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Coupling strength between omnivory loops and their one-species-delete subloops drives real food web stability

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Abstract

A central and fundamental issue in ecology is to understand the relationship between complexity and stability. Increased empirical evidences demonstrated no clear relationships between complexity metrics and stability, and recent food web loop analyses suggested that maximum loop weight as well as the summation ratio between 3- and 2-link feedback loop weights could be better estimators of system stability. However, the importance of longer loops than 3-link on the stability remains unclear. Here, we use 127 marine food webs and the matrix product and trace method to investigate the relationship between loops with maximum of 7 links and food web stability. We found that feedback metrics $|a_{2n+1}/a_{2n}|$, i.e., the ratio of the sums of $(2n + 1)$ -link and $2n$ -link loop weights, are strongly related with stability. These sum weight ratios can be regarded as the coupling strength between omnivory loops and their one-species-delete subloops, including the smallest three species and high-level omnivory ones. Further theoretical simulations of bioenergetic consumer-resource models with allometric constraints strengthen this finding. These results suggest that both longer loops and omnivory are important drivers of the food web stability.

Keywords Ecosystem community · Food webs · Feedback loops · Interaction strength · Stability · Matrix trace

Introduction

The stability of food webs is considered to be important for the maintenance of ecosystem functions such as carbon and nutrient cycles (de Vries et al. 2013). Current multiple anthropologic stresses on ecosystems have heightened the need to understand the mechanism underlying food web stability. The relation between the structure and stability of food webs has been widely studied (MacArthur 1955; Paine 1966), since key features to stability provide necessary information for both ecological theorists and operators for the restoration and management of ecosystems.

The complex-stability debate (McCann 2000) was initiated more than 50 years ago and has been a fundamental topic of ecological research since then (Jacquet et al. 2016). Network complexity, including species richness and connectance, was taken into consideration for food web stability

after May (1972) studied the relation between complexity and stability in theoretical random matrices and predicted that a system could be stable only if certain criteria were satisfied. Gardner and Ashby (1970) found that the connectance of large dynamic systems was critical for stability, and Tang et al. (2014) showed 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. It has become increasingly clear that the trophic interactions between predator and prey, depending on top-down and bottom-up effects and the patterning of strong and weak interactions, were crucial to food web stability (Brose et al. 2006; Neutel et al. 2007; Allesina and Tang 2012; Butler and O'Dwyer 2018; Tu et al. 2019).

A trophic interaction loop describes a pathway of interactions from a certain species through the web back to the same species without visiting other species more than once (Levins 1974; Neutel et al. 2002); hence, a loop is a closed chain of trophic links, which came into focus. Neutel et al. (2002) showed that the low loop weight of long loops, defined by the geometric mean of the absolute values of

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the interaction strengths in the loop, stabilizes complex food webs. Generally, it is the omnivorous loop that comprises a prey, a consumer of the prey and an omnivorous predator consuming both, that had the maximum loop weight, which limits the stability of the food web (Neutel et al. 2007). Analyzing the stability of an observed food web, the maximum weight of the omnivorous loop (Neutel et al. 2007; Mitchell and Neutel 2012; Michalska-Smith et al. 2015) as indicator of food web stability was refined into the ratio of the summed weights of 3- and 2-link trophic interaction feedback loops (Neutel and Thorne 2014). The understanding in terms of key feedback loops has revealed that it was not network complexity (the number of species or their connectance) that places constraints on system stability, but the energy-flow and biomass distribution in the trophic pyramid (Neutel et al. 2002). Specifically, it was shown that increased predation pressure over trophic levels leads to less stability (Neutel and Thorne 2014). Considering community matrices of a predator–prey system with Holling type I, II, III response, Neutel and Thorne (2015) showed that the relation between the dominant eigenvalue and 3- and 2-link feedback loop weights is very significant. Because of the complexity of empirical food webs, many empirical and theoretical studies concentrated on the smaller scale of subgraph (Milo et al. 2002; Arim and Marquet 2004; Bascompte and Melián 2005; Camacho et al. 2007; Paulau et al. 2015; Stouffer and Bascompte 2010; Li et al. 2021), i.e., trophic modules and network motifs, that mostly have three or four species.

Three-species trophic modules make up complex food webs and can be viewed as their simple building blocks (Stouffer and Bascompte 2010). Recent loop studies have been limited to 3- and 2-link loops and systems with 10–30 species (Neutel and Thorne 2014; Neutel et al. 2007). The importance of loops longer than 3-link on the stability remains unclear. Given that the long loops indicate longer food chains consisting of more complex top-down and bottom-up effects among species, which may provide new insights into how trophic interactions between predators and prey drive food web stability, Li et al. (2021) further found that swapping only two (pairs) of interaction strengths in the empirical Jacobian matrix may not affect the heaviest omnivorous loops with three species but could have a profound effect on food web stability. Therefore, there is a need to test how coupling strengths within longer feedback loops in empirical food webs drive food web stability. And there is a need to test the longer feedback metric from realistic empirical data (Neutel and Thorne 2016). For an ecosystem of n species or trophic groups, the longest loops may have n -link length that show very complicated structure and the most expensive computational cost, so only the total effect of three-link and two-link loops is researched up to present (Neutel and Thorne 2014), but longer loops should affect stability definitely.

In the present paper, we analyzed the stability of 127 natural marine ecosystems (Colléter et al. 2013, 2015) by calculating the weights of long loops with four or more links. The results indicated that not only 3- and 2-link, but also $(2n + 1)$ - and $2n$ -link ($n = 2, 3, \dots$) feedback loops ratios were related to food web stability. Nevertheless, $(2n)$ - and $(2n - 1)$ -link ($n = 2, 3, \dots$) feedback loops ratios showed little relationship to food web stability. Furthermore, a bioenergetic consumer-resource dynamic model with allometric constraints (Domínguez-García et al. 2019) was analyzed to confirm these findings.

Methods

Empirical food web models A total of 127 empirical marine food webs were used in this study. Biomass dynamics of trophic species is the basis of Ecopath, expressed in the form of coupled linear differential equations as

$$\frac{dB_i}{dt} = B_i \times (P/B)_i - f_i - \sum_j [B_j \times (Q/B)_j \times DC_{ji}] - M_{0i} \times B_i, \quad (1)$$

where B_i ($t \text{ km}^{-2}$) and $(P/B)_i$ (per year) are the biomass and production/biomass ratio, respectively, of trophic species i ; f_i ($t \text{ km}^{-2}$ per year) corresponds to fishery yields; $(Q/B)_j$ (per year) is the consumption/biomass ratio of predator j ; and DC_{ji} is the proportion of trophic species i in the diet of predator j . The mortality resource, M_{0i} (per year), is $(1 - EE_i) \times (P/B)_i$, where EE_i is the ecotrophic efficiency of i , corresponding to the fraction of production used in the food web. The model consists of functional groups rather than all of the species present since functional groups are a way of simplifying the high taxonomic diversity encountered in many communities and partly a way of describing the ecological roles or “functions” of different species. The concept is particularly important for modeling approaches that focus on understanding the behavior of ecological systems.

