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RECONCILING RESILIENCE ACROSS ECOLOGICAL SYSTEMS, SPECIES AND SUBDISCIPLINES

Research Article

Energetic constraints imposed on trophic interaction strengths enhance resilience in empirical and model food webs

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Abstract

- 1. Food web stability and resilience are at the heart of understanding the structure and functioning of ecosystems. Previous studies show that models of empirical food webs are substantially more stable than random ones, due to a few strong interactions embedded in a majority of weak interactions. Analyses of trophic interaction loops show that in empirical food webs the patterns of the interaction strengths prevent the occurrence of destabilizing heavy loops and thereby enhances resilience. Yet, it is still unexplored which biological mechanisms cause these patterns that enhance food web resilience.
- We quantified food web resilience using the real part of the maximum eigenvalue of the Jacobian matrix of the food web from a seagrass bed in the Yellow River Delta (YRD) wetland, that could be parametrized by the empirical data of the food web.
- 3. We found that the empirically based Jacobian matrix of the YRD food web indicated a much higher resilience than random matrices with the same element values but arranged in random ways. Investigating the trophic interaction loops revealed that the high resilience was due to a negative correlation between the negative and positive interaction strengths (per capita top-down and bottom-up effects, respectively) within positive feedback loops with three species. The negative correlation showed that when the negative interaction strengths were strong the positive was weak, and vice versa.
- 4. Our invented reformulation of loop weight in terms of biomasses and specific production rates showed that energetic properties of the trophic groups in the loop and mass-balance constraints, for example, the food uptake has to balance all losses, created the negative correlation between the interaction strengths. This result could be generalized using a dynamic intraguild predation model, which delivered the same pattern for a wide range of model parameters.
- 5. Our results shed light on how energetic constraints at the trophic group and food web level create a pattern of interaction strengths within trophic interaction loops that enhances food web resilience.

KEYWORDS

food web resilience, interaction strengths, intraguild predation, Jacobian matrix, trophic interaction loops

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1 | INTRODUCTION

One of the most pressing challenges in ecological research is the ongoing deterioration of ecosystems world-wide with dramatic losses of biodiversity and the concomitant threats to ecosystem resilience and services (e.g. IPBES, 2019; Mori et al., 2013). A central concept in understanding biodiversity dynamics is community stability, that is, the capacity of the community to withstand or recover from environmental change. Food webs depict the trophic interactions, that is, who eats whom, in biological communities. Trophic interactions are of fundamental importance to the dynamics and persistence of species in ecosystems. Therefore, food webs occupy a central position in community ecology and their stability and resilience are at the heart of understanding the structure and functioning of ecosystems (Moore et al., 2017).

Food web stability has been approached by experimentation (e.g. Paine, 1992) and mathematical modelling (e.g. May, 1972; Pimm & Lawton, 1977). One of the most well-known approaches to measure food web stability is modelling the food web structure in the form of a Jacobian matrix (sensu May, 1972). In a Jacobian the matrix elements denote the strengths of the trophic interactions among the trophic groups. This approach considers food web stability and resilience in terms of how the food web responds to a disturbance. This can include various kinds of disturbance-response situations. When the disturbance has a short-term transient character, it is seen as a momentary change in the state of the food web, in terms of population biomasses. Then food web stability denotes the capacity of the food web to return to its original equilibrium state, while food web resilience denotes the rate at which the food web returns to the original equilibrium. This type of food web resilience can be categorized as an example of the 'first face' of resilience (sensu Holling, 1996), that is, 'engineering resilience'. When, in contrast, the disturbance has a long-term persistent character, it is seen as a structural change in environmental conditions. Then food web stability and resilience capture the capacity of the food web to adapt to the new environmental conditions by moving towards a new equilibrium state as well as the pathways towards the new equilibrium. This type of resilience can be categorized as an example of Holling's second face of resilience, that is, 'ecological resilience'.

In the present paper, we adopted the Jacobian matrix approach to analyse engineering resilience of an empirical food web. In such an application, the value of the maximum eigenvalue serves as a measure of food web resilience as it represents the 'return time' of the community needed to return to the original equilibrium after a sufficiently small disturbance (Moore et al., 2004; Pimm, 1982; Pimm & Lawton, 1977). Short return times are interpreted as high engineering resilience (Angeler & Allen, 2016; Pimm, 1991). Overall, the larger the value of the maximum eigenvalue the less resilient the food web (Wootton & Stouffer, 2016; see further section Materials and Methods).

