

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

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Abstract:

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

Introduction

58

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

65 The complex-stability debate(Mccann, 2000) was initiated more than 50 years ago and has
66 been a fundamental topic of ecological research since then(Jacquet et al., 2016). Network com-
67 plexity, including species richness and connectance, were taken into consideration for food web
68 stability after May(May, 1972) studied the relation between complexity and stability in theoretical
69 random matrices and predicted that a system could be stable only if certain criteria were satis-
70 fied. Gardner(Gardner and Ashby, 1970) found that the connectance of large dynamic systems
71 was critical for stability, and Tang *et al.*(Tang et al., 2014) showed that a simple yet overlooked
72 feature of natural food webs, the correlation between the effects of consumers on resources and
73 those of resources on consumers, substantially accounts for their stability. It has become increas-
74 ingly clear that the trophic interactions between predator and prey, depending on top-down and
75 bottom-up effects and the patterning of strong and weak interactions was crucial to food web
76 stability(Allesina and Tang, 2012; Brose et al., 2006; Butler and O'Dwyer, 2018; Neutel et al., 2007;
77 Tu et al., 2019).

78 The trophic interaction loops came into focus, which describes a pathway of trophic inter-
79 actions from a given species without visiting other species more than once(Levins, 1974; Neutel
80 et al., 2002). Neutel(Neutel et al., 2002) showed that the low loop weight of long loops, defined by
81 the geometric mean of the absolute values of the interaction strengths in the loop, stabilizes com-
82 plex food webs. It is generally the omnivorous loop, comprising a prey, a consumer of the prey
83 and an omnivorous predator consuming both, had the maximum loop weight, limiting stability of

84 the food web(Neutel et al., 2007). Analyzing the stability of an observed food web, the maximum
85 weight of the omnivorous loop(Michalska-Smith et al., 2015; Mitchell and Neutel, 2012; Neutel
86 et al., 2007) as indicator of food web stability was refined into the ratio of the summed weights
87 of 3- and 2-link trophic interaction feedback loops(Neutel and Thorne, 2014). The understanding
88 in terms of key feedback loops has revealed that it was not network complexity (the number
89 of species or their connectance) that places constraints on system stability, but the energy-flow
90 and biomass distribution in the trophic pyramid(Neutel et al., 2002). Specifically, it was shown
91 that increased predation pressure over trophic levels leads to less stability(Neutel and Thorne,
92 2014). Considering a predator-prey system with Holling type I, II, III response, Neutel(Neutel
93 and Thorne, 2015) showed the relation between the maximum real part of the eigenvalues of
94 the community matrices without diagonal elements and the strengths of 3- and 2-link feedback
95 loops in these matrices is very significant. Because of the complexity of empirical food webs,
96 many empirical and theoretical studies concentrated on the smaller scale of subgraph(Arim and
97 Marquet, 2004; Bascompte and Melián, 2005; Camacho et al., 2007; Li et al., 2021; Milo et al., 2002;
98 Paulau et al., 2015; Stouffer and Bascompte, 2010), i.e., trophic modules and network motifs, that
99 mostly have three or four species.

100 Three-species trophic modules make up complex food webs and can be viewed as their simple
101 building blocks(Stouffer and Bascompte, 2010). Recent loop weight studies have been limited
102 coupling strength between 3- and 2-link loops and systems of 10-30 trophic groups(Neutel and
103 Thorne, 2014; Neutel et al., 2007). The importance of loops longer than 3-link on the stability
104 remains unclear. Given that the long loops indicates longer food chains consisting of more
105 complex top-down and bottom-up effects among species, which may provide new insights into
106 how trophic interactions between predators and prey drive food web stability, Li et al. (Li et al.,
107 2021) further found that swapping only two (pairs) of interaction strengths in the empirical
108 Jacobian matrix may didn't affect the heaviest omnivorous loops with three species but could
109 have a profoundly effect on food web stability. Therefore, there is a need to test how coupling
110 strengths within longer feedback loops in empirical food webs drive food web stability. And

111 there is a need to test the longer feedback metric from realistic empirical data (Neutel and Thorne,
 112 2016). Most marine ecosystems have complicated networks. In the present paper we analyzed the
 113 stability of 127 natural marine ecosystems (Colleter et al., 2013; Colltter et al., 2015) by calculating
 114 the weights of long loops with four or more links. The results indicated that not only 3- and 2-
 115 link, but also 5- and 4-link, 7- and 6-link feedback loops ratios were related to food web stability.
 116 Nevertheless 6- and 5-link, 4- and 3-link feedback loops ratios showed little relationship to food
 117 web stability. Furthermore, a bioenergetic consumer-resource dynamic model with allometric
 118 constraints (Domínguez-García et al., 2019) was analyzed to confirm these findings.

119 Methods

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

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

123 where B_i (t km^{-2}) and $(P/B)_i$ (per year) are the biomass and production/biomass ratio, respec-
 124 tively, of trophic species i ; Y_i (t km^{-2} per year) corresponds to fishery yields; $(Q/B)_j$ (per year)
 125 is the consumption/biomass ratio of predator j ; and DC_{ji} is the proportion of trophic species i
 126 in the diet of predator j . The mortality resource, M_{0i} (per year), is $(1 - EE_i) \times (P/B)_i$, where
 127 EE_i is the ecotropic efficiency of i , corresponding to the fraction of production used in the food
 128 web. These 127 marine ecosystem models, including continental shelf, open ocean, upwelling,
 129 bay, coastal lagoon, estuarine, and channel, published worldwide, were equipped in Ecopath
 130 with the Ecosim software's repository (Colleter et al., 2013; Colltter et al., 2015), and we ran them
 131 until a stable state (mass balance with $dB_i/dt = 0$) or the maximum number of steps was reached
 132 (unstable state). The ultimate biomass B_i^* was substituted in the Jacobian community matrix,