These 127 marine ecosystem models, including continental shelf, open ocean, upwelling, bay, coastal lagoon, estuarine, and channel, published worldwide, were equipped in Ecopath with the Ecosim software’s repository (Colléter et al. 2013, 2015), and we ran them until a stable state (mass balance with $dB_i/dt = 0$) or the maximum number of steps was reached (unstable state). The ultimate biomass B_i^* was substituted in the Jacobian community matrix (Jacquet et al. 2016):

$$\begin{pmatrix} 0 & \gamma_{ij} = (P/B)_j \times DC_{ji} \times \frac{B_j^*}{B_i^*} (i < j) \\ \gamma_{ij} = -(Q/B)_j \times DC_{ji} (i > j) & 0 \end{pmatrix}, i, j = 1, 2, \dots, n \quad (2)$$

where diagonal elements were set to zero, since we emphasized interspecific interaction strength between species and ignored intraspecific ones. Elements in the Jacobian matrix represent the trophic interaction strength between predator and its prey; specifically, the positive elements show the interaction of the prey on the predator, whereas the negative elements show the interaction of the predator on the prey.

Different from Neutel and Thorne (2014, 2016), which constructed a “normalized” matrix by dividing each row of the community matrix by the absolute value of the corresponding diagonal element, we used Michalska-Smith et al. (2015) method without “normalization.” Further details of the Ecopath modeling approach can be obtained at <http://ecobase.ecopath.org>.

Feedback metric A loop describes a pathway of interactions from a certain species through the web back to the same species without visiting other species more than once (Hofbauer and Sigmund 1988). Neutel et al. (2002) defined the loop weight as the geometric mean of the absolute values of the interaction strengths in the loop. For zero-diagonal matrices, Neutel and Thorne (2014) proposed a feedback metric expressed as a ratio of 3-link and 2-link feedback loops: $\sqrt[3]{| \frac{a_3}{a_2} |}$, where $a_2 = \sum \gamma_{ij} \gamma_{ji}$ represents the sum of all 2-link feedback loops and $a_3 = \sum (\gamma_{ij} \gamma_{jk} \gamma_{ki} + \gamma_{ik} \gamma_{kj} \gamma_{ji})$ is the sum of all 3-link feedback loops. γ_{ij} is an element of a Jacobian community matrix model (linearization of ordinary differential equations of dynamic systems):

$$\Gamma = \begin{pmatrix} \gamma_{11} & \gamma_{12} & \cdots & \gamma_{1n} \\ \gamma_{21} & \gamma_{22} & \cdots & \gamma_{2n} \\ \vdots & \vdots & \ddots & \vdots \\ \gamma_{m1} & \gamma_{m2} & \cdots & \gamma_{mn} \end{pmatrix} = \frac{\partial (dB_i/dt)}{\partial B_j} \Big|_{B^*}, \tag{3}$$

whose local stability is determined by the largest real part of the eigenvalues, where B_i is the biomass of the species, B^* is the equilibrium point, and $(dB_i/dt)|_{B^*} = 0$. For the smallest omnivorous structures, i is the bottom prey, j is the intermediate predator, and k is the omnivore. For an ecological network with three species, the characteristic polynomial of the Jacobian community matrix at equilibrium biomass can be expressed as $\lambda^3 + a_1 \lambda^2 + a_2 \lambda + a_3$ (Neutel and Thorne 2014), but with S species, $S > 3$, a_n cannot be obtained through the coefficients of the characteristic polynomial.

According to zero-diagonal Jacobian community matrix $\Gamma_0 = \begin{pmatrix} 0 & \gamma_{ji} \\ \gamma_{ij} & 0 \end{pmatrix}$, $a_2 = tr(\Gamma_0 \times \Gamma_0) = tr((\Gamma_0)^2)$ can be easily proved, where tr is the trace of the matrix, i.e., the sum of the diagonal elements. We can similarly hold $a_3 = tr((\Gamma_0)^3)$ and

$$a_n = tr((\Gamma_0)^n), n = 2, 3, \dots, \tag{4}$$

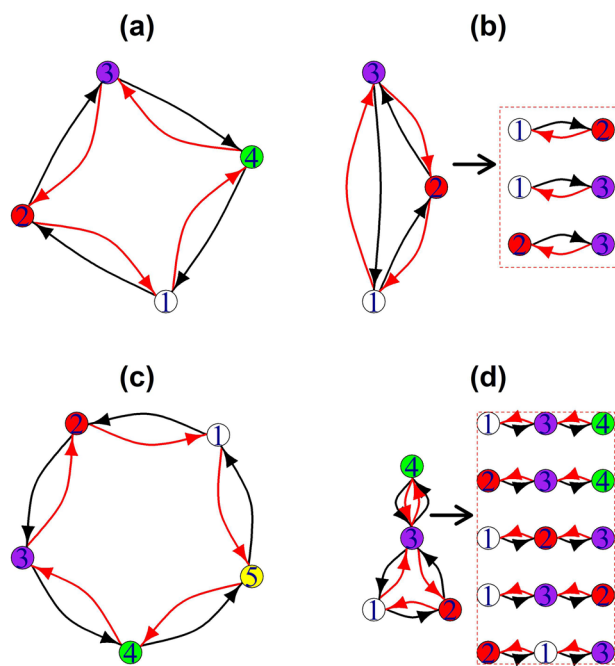


Fig. 1 Predator–prey feedback loop structure: **a** 4-link loop without repeated species (cycle in graph theory), which can be searched by Johnson’s algorithm (Johnson 1977); **b** Classic smallest omnivory loop and its three one-species-delete subloops (2-link loop); **c** 5-link loop without repeated species (cycle in graph theory); **d** High-level omnivory module (McLeod and Leroux 2021; Wootton 2017) and its five one-species-delete subloops (4-link loop). Our trace a_5 includes a high-level omnivory module and 5-link cycle (c), and the sum weight of the high-level omnivory module is far greater than that of 5-link cycle (c), so 5-link cycle (c) can be discarded. The same applies to 4-link cycle (a)

which have more simple program implementation than Neutel’s formula (Neutel and Thorne 2014). We extend feedback metric $\sqrt[3]{| \frac{a_3}{a_2} |}$ to $| \frac{a_n}{a_{n-1}} |^l$, $n = 4, 5, 6, \dots$, where the power l is introduced for more robustness of different food webs with various stability. In most case, the power l is one.