Originally, Jacobian matrices were randomly constructed, both in terms of sign structure and of the values of the matrix elements. In such random approaches, the random food webs lost the intrinsic relationships that reflect the energetic build-up of empirical food webs in terms of the distributions of biomasses and energy fluxes. However, the Jacobian matrix approach is also suitable to combine empirical information with mathematical analysis, as the values of the elements in the Jacobian matrix can be derived from measurements (e.g. Jacquet et al., 2016; de Ruiter et al., 1995). The food webs represented by such empirically constructed matrices were found to be substantially more resilient than randomly constructed food webs (Jacquet et al., 2016; Neutel et al., 2002; de Ruiter et al., 1995; Tang et al., 2014; Yodzis, 1981). The mechanism behind this high level of resilience was that within the more realistic and ecologically feasible values of interaction strengths (ISs), a majority of weak ISs dampen a few strong ISs, thus enhancing food web resilience (Brose et al., 2006; Emmerson & Raffaelli, 2004; Emmerson & Yearsley, 2004; Gellner & McCann, 2016; McCann et al., 1998; Paine, 1992; Rip et al., 2010).

A key finding for understanding the stabilizing effects of IS patterns comes from Neutel et al. (2002) by revealing the importance of 'trophic interaction loops' sensu Levins (1974). A trophic interaction loop connects the interactions among several trophic groups in a closed circuit, where a group is connected with any other groups only once along the same path. For instance, three groups of intraguild predation (IGP, Holt & Polis, 1997), comprising a prey, a consumer of the prey and an omnivorous predator consuming both, result in two omnivorous loops (Figure 1). The length of a loop is determined by the number of trophic groups involved and its weight is the geometric mean of the component ISs. The higher the maximum loop weight the less stable the Jacobian matrix (Neutel et al., 2002, 2007). It has indeed been found that the maximum loop weight in the empirically based matrices is much lower than that in the randomized matrices (Neutel et al., 2002).

The concept of maximum loop weight provides a link between observed stabilizing patterns of ISs and mathematical theory of food web resilience. Yet, further clarification is needed to understand the biological mechanisms preventing that in empirical food webs such heavy loops occur as in the corresponding random webs. Because the values of ISs are derived from the energetic structure of the food web, the question becomes how the energetic build-up in food webs prevents heavy loops.

In the present paper, we approach this question by analysing resilience of the seagrass food web in the Yellow River Delta (YRD) wetland (Figure 1). The description of the YRD food web entails the biomasses of 14 trophic groups (and a detritus pool) and the fluxes among them (Li, Yang, Sun, et al., 2021). We constructed a Jacobian matrix of the food web and investigated the maximum loop weight to identify biological mechanisms that underly food web resilience. We hypothesize that the interaction strengths in the empirically based YRD food web model are arranged in such a way that heavy loops are prevented. Furthermore, that this arrangement is controlled by food web energetics in terms of the distribution of biomasses and fluxes. To test these hypotheses, we compared the resilience of the YRD food web with that of randomized matrices through multiple random permutations of ISs (Yodzis, 1981). We also compared the maximum loop weight of the YRD matrix with that of the randomized matrices. This revealed that the YRD food web had no heavy loops due to a negative correlation between negative and positive ISs within loops. We then invented a reformulation of loop weight to see how this negative correlation results



FIGURE 1 (a) Feeding diagram of the food web from a seagrass bed in the Yellow River Delta wetland. (b) Three trophic groups with intraguild predation (IGP), where the top group shrimps (t) feeds on the intermediate group zooplankton (i) and competes with zooplankton feeding also on the bottom group phytoplankton (b). Black arrows denote the fluxes F_{bi} , F_{bt} and F_{it} , meaning the flux from phytoplankton to zooplankton, from phytoplankton to shrimps and from zooplankton to shrimps respectively. (c) Two trophic interaction loops derived from the IGP module (i.e. omnivorous loops). Negative and positive interaction strengths are represented by red and green arrows respectively. The positive feedback omnivorous loop consists of two negative interaction strengths (α_{it} and α_{bi}) and one positive interaction strength (α_{tb}), and the negative feedback omnivorous loop consists of two positive interaction strengths (α_{ib} and α_{ti}) and one negative interaction strength (α_{tb}).