133 (Jacquet et al., 2016)

$$\begin{pmatrix} 0 & (P/B)_j \times DC_{ji} \times \frac{B^*}{B_i} \\ -(Q/B)_j \times DC_{ji} & 0 \end{pmatrix}, \quad (2)$$

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

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

144 **Theoretical food web model.** Following Domnguez (Domínguez-García et al., 2019), we con-
145 structed the simulation model step by step using the niche model (Williams and Martinez, 2000)
146 and employed a bioenergetic consumer-resource model with allometric constraints,

$$\frac{dB_i}{dt} = r_i G_i B_i + B_i \sum_{j \in \text{prey}} e_{0j} F_{ij} - \sum_{k \in \text{pred}} B_k F_{ki} - x_i B_i - d_i B_i, \quad (3)$$

147 where the interaction term is defined as

$$F_{ij} = \frac{\omega_i a_{ij} B_j^{1+q}}{m_i (1 + \omega_i \sum_{k \in \text{prey}} a_{ik} h_{ik} B_k^{1+q})}. \quad (4)$$

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

150 We simulated the biomass of each species by Eqn. (3) in the R language, where the function
151 *runsteady* in library *rootSolve* solves the steady-state condition of ordinary differential equations
152 (ODEs) by dynamically running until the summed absolute values of the derivatives become
153 smaller than some predefined tolerance, and the function *jacobian.full* in library *rootSolve* estimates
154 the Jacobian matrix at the steady state. The rows and columns corresponding to the extinct

155 species and bottom prey were deleted, and the diagonal was substituted with zeros without
 156 normalization by diagonal elements, which formed the final community matrices to calculate the
 157 maximum real parts of the eigenvalues $Re(\lambda_{max})$ and feedback levels $a_n, n = 2, \dots, 7$. Herewith
 158 the assumed diagonal values of zero will let the matrices have some positive eigenvalues. In this
 159 way, this cannot be defined as the stability of the matrix in a strict mathematical sense, the values
 160 of $Re(\lambda_{max})$ can then indicate the level of stability. That is, the value of the $Re(\lambda_{max})$ is larger, the
 161 food web become more unstable(Neutel and Thorne, 2014; Neutel et al., 2002).

162 **Feedback metric.** A loop describes a pathway of interactions from a certain species through
 163 the web back to the same species without visiting other species more than once. (Hofbauer and
 164 Sigmund, 1988) Neutel(Neutel et al., 2002) defined the loop weight as the geometric mean of
 165 the absolute values of the interaction strengths in the loop. For zero-diagonal matrices, Neu-
 166 tel(Neutel and Thorne, 2014) proposed a feedback metric expressed as a ratio of 3-link and 2-link
 167 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
 168 $a_3 = \sum(\gamma_{ij}\gamma_{jk}\gamma_{ki} + \gamma_{ik}\gamma_{kj}\gamma_{ji})$ is the sum of all 3-link feedback loops. γ_{ij} is an element of a Jacobian
 169 community matrix model (linearization of ordinary differential equations of dynamic systems),

$$\Gamma = \begin{pmatrix} \gamma_{11} & \gamma_{12} & \cdots & \gamma_{1n} \\ \gamma_{21} & \gamma_{22} & \cdots & \gamma_{2n} \\ \vdots & \vdots & \ddots & \vdots \\ \gamma_{m1} & \gamma_{m2} & \cdots & \gamma_{mn} \end{pmatrix} = \frac{\partial(dB_i/dt)}{\partial B_j} \Big|_{B^*}, \quad (5)$$

170 whose local stability is determined by the largest real part of the eigenvalues of these matrices
 171 on three kinds of food webs, where B_i is the biomass of the species, B^* is the equilibrium point,
 172 and $(dB_i/dt)|_{B^*} = 0$. For the smallest omnivorous structures, i is the bottom prey, j is the
 173 intermediate predator, and k is the omnivore. For an ecological network with three species,
 174 the characteristic polynomial of the Jacobian community matrix at equilibrium biomass can be
 175 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
 176 be obtained through the coefficients of the characteristic polynomial.

177 According to zero-diagonal Jacobian community matrix $\Gamma_0 = \begin{pmatrix} 0 & \gamma_{ji} \\ \gamma_{ij} & 0 \end{pmatrix}$, $a_2 = tr(\Gamma_0 \times \Gamma_0) =$
 178 $tr((\Gamma_0)^2)$ can be easily proved, where tr is the trace of the matrix, i.e., the sum of the diagonal
 179 elements. We can similarly hold $a_3 = tr((\Gamma_0)^3)$ and

$$a_n = tr((\Gamma_0)^n), n = 2, 3, \dots, \quad (6)$$

180 which have more simple program implementation than Neutel's formula.(Neutel and Thorne,
 181 2014) We extend feedback metric $\sqrt[3]{|\frac{a_3}{a_2}|}$ to $|\frac{a_n}{a_{n-1}}|^\alpha$, $n = 4, 5, 6, \dots$, where the power α is intro-
 182 duced for more robustness of different food webs with various stability.