Feedback loop structure Five-link feedback loops applied in our trace method are depicted in Fig. 1c and d, and loops with an edge from one species to itself can be neglected since diagonal intraspecific strengths in our Jacobian community matrices are zero. Loops of Fig. 1c are cycles in graph theory that can be searched out by Johnson’s algorithm (Johnson 1977), and the left part of Fig. 1d is a high-level omnivory module (McLeod and Leroux 2021; Wootton 2017) compared to a classic omnivory loop (left part of Fig. 1b). Our trace a_5 can be divided into the sum weight of high-level omnivory modules, which is dominant, since it far outweighs the other (Fig. 5b), and the sum weight of 5-link cycles, which can be omitted. For all of the zero-diagonal

community matrices, a_2 and a_3 by our trace method are just double and triple sum weights of 2- and 3-link loops found by Johnson’s algorithm (Fig. 5b).

Feedback loops of toy omnivory model To better explain the idea of feedback loops, a toy Lotka-Volterra Intraguild Predation (IGP) Model of three groups (Holt and Polis 1997), comprising a basal resource, an intermediate predator on resource, and an omnivorous predator consuming both, is defined as

$$\begin{aligned} \frac{dP}{dt} &= P(b'a'R + \beta\alpha N - m'), \\ \frac{dN}{dt} &= N(abR - m - \alpha P), \\ \frac{dR}{dt} &= R(r(1 - R/K) - aN - a'P). \end{aligned} \tag{5}$$

The P , N , and R are the densities of the omnivorous predator, intermediate predator, and basal resource, respectively. The quantities $a'R$ and αN are functional responses of the top predator to the resource and intermediate predator, respectively; aR is the functional response of the intermediate predator to the basal resource; and m and m' are density-independent mortality rates. The parameters b and b' convert resource consumption into reproduction for the intermediate and omnivorous predator, respectively; the parameter β scales the benefit enjoyed by the omnivory from its consumption of intermediate predator. We deliberately use the symbol α to denote mortality inflicted on the intermediate predator by the top predator, because in some circumstances, such mortality could be viewed as interspecific interference competition and might be measured by a competition coefficient (even though the actual mechanism is mortality from predation). Finally, the basal resource when alone grows according to a logistic model with carrying capacity K , each consumer has linear functional responses, and consumer growth is proportional to the rate of consumption. For instance, phytoplankton, zooplankton, and shrimps form an IGP food chain (Fig. 2a) where phytoplankton is the basal resource, zooplankton is the intermediate predator, and shrimps are the omnivorous predator.

To evaluate local stability of the full three-species equilibrium P^* , N^* , and R^* at which growth rates reach zero, we follow standard Jacobian matrix procedures (May 1972). The elements in the Jacobian matrix near equilibrium which equal the partial derivative of the population growth equation of the species corresponding to row i with respect to the species corresponding to column j , evaluated at equilibrium, are regarded as interaction strengths (Laska and Wootton 1998), which conceptually represent the direct effect of an individual of one species on the total population of another species at or near equilibrium. This definition

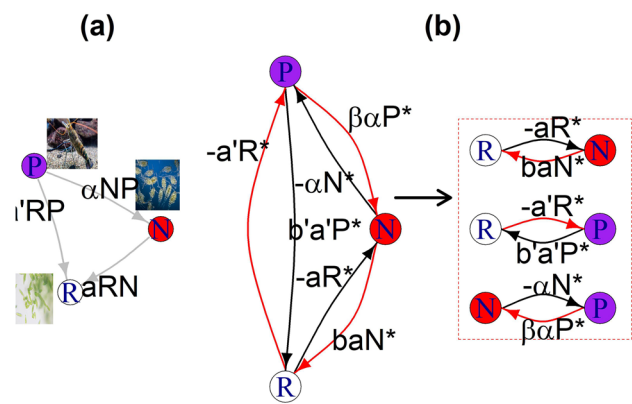


Fig. 2 A toy Lotka-Volterra Intraguild Predation Model with three species and feedback loops based on Jacobian matrix: The omnivorous feeding rates loop (a) generates two trophic interaction loops (b), one negative clockwise loop $(-a'R^*)(\beta\alpha P^*)(baN^*)$ and one positive anti-clockwise loop $(-a'R^*)(-\alpha N^*)(b'a'P^*)$. a Predator–prey relationship in the IGP model (Eq. 5) taking phytoplankton, zooplankton, and shrimps as examples, intermediate predator zooplankton consume aRN basal resource phytoplankton per unit time, meanwhile omnivorous shrimps eat zooplankton αNP and phytoplankton $a'RP$ per unit time. b There are 3 two-link feedback loops with all negative weights causing stability and 2 three-link loops with one negative weight and one positive weight leading to instability in the Jacobian matrix (Eq. 6) induced from model (Eq. 5)

has received considerable attention in food web models. The Jacobian matrix of model (5) is as follows:

$$\begin{pmatrix} \gamma_{11} & \gamma_{12} & \gamma_{13} \\ \gamma_{21} & \gamma_{22} & \gamma_{23} \\ \gamma_{31} & \gamma_{32} & \gamma_{33} \end{pmatrix} = \begin{pmatrix} 0 & \beta\alpha P^* & b'a'P^* \\ -\alpha N^* & 0 & baN^* \\ -a'R^* & -aR^* & -\frac{rR^*}{K} \end{pmatrix}. \tag{6}$$

For testing the local stability of the equilibrium, a small and temporary perturbation is added to phytoplankton from equilibrium, for example (also can be to two or all species, one for simplicity and easy explanation), and then three growth rates all change to be nonzero. The growth rate of phytoplankton must be greater than zero for its density increment from equilibrium, so phytoplankton growth rate must be pulled back through interaction strengths γ_{31} and γ_{32} . There are three possible paths to do it, one is $\gamma_{32}\gamma_{23} = (-aR^*)(baN^*)$ called two-link feedback loop, implying abundant phytoplankton enriches zooplankton and more zooplankton eat increased phytoplankton conversely. The other two are three-link feedback loops $\gamma_{32}\gamma_{21}\gamma_{13} = (-aR^*)(-\alpha N^*)(b'a'P^*)$ having positive weight to enlarging phytoplankton and instability (Fig. 2b black arrow) and $\gamma_{31}\gamma_{12}\gamma_{23} = (-a'R^*)(\beta\alpha P^*)(baN^*)$ having negative weight to decreasing phytoplankton and leading more stability (Fig. 2b red arrow).

Negative loop can be explained as that increasing phytoplankton brings about zooplankton and shrimps which will

eat additional phytoplankton to go back to the original equilibrium, whereas positive loop is that increasing phytoplankton directly flourishes shrimps which consume more zooplankton and fading zooplankton will strengthen phytoplankton far away the equilibrium. The system's stability can be determined by the total effects of negative and positive feedback loops of different lengths. For an ecosystem of n species or trophic groups, the longest loops may have n -link lengths that show very complicated structure and the most expensive computational cost, so only the total effect of three-link and two-link loops is researched up to present (Neutel and Thorne 2014), but longer loops should affect stability definitely.