from the energetic constraints imposed on the structure of empirical food web. These energetic constraints accounted for energetic properties of trophic groups (e.g. biomasses and specific production rates) and mass-balanced constraints at the trophic group and food web level. Mass-balanced constraints at the trophic group level imply that the food uptake of a trophic group has to balance losses by its excretion, respiration and mortality. At the food web level, such constraints imply that consumer production can only be a fraction of its total prey production, that when an omnivorous predator receives a large proportion of its diet from one species then it will consume other species less, and that the production of a prey shared by different consumers can only be consumed once. Finally, we constructed a dynamic IGP model to investigate the generality of our results, in particular the negative correlations between negative and positive interaction strengths in loops and the role of energetic constraints.

2 | MATERIALS AND METHODS

2.1 | Structure of the Yellow River Delta food web

The YRD food web (Figure 1) comes from a seagrass bed, located on the coast of the Bohai Sea of northeast China, being ca. 20 km away from the river mouth. Based on field and laboratory observations, we distinguished 14 trophic groups and detritus represented by suspended particulate matter (Figure 1); herewith, a trophic group means a grouping of organisms sharing the same prey and predators. Food web fluxes were derived from measurements of biomasses, stable carbon and nitrogen isotope ratios, a Bayesian isotope mixing model, and assuming that the quantitative food web model is at steady state (Li, Yang, Sun, et al., 2021).

The food web had 34 trophic links among the 14 trophic groups, with a linkage density and connectance of 2.43 and 0.17, respectively, which is similar to many other aquatic food webs (Dunne et al., 2002). Regarding the primary producers, the production of seagrass and cordgrass *Spartina alterniflora* was rather low relative to their high biomasses and vice versa for phytoplankton and microphytobenthos (Table S1). Bivalves and gastropods dominated the consumer biomass, but zooplankton, the fish species So-iuy mullet *Planiliza haematocheila*, shrimps and polychaetes contributed also substantially to food web energetics due to their relatively high specific production rates (i.e. production to biomass ratios, *P/B*). The magnitude of fluxes generally decreased from low to high trophic positions, covering a range of three orders of magnitudes (Table S2).

2.2 | Assessing the resilience of the YRD food web

To derive the Jacobian matrix, the YRD food web was modelled in terms of generalized Lotka-Volterra differential equations sensu de Ruiter et al. (1995), in which the dynamics of producer biomass can be described as follows:

$$\frac{dX_i}{dt} = X_i \left(r_i - \sum_{j=1}^n a_{ij} X_j \right), \tag{1}$$

where X_i and X_j are the biomass of trophic group *i* and trophic group *j* respectively. *r* is the intrinsic growth rate and a_{ij} is the attack rate of *i* on *i*.

The dynamics of consumer biomass can be described as:

$$\frac{dX_i}{dt} = X_i \left(\sum_{j=1}^n e_j a_{jj} X_j - \sum_{j=1}^n a_{ij} X_j - d_i \right),$$
(2)

where e_i is the conversion efficiency of trophic group *i*, and d_i is the specific death rate of *i*.

The Jacobian matrix was derived in the equilibrium state as the partial derivatives of the Lotka–Volterra differential equations (May, 1972). The values of the matrix elements were derived from the observed biomasses, the estimated fluxes and energy conversion efficiencies (Li, Yang, Sun, et al., 2021) following de Ruiter et al. (1995). The flux F_{ij} (flux from trophic group *i* to trophic group *j*, g DW m⁻² year⁻¹, where DW is dry weight) in the equilibrium state can be expressed as $F_{ij} = a_{ij}X_i^*X_j^*$. This implies that the negative interaction strength (IS) of predator *j* on prey *i* (α_{ij}) representing the per capita top-down effect becomes:

$$\alpha_{ij} = \left(\frac{\partial \frac{dX_i}{dt}}{\partial X_j}\right)^* = -a_{ij}X_i^* = -\frac{F_{ij}}{B_j}.$$
(3)

where B_j is the biomass (g DW m⁻²) of predator *j* based on field survey data, and we set $B_j = X_j^*$ in the equilibrium state (de Ruiter et al., 1995).