183 **Feedback loop structure.** Five-link feedback loops applied in our trace method are depicted in
 184 Fig. 1(c,d), and loops with an edge from one species to itself can be neglected since diagonal
 185 intraspecific strengths in our Jacobian community matrices are zero. Loops of Fig. 1(c) are cycles
 186 in graph theory that can be searched out by Johnson's algorithm,(Johnson, 1977) and the left
 187 part of Fig. 1(d) is a high-level omnivory module(McLeod and Leroux, 2021; Wootton, 2017)
 188 compared to a classic omnivory loop (left part of Fig. 1(b)). Our trace a_5 can be divided into the
 189 sum weight of high-level omnivory modules, which is dominant, since it far outweighs the other
 190 (Fig. 5(b)), and the sum weight of 5-link cycles, which can be omitted. For all of the zero-diagonal
 191 community matrices, a_2 and a_3 by our trace method are just double and triple sum weights of 2-
 192 and 3-link loops found by Johnson's algorithm (Fig. 5(b)).

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

$$\begin{aligned} \frac{dP}{dt} &= P(b'a'R + \beta\alpha N - m'), \\ \frac{dN}{dt} &= N(abR - m - \alpha P), \\ \frac{dR}{dt} &= R(r(1 - R/K) - aN - a'P). \end{aligned} \quad (7)$$

197 The P , N , and R are the densities of the omnivorous predator, intermediate predator, and basal

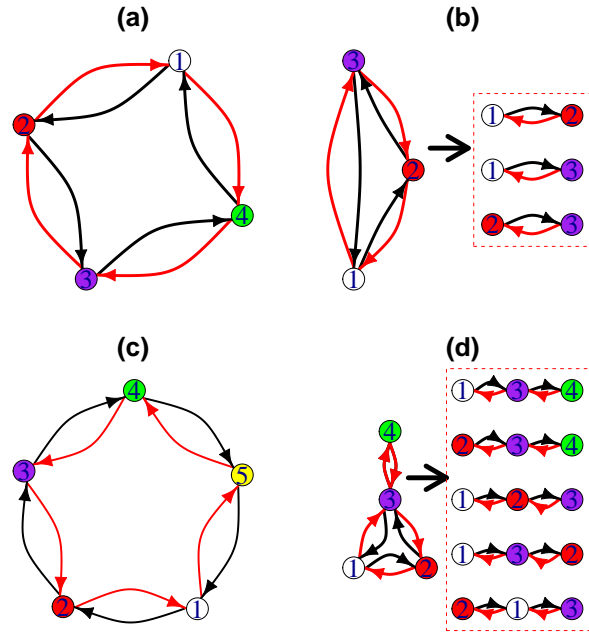


Figure 1: Predator-prey feedback loop structure: (a) 4-link loop without repeated species (cycle in graph theory), which can be searched by Johnson’s algorithm(Johnson, 1977); (b) Classic smallest omnivory loop and its three one-species-delete subloops (2-link loop); (c) 5-link loop without repeated 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).

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

211 To evaluate local stability of the full three-species equilibrium P^* , N^* and R^* at which growth
 212 rates reach zero, we follow standard Jacobian matrix procedures(May, 1972). The elements in
 213 the Jacobian matrix near equilibrium which equal the partial derivative of the population growth
 214 equation of the species corresponding to row i with respect to the species corresponding to
 215 column j , evaluated at equilibrium, are regarded as interaction strengths(Laska and Wootton,
 216 1998), which conceptually represent the direct effect of an individual of one species on the total
 217 population of another species at or near equilibrium. This definition has received considerable
 218 attention in food web models. The Jacobian matrix of model (7) is as follows:

$$\begin{pmatrix} \gamma_{11} & \gamma_{12} & \gamma_{13} \\ \gamma_{21} & \gamma_{22} & \gamma_{23} \\ \gamma_{31} & \gamma_{32} & \gamma_{33} \end{pmatrix} = \begin{pmatrix} 0 & \beta\alpha P^* & b'a'P^* \\ -\alpha N^* & 0 & baN^* \\ -a'R^* & -aR^* & -\frac{rR^*}{K} \end{pmatrix}. \quad (8)$$

219 For testing the local stability of the equilibrium, a small and temporary perturbation is
 220 added to phytoplankton from equilibrium for example(also can be to two or all species, one
 221 for simplicity and easy explanation), then three growth rates all change to be nonzero. The

222 growth rate of phytoplankton must be greater than zero for its density increment from equi-
 223 librium, so phytoplankton growth rate must be pulled back through interaction strengths γ_{31}
 224 and γ_{32} . There are three possible paths to do it, one is $\gamma_{32}\gamma_{23} = (-aR^*)(baN^*)$ called two-
 225 link feedback loop, implying abundant phytoplankton enriches zooplankton and more zoo-
 226 plankton eat increased phytoplankton conversely. The other two is three-link feedback loops
 227 $\gamma_{32}\gamma_{21}\gamma_{13} = (-aR^*)(-\alpha N^*)(b'a'P^*)$ having positive weight to enlarging phytoplankton and in-
 228 stability (Fig. 2(b) black arrow) and $\gamma_{31}\gamma_{12}\gamma_{23} = (-a'R^*)(\beta\alpha P^*)(baN^*)$ having negative weight
 229 to decreasing phytoplankton and leading more stability(Fig.2(b) red arrow).

230 Negative loop can be explained as that increasing phytoplankton brings about zooplankton
 231 and shrimps which will eat additional phytoplankton to go back to the original equilibrium,
 232 whereas positive loop is that increasing phytoplankton directly flourish shrimps which consume
 233 more zooplankton and fading zooplankton will strengthen phytoplankton far away the equi-
 234 librium. The system's stability can be determined by the total effects of negative and positive
 235 feedback loops of different lengths. For a ecosystem of n species or trophic groups, the longest
 236 loops may have n -link length that show very complicated structure and the most expensive
 237 computational cost, so only total effect of three-link and two-link loops are researched up to
 238 present(Neutel and Thorne, 2014), but longer loops should affect stability definitely.