For the diagonal values in Jacobian matrix at the equilibrium, denoting intraspecific interference, we lacked empirical information to identify them. There are several ways to "deal" with the diagonal values (Altena et al. 2014). We choose to set all diagonal values equal to zero (Neutel and Thorne 2014; Rip and McCann 2011; Tang et al. 2014). This implies that the matrix will have some eigenvalues with positive real parts, and then, we cannot speak of stability of the matrix in the strict, mathematical sense, but the real part of the maximum eigenvalue ($Re(\lambda_{max})$) can then indicate the level of resilience. The lower the value of the $Re(\lambda_{max})$, the more resilient the food web (Neutel and Thorne 2014; Tang et al. 2014).

Theoretical food web model Following Domínguez-García et al. (2019), we constructed the simulation model step by step using the niche model (Williams and Martinez 2000) and employed a bioenergetic consumer-resource model with allometric constraints:

$$\frac{dB_i}{dt} = r_i G_i B_i + B_i \sum_{j \in \text{prey}} e_{0j} F_{ij} - \sum_{k \in \text{pred}} B_k F_{ki} - x_i B_i - d_i B_i, \quad (7)$$

where the interaction term is defined as

$$F_{ij} = \frac{\omega_i c_{ij} B_j^{1+q}}{m_i (1 + \omega_i \sum_{k \in \text{prey}} c_{ik} h_{ik} B_k^{1+q})}. \quad (8)$$

The synthetic parameterization of the model is discussed in Supplementary Information in Domínguez-García et al. (2019).

We simulated the biomass of each species by Eq. (7) in the R language, where the function *runsteady* in library *rootSolve* solves the steady-state condition of ordinary differential equations (ODEs) by dynamically running until the summed absolute values of the derivatives become smaller than some predefined tolerance, and the function *jacobian.full* in library *rootSolve* estimates the Jacobian matrix at the steady state. The rows and columns corresponding to the extinct species and bottom prey were deleted, and the diagonal was substituted with zeros without normalization

by diagonal elements, which formed the final community matrices to calculate the maximum real parts of the eigenvalues $Re(\lambda_{max})$ and feedback levels a_n , $n = 2, \dots, 7$. Herewith, the assumed diagonal values of zero will let the matrices have some positive eigenvalues. In this way, this cannot be defined as the stability of the matrix in a strict mathematical sense; the values of $Re(\lambda_{max})$ can then indicate the level of stability. That is, if the value of the $Re(\lambda_{max})$ is larger, the food web becomes more unstable (Neutel and Thorne 2014; Neutel et al. 2002).

Results

Complexity-stability relation We first investigated the relation between stability and classic complexity descriptors, i.e., species richness S ; connectance C ; standard deviation of interaction strength (IS) σ ; coefficient of variation of IS σ/E , where E is the mean of IS; skewness and kurtosis of IS. We observed no relation between food web stability and species richness and connectance, neither with skewness nor kurtosis (Fig. 3a, b, f, g). The standard deviation of IS σ is an important factor for food web stability. Coefficient of variation σ/E and May's complexity criterion $\sigma\sqrt{SC}$ (May 1972) implied little dependence on the stability. Standard deviation σ and related metrics are not critical to determining food web stability (Fig. 3c–e), and other metrics of the substructure beyond basic statistics of interaction strength should be considered.

Weight sum ratio determines stability Surprisingly, we found that predator–prey feedback metrics $|a_3/a_2|$, $|a_5/a_4|$, and $|a_7/a_6|$ were strongly related to the matrix stability measure $Re(\lambda_{max})$, and their slopes gradually decreased, which implied that $|a_3/a_2|$ contributed most to the stability of an ecosystem among the three metrics (Fig. 4a). It was noted that $|a_4/a_3|$ and $|a_6/a_5|$ exhibited almost no relation with stability $Re(\lambda_{max})$ (Fig. 4b, c). Pairwise metrics (Tang et al. 2014) also showed little correlation with stability with $R^2 = 0.36$ (Fig. 4d), which satisfied the opinions in Neutel and Thorne (2016) and Jacquet et al. (2016) but contradicted the results in Michalska-Smith et al. (2015). Predator–prey feedback metrics $|a_{2n+1}/a_{2n}|$, $n = 1, 2, \dots$ are generally good indicators of stability, but $|a_{2n}/a_{2n-1}|$, $n = 2, 3, \dots$ are not.

Feedback loop weight decomposition Since cycles greater than five are numerous for large ecological networks, we selected 74 smaller Ecopath marine models and identified all of their 2-, 3-, 4-, and 5-links cycles from our 127 models using Johnson's algorithm. The cumulative proportion curves were almost the same whether subtracting the sum weight of 4- and 5-link cycles from our sum weights a_4 and a_5 , respectively