Similarly, the positive IS of prey *i* on predator *j* (α_{ji} , here we restrict the Jacobian matrix to biological interactions and leave out interactions to and from the detritus pool; Neutel & Thorne, 2014) representing the per capita bottom-up effect becomes:

$$\alpha_{ji} = \left(\frac{\partial \frac{dX_j}{dt}}{\partial X_i}\right)^* = e_j a_{ji} X_j^* = \frac{e_j F_{ij}}{B_i}.$$
(4)

In this way we could parametrize all off-diagonal values to obtain the empirical matrix. For the diagonal values, denoting intraspecific interference, we lacked empirical information. There are several ways to 'deal' with the diagonal values (see e.g. van Altena et al., 2016). We choose to set all diagonal values equal to zero (Neutel & Thorne, 2014; Rip & 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(λ_{max})) can then indicate the level of resilience. The lower the value of the Re(λ_{max}), the more resilient the food web (Neutel & Thorne, 2014; Wootton & Stouffer, 2016).

2.3 | Randomizations in the empirical matrix of the YRD food web

To get insights in underlying mechanisms of the YRD food web resilience, we applied four randomizations on the empirical matrix (see Figure S1 the schematic representation of the four randomizations). All four randomizations conserve the empirical YRD food web topological structure (i.e. who eats whom), sign structure (+, -) and the values of ISs, but randomize the placing of ISs in the empirical matrix (Yodzis, 1981). This implies that we kept the trophic interactions among trophic groups in place but changed the absolute values of the strengths of these interactions. Comparing the Re(λ_{max}) for a random matrix with that of the empirical matrix reveals which patterns of IS are critical to food web resilience.

The first two randomizations, 1 and 2, were meant to test whether the empirical matrix included a pattern of ISs that enhances food web resilience. For randomization 1, we got a completely random matrix via randomly swapping predator-prey pairing of ISs (i.e. α_{ij} and α_{ji} for each trophic link, see Equations 3 and 4) 1,000 times for each random matrix, except that we still conserved the linkage between the negative and positive ISs for each pair (sensu Yodzis, 1981). Then we repeated this 1,000 times to achieve 1,000 random matrices. For randomization 2, we got an even more randomized matrix in which also the pairing of ISs was lost via randomly swapping all positive elements and negative elements 1,000 times for each random matrix (Tang et al., 2014). This allows us to further determine the role of pairing of ISs. We repeated this also 1,000 times to achieve 1,000 random matrices.

The two other types of randomization, randomization 3 and 4, were meant to see whether there are any single (pairs of) ISs that are critical ('keynote interactions') to food web resilience. In these randomizations, the permutations were restricted to swapping only two pairs of ISs (randomization 3) or two single ISs with the same sign (i.e. either two positive values or two negative values, randomization 4). In both randomization we systematically covered all exchange possibilities. Since we have 34 trophic links resulting in 34 pairs of ISs in the empirical matrix, we had for randomization 3 and 4 561 (34*33/2 = 561) and 1,122 (34*33 = 1,122) random matrices, respectively.

One-sample t tests were used to compare the average values of $\text{Re}(\lambda_{\max})$ and maximum loop weight (cf. Section 2.4 in Materials and Methods) of the randomized matrices with those of the empirical matrix. For these t tests we used version 20.0 of Statistical Package for the Social Sciences (SPSS) software (www.ibm.com/analytics/us/en/technology/spss/).

2.4 | Analysis of trophic interaction loops

A trophic interaction loop is a closed chain of interactions starting from a certain trophic group and going back to the same group with visiting other groups only once. For example, an IGP module consisting of three trophic groups generates two feedback loops (Figure 1): one positive (a clockwise loop comprising two negative ISs and one positive IS) and one negative feedback loop (an anti-clockwise loop comprising one negative IS and two positive ISs). Here, positive or negative feedback means that the product of all component ISs in the loop is positive or negative.