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

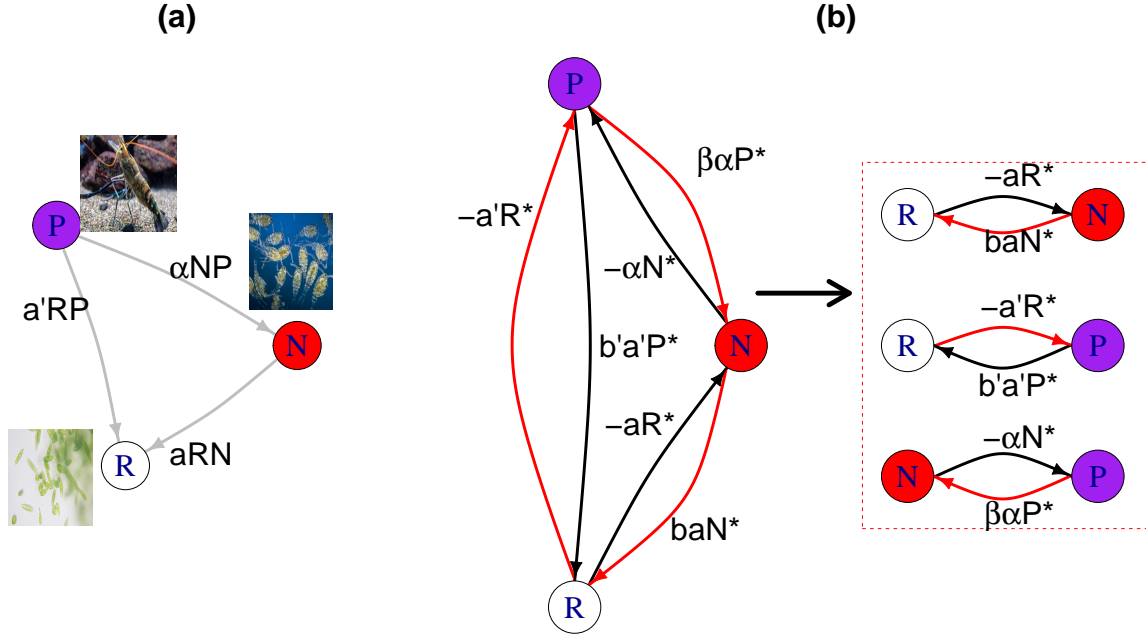


Figure 2: A toy Lotka-Volterra Intraguild Predation Model with three species and feedback loops based on Jacobian matrix: The omnivorous feeding rates loop (a) generates two trophic interaction loops (b), one negative clockwise loop $(-a'R^*)(\beta\alpha P^*)(baN^*)$ and one positive anti-clockwise loop $(-aR^*)(-\alpha N^*)(b'a'P^*)$. (a) Predator prey relationship in the IGP model(Eqn. 7) taking phytoplankton, zooplankton and shrimps as example, 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(Eqn. 8) induced from model(Eqn. 7).

Results

247

248 **Complexity-stability relation.** We first investigated the relation between stability and classic
249 complexity descriptors, i.e., species richness S ; connectance C ; standard deviation of interaction
250 strength (IS) σ ; coefficient of variation of IS σ/E , where E is the mean of IS; skewness and
251 kurtosis of IS. We observed no relation between food web stability and species richness and
252 connectance, neither with skewness nor kurtosis (Fig. 3(a,b,f,g)). The standard deviation of IS,
253 σ , is a considerable factor for food web stability because both itself and its combinations, such
254 as coefficient of variation σ/E and May's complexity criterion $\sigma\sqrt{SC}$ (May, 1972) implied some
255 dependence on the real part of the maximum eigenvalue for p values less than 0.05, but their
256 R^2 values were near 0.1, suggesting that σ and related metrics are not critical to determining
257 food web stability (Fig. 3(c,d,e)), and other metrics of the substructure beyond basic statistics of
258 interaction strength should be considered.

259 **Weight sum ratio determines stability.** Surprisingly, we found that predator-prey feedback met-
260 rics $|a_3/a_2|$, $|a_5/a_4|$, and $|a_7/a_6|$ were strongly related to the matrix stability measure $Re(\lambda_{max})$,
261 and their slopes gradually decreased, which implied that $|a_3/a_2|$ contributed most to the stability
262 of an ecosystem among the three metrics (Fig. 4(a)). It was noted that $|a_4/a_3|$ and $|a_6/a_5|$ ex-
263 hibited almost no relation with stability $Re(\lambda_{max})$ (Fig. 4(b,c)), since there were no omnivores in
264 4- and 6-link feedback loops (McLeod and Leroux, 2021; Wootton, 2017). Pairwise metrics (Tang
265 et al., 2014) also showed little correlation with stability with $R^2 = 0.36$ (Fig. 4(d)), which satis-
266 fied the opinions in (Jacquet et al., 2016; Neutel and Thorne, 2016) but contradicted the results
267 in (Michalska-Smith et al., 2015). Predator-prey feedback metrics $|a_{2n+1}/a_{2n}|^\alpha, n = 1, 2, \dots$ are
268 generally good indicators of stability, but $|a_{2n}/a_{2n-1}|^\alpha, n = 2, 3, \dots$ are not.