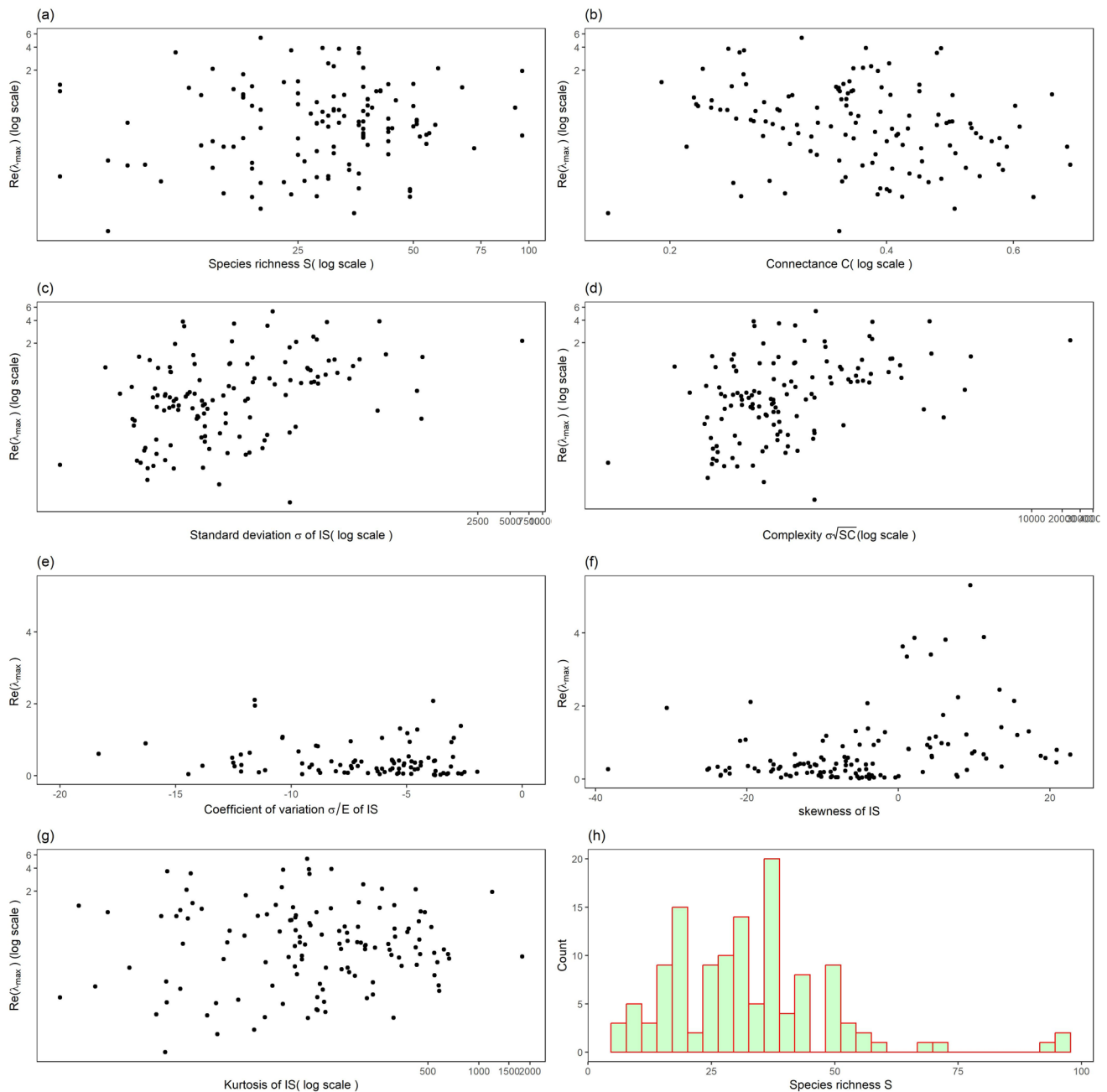


Fig. 3 Food web stability related to basic metrics of IS across 127 natural Ecopath models of marine ecosystems based on empirically parameterized community matrices: **a** Number of species S at log2 scale for xy axis ($R^2 = 0.009, p = 0.28$). **b** Connectance $C = L/S^2$, where L is the number of links at log2 scale for xy axis ($R^2 = 0.001, p = 0.76$). **c** Standard deviation σ of IS at log2 scale for

xy axis ($R^2 = 0.08, p = 0.0014$). **d** May's complexity $\sigma\sqrt{SC}$ of IS at log2 scale for xy axis ($R^2 = 0.12, p < 10^{-6}$). **e** Coefficient of variation σ/E , where E is the mean of IS ($R^2 = 0.11, p = 0.0006$). **f** Skewness of IS ($R^2 = 0.004, p = 0.48$). **g** Kurtosis of IS at log2 scale for xy axis ($R^2 = 0.0005, p = 0.79$). **h** Histogram of species richness

(Fig. 5a). The sum weights a_n and a_{n-1} must have different signs, i.e., a_2, a_5 , and a_6 are negative and a_3, a_4 , and a_7 are positive. The magnitudes of a_n grew exponentially, but the ratios a_n/a_{n-1} seemed to vary around a constant for different ecological systems (Fig. 5a). For 2- and 3-links, sum loop weights of our matrix trace method are exactly two and three times as

much as that of cycles with no repeat nodes, but our method's sum weights far outweigh that of cycles in 4- and 5- links (Fig. 5b), so omnivory loops are dominant in loop weight analyses. For a natural marine Ecopath food web (Eritrea's coral reef model (Tsehaye and Nagelkerke 2008)), geometric mean loop weights of different lengths searched out by Johnson's