269 **Feedback loop weight decomposition.** Since cycles greater than five are numerous for large
270 ecological networks, we selected 74 smaller Ecopath marine models and identified all of their
271 2-, 3-, 4-, and 5-links cycles from our 127 models using Johnson's algorithm. The cumulative
272 proportion curves were almost the same whether subtracting the sum weight of 4- and 5-link

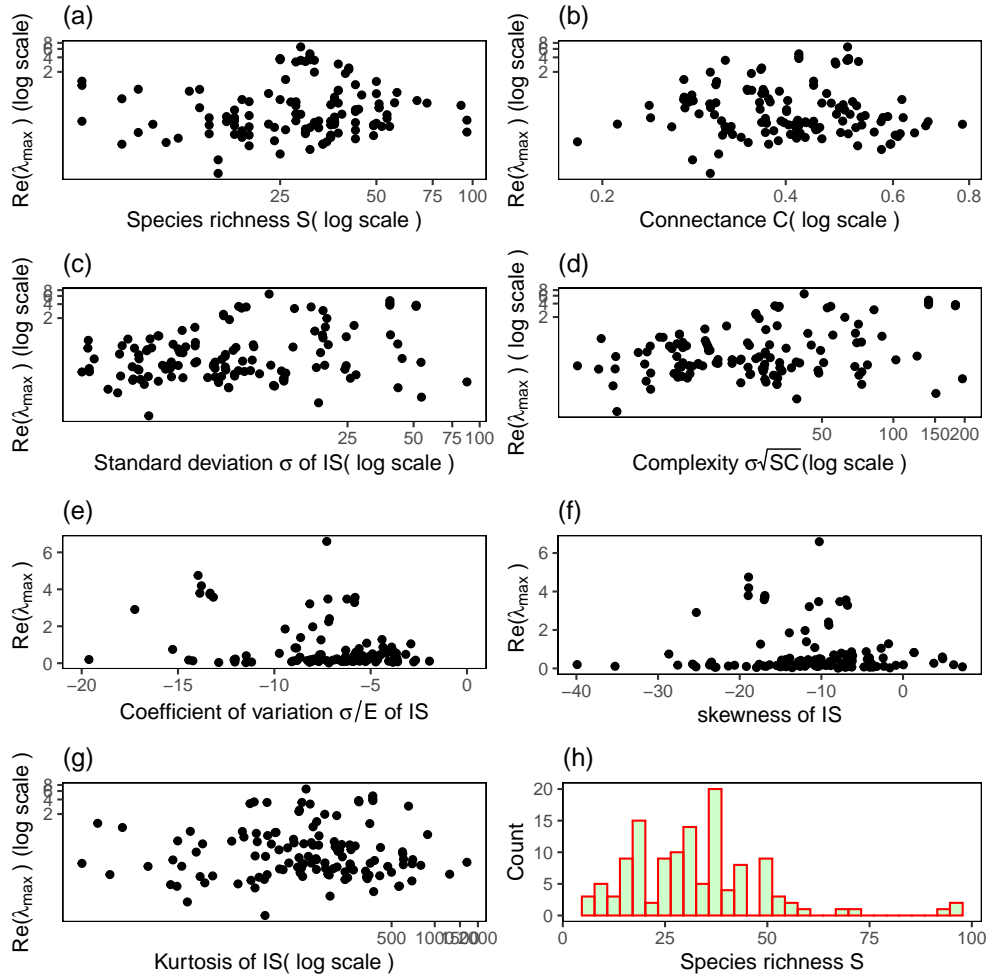


Figure 3: Food web stability related to basic metrics of IS across 127 natural Ecopath models of marine ecosystems based on empirically parameterized community matrices: (a) Number of species S at log₂ scale for xy axis ($R^2 = 0.009, p = 0.28$); (b) Connectance $C = L/S^2$, where L is the number of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

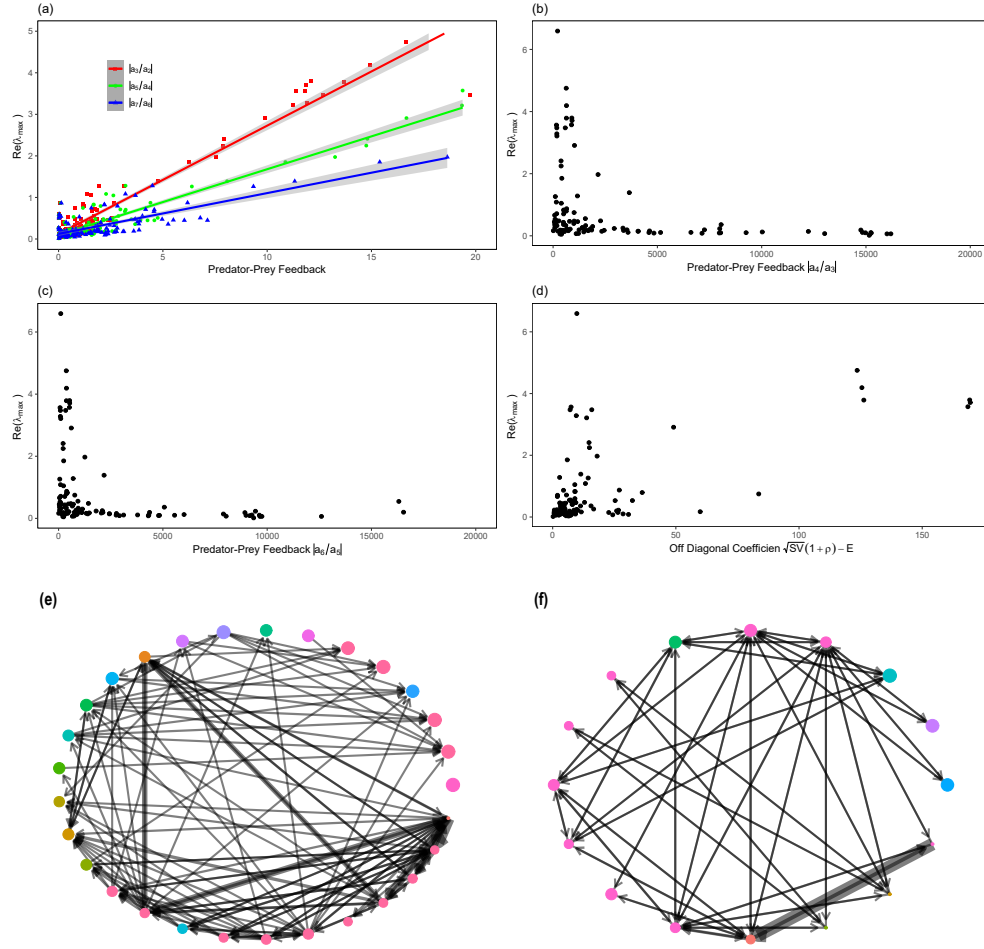


Figure 4: Performance of extended feedback metrics and pairwise metric against stability $Re(\lambda_{max})$ across 127 natural Ecopath models of marine ecosystems based on empirically parameterized community matrices, where S is the number of species or trophic species; and E, V, ρ are the mean, variance, 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

273 cycles from our sum weights a_4 and a_5 respectively (Fig. 5(a)). The sum weights a_n and a_{n-1}
 274 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
 275 magnitudes of a_n grew exponentially, but the ratios a_n/a_{n-1} seemed to vary around a constant
 276 for different ecological systems (Fig. 5(a)). For 2- and 3-links, sum loop weights of our matrix
 277 trace method are exactly two and three times as much as that of cycles with no repeat nodes,
 278 but our method's sum weights far outweigh that of cycles in 4- and 5- links(5(b)), so omnivory
 279 loops are dominant in loop weight analyses. For a natural marine Ecopath food web (Eritrea's
 280 coral reef model(Tsehaye and Nagelkerke, 2008)), geometric mean loop weights of different
 281 lengths searched out by Johnson's algorithm were almost symmetric at zero (Fig. 5(d)), so the
 282 maximum loop weight and sum loop weight had strong correlation for a fixed-length loop. This
 283 phenomenon also existed in other models(Neutel et al., 2002, 2007). Maximum loop weights of
 284 3-links were almost the maximum of all lengths, and only a few maxima of all lengths occurred
 285 at other links (Fig. 5(c,d)); therefore, a regression line between maximum loop weights of all link
 286 lengths and food web stability coincides with that between the maximum loop weight of 3-link
 287 and food web stability(Kuiper et al., 2015; Mitchell and Neutel, 2012; Neutel et al., 2007) (Fig.
 288 5(c)), with $R^2 = 0.722$ less than the effect of the sum weight ratio a_3/a_2 ($R^2 = 0.9$) in Fig. 4(a).
 289 **Theoretical simulations.** Simulations with the bioenergetic consumer-resource model(Domínguez-
 290 García et al., 2019) revealed that the vulnerability of a system (larger $Re(\lambda_{max})$ leads to more
 291 chance of instability) could be roughly predicted by the predator-prey feedback metrics $|a_{2n+1}/a_{2n}|^{2/2n+1}$
 292 , $n = 1, 2, \dots$ (Fig. 6(a-c)); even when long loops tended to be relatively weak(Neutel et al., 2007).
 293 The ratio of total odd- to even-link loops (minus 1) can capture the stability of food webs, but the
 294 ratio of total even- to odd-link loops (also minus 1) cannot (Supplementary Fig. ??). The exponent
 295 of the ratio $|a_{2n+1}/a_{2n}|$, chosen as $2/(2n + 1)$ in our simulation, was found to be a key parame-
 296 ter to predict $Re(\lambda_{max})$, whose numerator 2 is absolutely necessary in our simulation, and whose
 297 denominator $2n + 1$ can be regarded as the geometric mean of the $(2n + 1)$ -link loop weights,
 298 while the exponents in Ecopath models and their randomization tests were all set to 1 for good
 299 performance. The sensitivity of the exponent of the ratio against stability is discussed in the Sup-