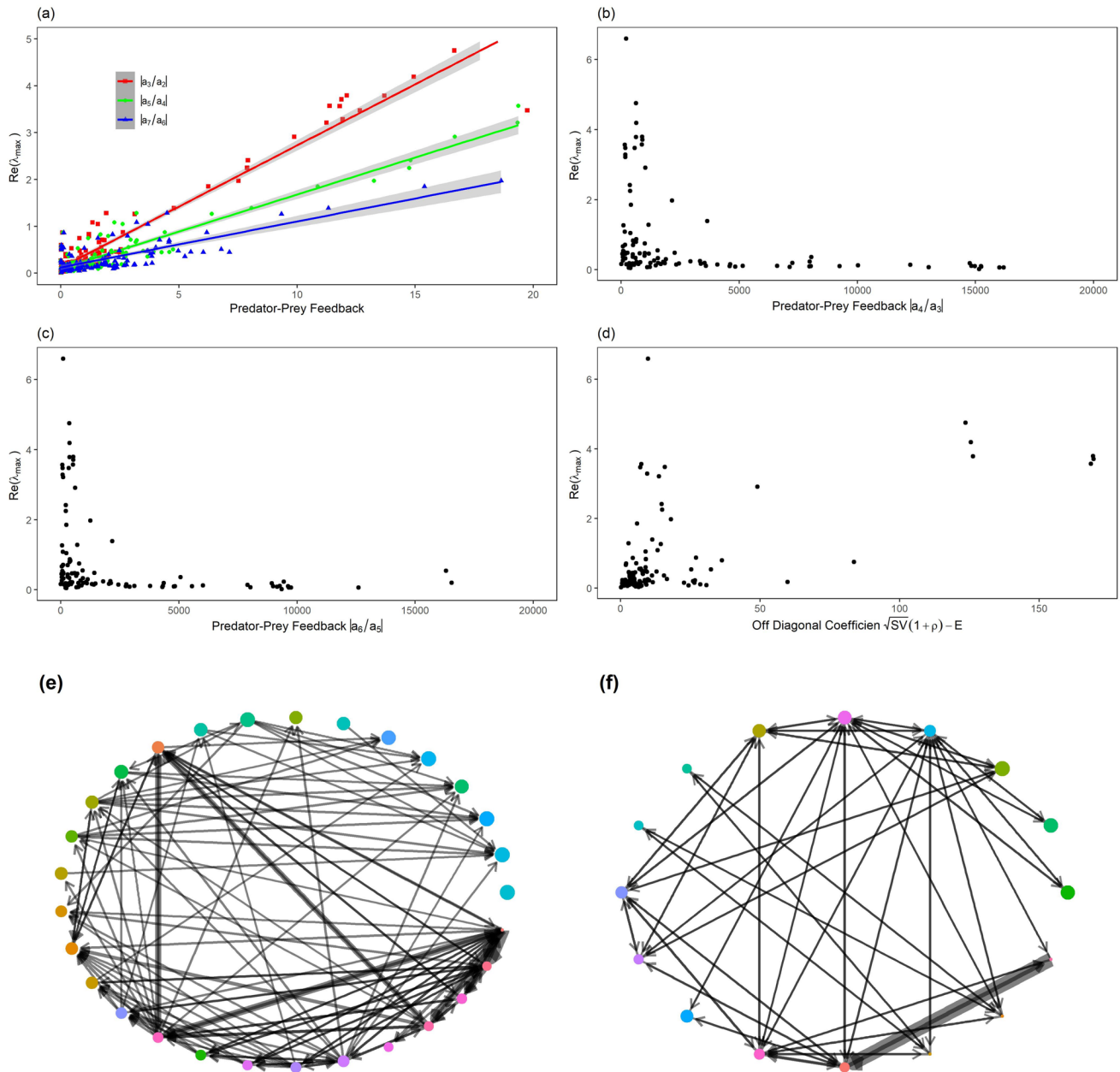


Fig. 4 Performance of extended feedback metrics and pairwise metric against stability $Re(\lambda_{max})$ across 127 natural Ecopath models of marine ecosystems based on empirically parameterized community matrices. S is the number of species or trophic species, and E , V , and ρ are the mean, variance, and Pearson linear correlation coefficient of off-diagonal elements of the Jacobian community matrix, respectively: **a** Feedback levels $|a_3/a_2|$, $|a_5/a_4|$, and $|a_7/a_6|$ showed excellent correlation with stability, with $R^2 = 0.9, 0.91, 0.9$, respectively, and all p values less than 10^{-16} . However, $|a_4/a_3|$ and $|a_6/a_5|$ could not determine food web stability (**b**, **c**) and the pairwise metric (**d**)

obtained the same conclusion as (**b**, **c**). The points in (**d**) showed no concentration trend although R^2 equaled 0.36 and its p -value was less than 0.05. Note that all of the diagonal elements were set at zero, and off-diagonal elements had no scaling by diagonal elements. **e** Interaction strengths of the most unstable system (the largest $Re(\lambda_{max})$) among 127 marine food webs. Node sizes of group species were drawn according to their trophic levels, and edge widths represented their strengths. Interaction strengths with absolute value less than 0.15 were neglected. **f** Interaction strengths of the most stable system (the smallest $Re(\lambda_{max})$) among 127 marine food webs

algorithm were almost symmetric at zero (Fig. 5d), so the maximum loop weight and sum loop weight had strong correlation for a fixed-length loop. This phenomenon also existed in other models (Neutel et al. 2002, 2007). Maximum loop weights of

3-links were almost the maximum of all lengths, and only a few maxima of all lengths occurred at other links (Fig. 5c, d); therefore, a regression line between maximum loop weights of all link lengths and food web stability coincides with that

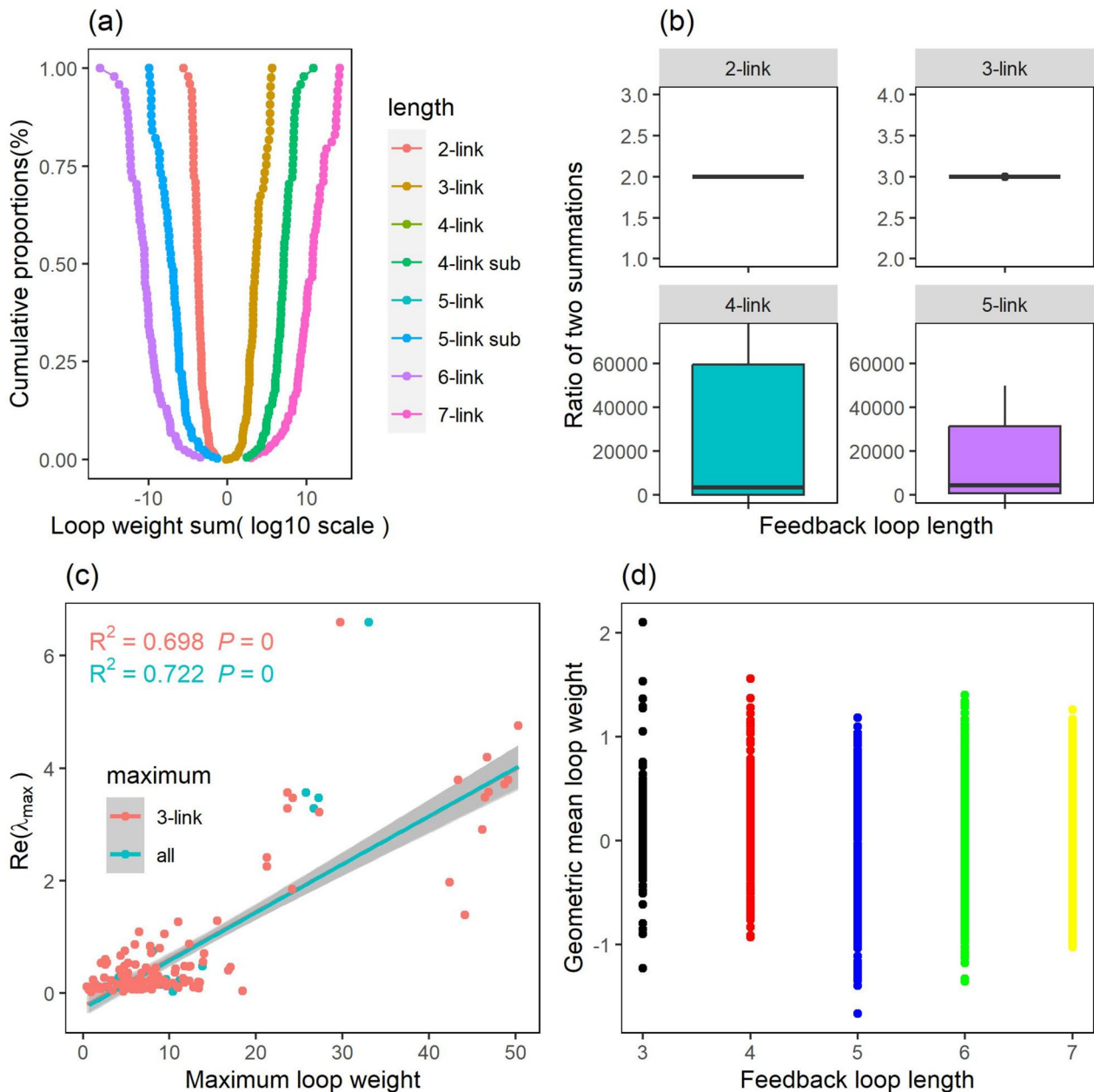


Fig. 5 Relation among loop weights in empirical marine Ecopath food webs, where loop weight is the product of interaction strengths without averaging: **a** Sum loop weight a_n of different lengths by our trace method in selected 74 models. *5-link sub* means that the sum weight of 5-link cycles found by Johnson's algorithm (Johnson 1977) is subtracted from a_5 so that only high-level omnivory modules (left part of Fig. 1d) are left. Curves of *5-link sub* and *4-link sub* disappear because they overlap with 5-link and 4-link curves. **b** Ratio of sum loop weights of two methods in

selected 74 models. The numerator is our trace method, and the denominator is cycles found by Johnson's algorithm. Cycle is loop without repeated species (Fig. 1a–c); **c** linear regression between maximum loop weight and system stability in all our 127 marine food webs. One maximum is restricted in 3-link feedback loops, and the other is covered with all lengths of loops as far as possible in computer's computing ability; **d** geometric mean loop weight of different lengths in no. 35 food webs with 25 species (Eritrea's coral reef model (Tsehaye and Nagelkerke 2008))

between the maximum loop weight of 3-link and food web stability (Neutel et al. 2007; Mitchell and Neutel 2012; Kuiper et al. 2015) (Fig. 5c), with $R^2 = 0.722$ less than the effect of the sum weight ratio a_3/a_2 ($R^2 = 0.9$) in Fig. 4a.