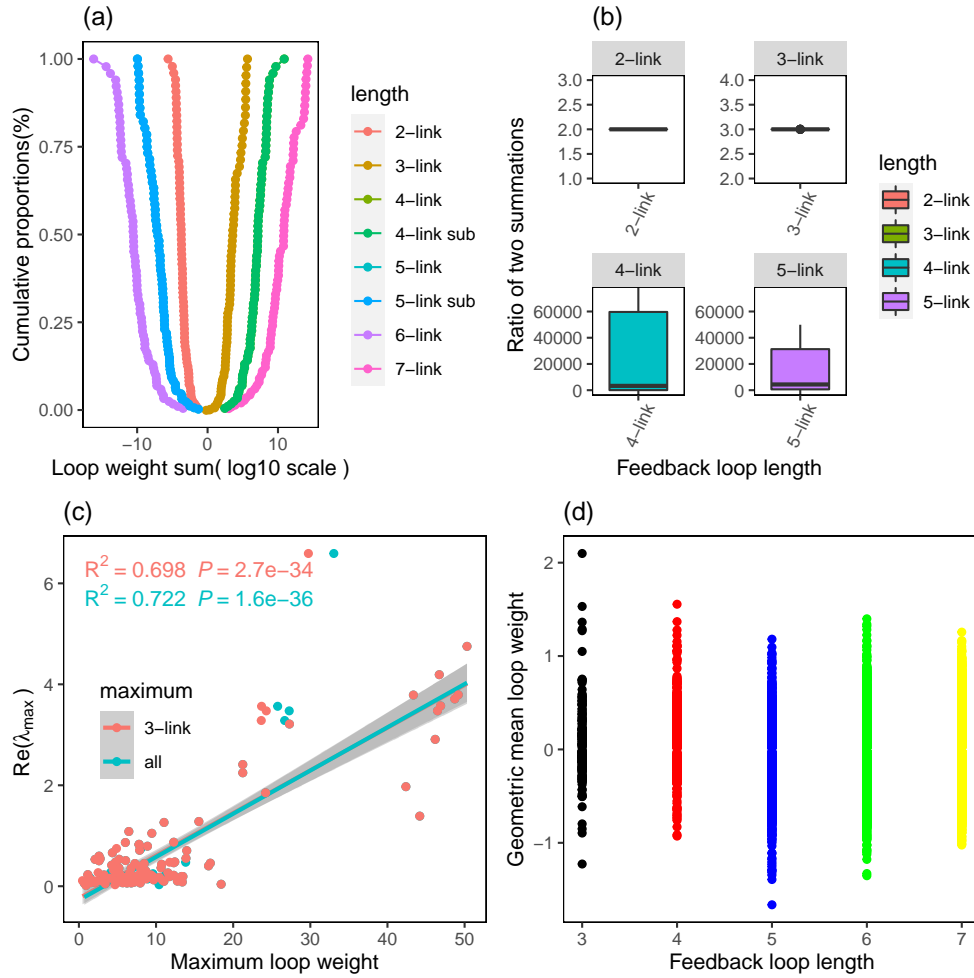


Figure 5: Relation among loop weights in empirical marine Ecopath food webs, where loop weight is the product of interaction strengths without averaging: (a) Sum loop weight a_n of different lengths by our trace method in selected 74 models. *5-link sub* means that the sum weight of 5-link cycles found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

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

304 Discussion

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

314 We discovered that feedback metrics $|a_{2n+1}/a_{2n}|^\alpha$, i.e., the ratio of the sums of $(2n + 1)$ -
315 link and $2n$ -link loop weights, have a good relation with stability (the real part of the dominant
316 eigenvalue) of community matrices. Why can the sum weight ratios $a_3/a_2, a_5/a_4, a_7/a_6$ capture
317 food web stability? As we know, a_3 is the total effect of classic omnivory loops (generated by
318 intraguild predation module), which plays an important role in a food web(Arim and Marquet,
319 2004; Bascompte and Melián, 2005; Camacho et al., 2007; Holt and Huxel, 2007; Milo et al., 2002;
320 Paulau et al., 2015). If we delete one species in turn, three 2-link predator-prey feedback loops,
321 whose total effect is measured by a_2 , occur independently (Fig. 1(b)). Consequently, the ratio
322 a_3/a_2 reflects coupling strength(Mougi, 2018; Mougi and Kondoh, 2016) which holds information
323 about ecological network stability. Two 3-link loops can be thought as three 2-link loops and two
324 5-link loops as five 4-link loops(Fig. 1(b,d)), since the loops without repeated species(Fig. 1(c)

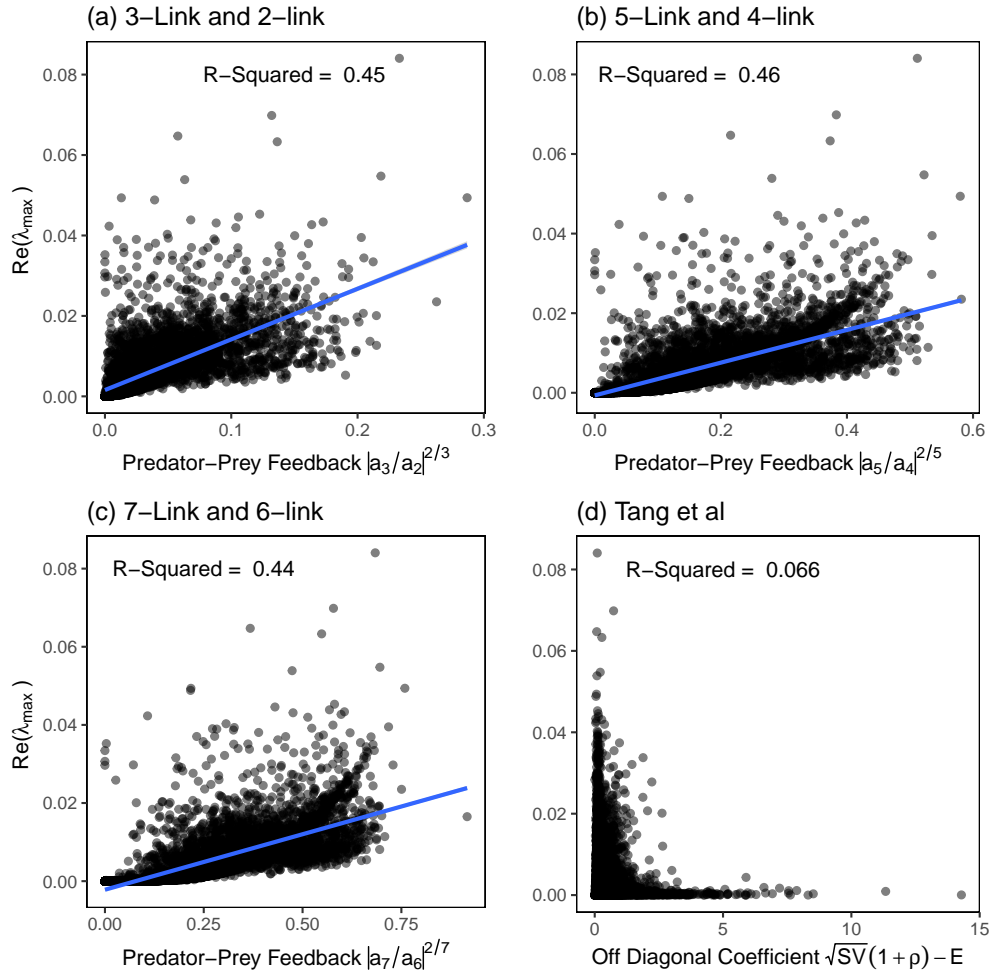


Figure 6: Performance of extended feedback metrics $|a_{2n+1}/a_{2n}|^{2/2n+1}$ and pairwise metric (Tang et al., 2014) $\sqrt{SV}(1 + \rho) - E$ against stability $Re(\lambda_{max})$ in simulation models (Domínguez-García et al., 2019) with species richness ranging from 5 to 100 species, repeated 50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

325) called cycles in graph theory are insignificant to omnivorous loops(Fig. 1(b,d)). These loops
326 have positive and negative weights which lead to instability and stability. For all n-link loops,
327 their total weight is represent as a_n , so a_3/a_2 and a_5/a_4 show coupling strength.

328 The main body of a_5 is a high-level omnivory module(McLeod and Leroux, 2021; Wootton,
329 2017)(left part of Fig. 1(d)). In the same way, if we delete one species in turn, five 4-link predator-
330 prey feedback loops, whose total effect is measured by a_4 , emerge independently (Fig. 1(d)).
331 Information about ecological network stability is also captured by coupling strength a_5/a_4 . If the
332 omnivory modules are more tightly coupled to their one-species-delete subloops, the food web
333 is more stable, since a_4 and a_6 have no omnivory structure, and fail to discover information about
334 food web stability (Fig. 4(b,c)).

335 If we randomly generate a Jacobian community matrix, a_n/a_{n-1} cannot predict stability re-
336 gardless of shuffling the positive elements to the upper triangle and negative ones to the lower
337 triangle (Supplementary Fig. ?? and ??), so there must be some conditions on the community
338 matrix for our results. We performed eight randomization tests H1-H8,(Jacquet et al., 2016) to
339 remove one or several properties of natural food webs and compute the stability of the permuted
340 community matrices. H1-H8 randomization tests of Jacobian community matrices of the 127 Eco-
341 path empirical marine ecosystems revealed that feedback metric $|a_5/a_4|$ almost played the same
342 role as $|a_3/a_2|$. Feedback metric $|a_3/a_2|$ had a better relation with stability than pairwise metric
343 $\sqrt{SV}(1 + \rho) - E$ in H2, H4, and H8 tests, but a worse one in H5, H6, and H7 tests, and both
344 seemed to have little correlation with stability in H1 and H3 tests (Supplementary Fig. ?? and ??).
345 In the same way, $|a_4/a_3|$ could not capture the stability of food webs (Supplementary Fig. ??). In
346 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
347 less than values in 127 Ecopath natural food webs. One reason is that our simulation have more
348 than 127 data points and large data could reduce the p value. Another is that Jacobian community
349 matrices of our simulation systems are directly and numerically computed at equilibrium points,
350 while those of Ecopath ecosystems are manually calculated by stable state biomass (Eqn. 2),
351 which are more dependent on off-diagonal elements. Our randomization tests by removing one

352 or several properties of natural food webs and a bioenergetic consumer-resource dynamic model
353 with allometric constraints (Domínguez-García et al., 2019) further confirmed these findings and
354 gave more insights into the underlying mechanisms.

355 Early studies concentrating on 3- and 2-link feedback loops for long loops contained relatively
356 many weak links and were time-consuming to explore. Since we computed the total weight a_n
357 of n -link feedback loops, there was no need to find every loop path and calculate its weight.
358 Matrix multiplication and traces could be applied for easy computation (Eqn. 6). Although the
359 long-loop weight is weak, its number is always large enough to have a non-negligible effect, and
360 the ratio between two tiny numbers may be large. Therefore, long feedback loops may affect
361 the stability of food webs. It is surprising that feedback levels $|a_{2n}/a_{2n-1}|$ seem to have little
362 correlation with stability; this needs further theoretical confirmation. A rough explanation is
363 based on theorems in linear algebra that the eigenvalues $\lambda((\Gamma_0)^n)$ of $(\Gamma_0)^n$ are the n -th power of
364 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
365 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
366 λ_i is the i -th eigenvalue. So, if the dominant eigenvalue $\lambda_1 = \lambda_{max}$ far outweighs the others,
367 then $\lambda_1^{2n+1} + \dots + \lambda_s^{2n+1}$ can be approximated by λ_1^{2n+1} , and $|a_{2n+1}/a_{2n}| \approx |\lambda_1| = |\lambda_{max}| = \lambda_{max}$,
368 since $\lambda_{max} > 0$, on account of the absence of intraspecific strength (diagonal elements) in the
369 community matrix. In the other case, if all eigenvalues center on their mean with small deviation
370 and are almost equal, then we can also approximate $|a_{2n+1}/a_{2n}|$ by the largest eigenvalue λ_{max} .
371 But to find the pattern of interaction strength in the community matrix to ensure these conditions
372 is a great challenge.

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Conflict of Interest

376

377 The authors declare that they have no conflict of interest.

Author Contributions

378

379 J.F. designed the research and discussed the framework with S.L. and R.W. S.L., J.F. and X.L.
380 conducted research. Y.J., R.W., X.M., W.Y., T.S., P.R. and Y.S. contributed to the analysis. S.L. and
381 J.F. wrote the paper and T.S., P.R. edited the paper, as well as input from all co-authors.

Data accessibility statement

382

383 Data available from the Figshare Digital Repository: [https://doi.org/10.6084/m9.figshare.](https://doi.org/10.6084/m9.figshare.16622305.v1)
384 [16622305.v1](https://doi.org/10.6084/m9.figshare.16622305.v1). The code supporting the results(mainly R scripts and partly Python code for
385 graph cycles) should be archived in Zenodo and the DOI will be included at the end of the article
386 if the manuscript is accepted.

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