Theoretical simulations Simulations with the bioenergetic consumer-resource model (Domínguez-García et al. 2019) revealed that the vulnerability of a system (larger $Re(\lambda_{max})$) leads to more chance of instability) could be roughly predicted by the

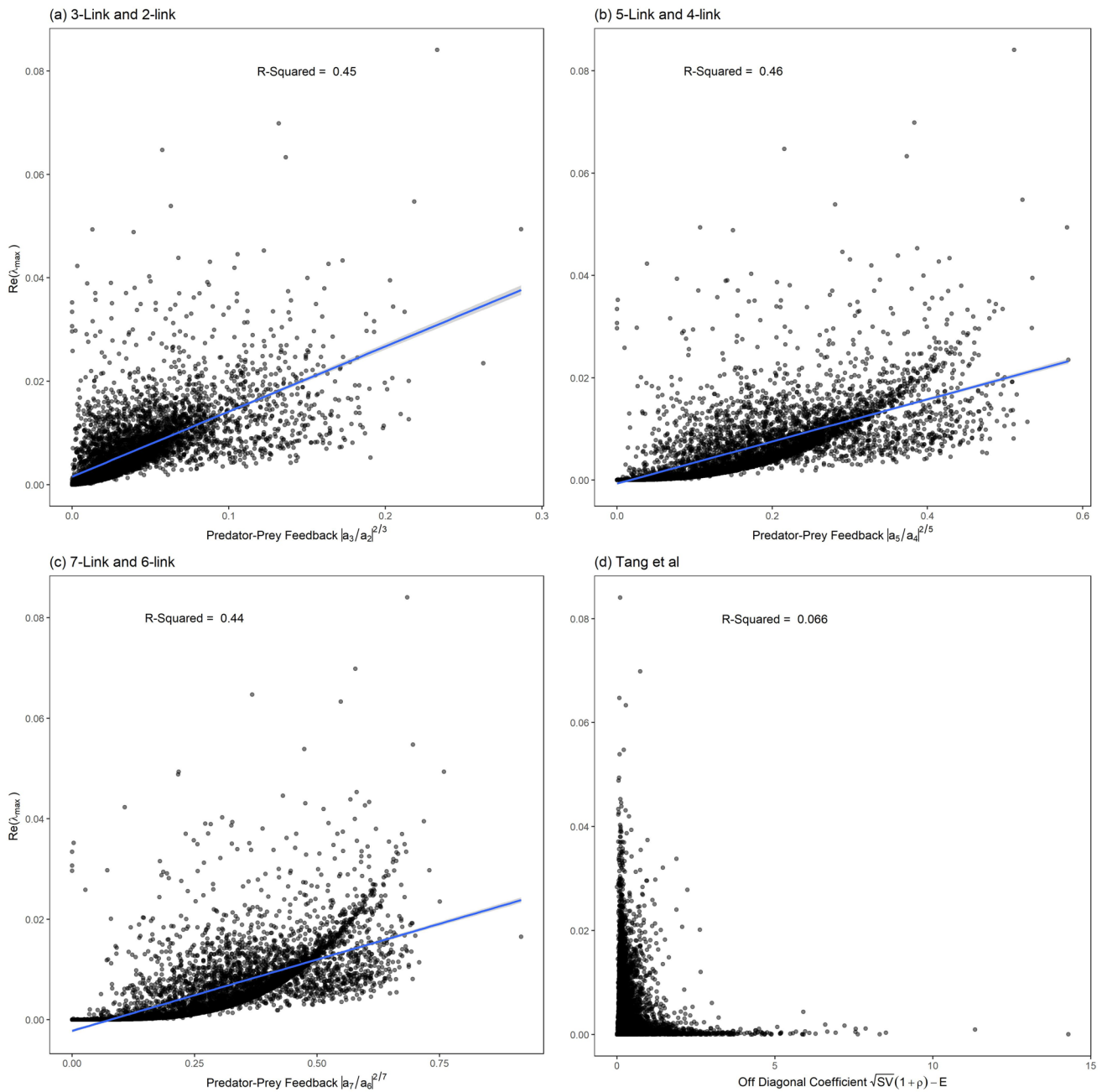


Fig. 6 Performance of extended feedback metrics $|a_{2n+1}/a_{2n}|^{2/2n+1}$ and pairwise metric (Tang et al. 2014) $\sqrt{SV(1+\rho)} - E$ against stability $Re(\lambda_{max})$ in simulation models (Domínguez-García et al. 2019) with species richness ranging from 5 to 100 species, repeated 50

times for each species: **a** Predator–prey feedback metric $|a_3/a_2|^{2/3}$ against stability; **b** predator–prey feedback metric $|a_5/a_4|^{2/5}$ against stability; **c** predator–prey feedback metric $|a_7/a_6|^{2/7}$ against stability; **d** Tang et al. (2014) pairwise metric against stability

predator–prey feedback metrics $|a_{2n+1}/a_{2n}|^{2/2n+1}$, $n = 1, 2, \dots$ (Fig. 6a–c), even when long loops tended to be relatively weak (Neutel et al. 2007). The ratio of total odd- to even-link loops (minus 1) can capture the stability of food webs, but the ratio of total even- to odd-link loops (also minus 1) cannot (Supplementary Fig. S7). The exponent of the ratio $|a_{2n+1}/a_{2n}|$, chosen as $2/(2n + 1)$ in our simulation, was found to be a key

parameter to predict $Re(\lambda_{max})$, whose numerator 2 is absolutely necessary in our simulation and whose denominator $2n + 1$ can be regarded as the geometric mean of the $(2n + 1)$ -link loop weights, while the exponents in Ecopath models and their randomization tests were all set to 1 for good performance. The sensitivity of the exponent of the ratio against stability is discussed in the Supplement. As expected, species richness,

connectance, and May's criteria showed no relationships with food web stability (Supplementary Fig. S6), and Tang's pairwise metric $\sqrt{SV(1 + \rho) - E}$ (Tang et al. 2014) also had weak correlation with the stability of the simulating bioenergetic consumer-resource systems (Fig. 6d).

Discussion

Beyond complexity-stability relationships, substructure in complex network (network motifs), from pairwise correlation (Tang et al. 2014) to the smallest omnivorous loops (3-link feedback loops), (Tang et al. 2014; Neutel et al. 2007; Mitchell and Neutel 2012; Neutel and Thorne 2015; Neutel et al. 2002; Neutel and Thorne 2014; Michalska-Smith et al. 2015; Neutel and Thorne 2016), has become an important research focus in food web ecology. A maximum three-species omnivorous loop weight stands out in relation to stability among the multitude of feedback loops, and the ratio of the sum weights of 3- to 2-link feedback loops a_3/a_2 has been proposed (Neutel and Thorne 2014), but no one has considered the correlation between long-link feedback loops and stability in empirical food webs.

We discovered that feedback metrics $|a_{2n+1}/a_{2n}|$, i.e., the ratio of the sums of $(2n + 1)$ -link and $2n$ -link loop weights, have a good relation with stability (the real part of the dominant eigenvalue) of community matrices. Why can the sum weight ratios $a_3/a_2, a_5/a_4, a_7/a_6$ capture food web stability? As we know, a_3 is the total effect of classic omnivory loops (generated by intraguild predation module), which plays an important role in a food web (Holt and Huxel 2007; Milo et al. 2002; Arim and Marquet 2004; Bascompte and Melián 2005; Camacho et al. 2007; Paulau et al. 2015). If we delete one species in turn, three 2-link predator-prey feedback loops, whose total effect is measured by a_2 , occur independently (Fig. 1b). Consequently, the ratio a_3/a_2 reflects coupling strength (Mougi and Kondoh 2016; Mougi 2018) which holds information about ecological network stability. Two 3-link loops can be thought as three 2-link loops and two 5-link loops as five 4-link loops (Fig. 1b, d), since the loops without repeated species (Fig. 1c) called cycles in graph theory are insignificant to omnivorous loops (Fig. 1b, d). These loops have positive and negative weights which lead to instability and stability. For all n -link loops, their total weight is represent as a_n , so a_3/a_2 and a_5/a_4 show coupling strength.

The main body of a_5 is a high-level omnivory module (McLeod and Leroux 2021; Wootton 2017) (left part of Fig. 1d). In the same way, if we delete one species in turn, five 4-link predator-prey feedback loops, whose total effect is measured by a_4 , emerge independently (Fig. 1d). Information about ecological network stability is also captured by coupling strength a_5/a_4 . If the omnivory modules are more tightly coupled to their one-species-delete subloops, the food web is more stable, since a_4 and a_6 have no omnivory

structure and fail to discover information about food web stability (Fig. 4b, c).

Expected changes in varying environmental conditions will be reflected in food web architecture; the dynamics of weights is a key character accounting for food web stability. The food web models are obviously not complete and miss some properties of species that might be important for food web stability, i.e., switching. It is very valuable to study switching abilities of consumer for species migration. It depends on how we define "switching." In the original literature on switching, it is meant that consumers have a "disproportionately" preference for the more abundant prey. This does not change the architecture of the web (who eats whom) but also the fluxes. Such switching generates frequency-dependent selection in favor of the "rare" prey and hence promotes stability. The above will generate different community matrices, which is equal to add new food webs. In order to get the same effect, we randomly generate a Jacobian community matrix, a_n/a_{n-1} cannot predict stability regardless of shuffling the positive elements to the upper triangle and negative ones to the lower triangle (Supplementary Figs. S1 and S2), so there must be some conditions on the community matrix for our results. We performed eight randomization tests H1–H8 (Jacquet et al. 2016) to remove one or several properties of natural food webs and compute the stability of the permuted community matrices. H1–H8 randomization tests of Jacobian community matrices of the 127 Ecopath empirical marine ecosystems revealed that feedback metric $|a_5/a_4|$ almost played the same role as $|a_3/a_2|$. Feedback metric $|a_3/a_2|$ had a better relation with stability than pairwise metric $\sqrt{SV(1 + \rho) - E}$ in H2, H4, and H8 tests, but a worse one in H5, H6, and H7 tests, and both seemed to have little correlation with stability in H1 and H3 tests (Supplementary Figs. S3 and S5). In the same way, $|a_4/a_3|$ could not capture the stability of food webs (Supplementary Fig. S4). In our simulation models, the R^2 of $a_3/a_2, a_5/a_4$, and a_7/a_6 were all about 0.45 (Fig. 6) which was less than values in 127 Ecopath natural food webs. One reason is that our simulation has more than 127 data points, and large data could reduce the p value. Another is that Jacobian community matrices of our simulation systems are directly and numerically computed at equilibrium points, while those of Ecopath ecosystems are manually calculated by stable state biomass (Eq. 2), which are more dependent on off-diagonal elements. Our randomization tests by removing one or several properties of natural food webs and a bioenergetic consumer-resource dynamic model with allometric constraints (Domínguez-García et al. 2019) further confirmed these findings and gave more insights into the underlying mechanisms.

Early studies concentrating on 3- and 2-link feedback loops for long loops contained relatively many weak links

and were time-consuming to explore. Since we computed the total weight a_n of n -link feedback loops, there was no need to find every loop path and calculate its weight. Matrix multiplication and traces could be applied for easy computation (Eq. 4). Although the long-loop weight is weak, its number is always large enough to have a non-negligible effect, and the ratio between two tiny numbers may be large. Therefore, long feedback loops may affect the stability of food webs. It is surprising that feedback levels $|a_{2n}/a_{2n-1}|$ seem to have little correlation with stability; this needs further theoretical confirmation. A rough explanation is based on theorems in linear algebra that the eigenvalues $\lambda((\Gamma_0)^n)$ of $(\Gamma_0)^n$ are the n -th power of the eigenvalues of Γ_0 , i.e., $\lambda((\Gamma_0)^n) = (\lambda(\Gamma_0))^n$, and since the trace of a matrix is the sum of all its eigenvalues, then we can obtain $|a_{2n+1}/a_{2n}| = |(\lambda_1^{2n+1} + \dots + \lambda_s^{2n+1})/(\lambda_1^{2n} + \dots + \lambda_s^{2n})|$, where λ_i is the i -th eigenvalue. So, if the dominant eigenvalue $\lambda_1 = \lambda_{max}$ far outweighs the others, then $\lambda_1^{2n+1} + \dots + \lambda_s^{2n+1}$ can be approximated by λ_1^{2n+1} , and $|a_{2n+1}/a_{2n}| \approx |\lambda_1| = |\lambda_{max}| = \lambda_{max}$, since $\lambda_{max} > 0$, on account of the absence of intraspecific strength (diagonal elements) in the community matrix. In the other case, if all eigenvalues center on their mean with small deviation and are almost equal, then we can also approximate $|a_{2n+1}/a_{2n}|$ by the largest eigenvalue λ_{max} . But to find the pattern of interaction strength in the community matrix to ensure these conditions is a great challenge.

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Declarations

Conflict of interest The authors declare no competing interests.

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