Loop weight is defined as the geometric mean of the absolute values of the ISs in a loop:

$$LW_{(k)} = \sqrt[k]{|\alpha_{12}\alpha_{23}\cdots\alpha_{k1}|},$$
(5)

where $LW_{(k)}$ is the loop weight (year⁻¹) of a loop of length *k* (containing *k* trophic group). In this study, we examined all loops up to a length of 8 (Neutel et al., 2002) for the YRD food web and for each random food web.

The maximum loop weight has been proposed as an indicator for the stability of the Jacobian matrix (Neutel et al., 2002). In the present analysis maximum loop weight should correlate with the maximum eigenvalue of the Jacobian matrix indicating food web resilience. Hence, the lower the maximum loop weight the more resilient the food web. Given that the heaviest omnivorous loops strongly govern food web resilience (Neutel et al., 2007, Figure 1 and Figure S2), and positive feedback loops lead to unstable system behaviour (Li & Moyle, 1981), we focused on positive feedback omnivorous loops (LW_{PFOI}). To understand what biological properties of the trophic groups within the loop determine loop weight, we invented a reformulation of the LW_{PFOL} in terms of a function of P/B ratios and the biomass ratio between the top and the bottom trophic group B_t/B_h (see below). P/B ratios determine the weightspecific turnover rates of energy of the component trophic groups and reflect their metabolic activity, depending, for example, on their growth and death rates. They are ultimately related to ISs, that is, high P/B ratios promote strong ISs and vice versa (Rooney et al., 2006). For example, a predator with a high P/B ratio will consume a high amount of prey relative to its own biomass and thus exert a strong grazing pressure on its prey, that is, a pronounced negative IS. The absolute values of ISs involved in a PFOL can be biologically expressed as:

$$\left|\alpha_{bi}\right| = \frac{F_{bi}}{B_i} = \frac{f_{bi}F_i}{B_i} = \frac{f_{bi}P_i}{e_iB_i},\tag{6}$$

$$\left|\alpha_{it}\right| = \frac{F_{it}}{B_t} = \frac{f_{it}F_t}{B_t} = \frac{f_{it}P_t}{e_tB_t},\tag{7}$$

$$\alpha_{tb} = \frac{e_t F_{bt}}{B_b} = \frac{e_t f_{bt} F_t}{B_b} = \frac{f_{bt} P_t}{B_b} = \frac{f_{bt} P_t B_t}{B_t B_b},$$
(8)

where f_{kj} reflects the diet composition of consumer *j* (dimensionless) and represents the proportion of a given prey *k* contributing to the diet of the consumer *j*, therefore, $F_{kj} = f_{kj}F_j$, where F_j is the total ingestion of consumer *j*. P_j is the production, being the product of F_j and its conversion efficiency e_j , $P_j = e_jF_j$. Equations (6) and (7) reveal that α_{bi} and α_{it} are proportional to the values of P_i/B_i and P_t/B_t respectively. α_{tb} is proportional to the product of P_t/B_t and B_t/B_b (Equation 8). Thus, the loop weight of PFOLs can be expressed as:

$$LW_{PFOL} = \sqrt[3]{|\alpha_{bi}\alpha_{it}\alpha_{tb}|} = \left(\frac{F_{bi}}{B_i}\frac{F_{it}}{B_t}\frac{e_tF_{bt}}{B_b}\right)^{1/3} = \left(\mu\frac{P_i}{B_i}\frac{P_t}{B_t}\frac{P_t}{B_t}\frac{B_t}{B_b}\right)^{1/3},$$
(9)

$$u = \frac{f_{bi}f_{it}f_{bt}}{e_i e_t},\tag{10}$$

where the diet compositions are subject to energetic mass-balance constraints and satisfy $0 < f_{bi} \le 1$ and $0 < f_{it} + f_{bt} \le 1$. That is, for example, the omnivore can only comprise either a high share of the bottom trophic group or the intermediate consumer.

2.5 | Intraguild predation modelling

To theoretically investigate the generality of the effects of the pattern of ISs and the energetic properties of the trophic groups in the PFOLs on food web resilience, we constructed a dynamic model of a food web of three trophic groups with IGP (Holt & Polis, 1997; Figure 1). The biomass dynamics of the three trophic groups (X_b , X_i and X_t) are given by the following ordinary differential equations:

$$\frac{dX_b}{dt} = X_b \left[r \left(1 - \frac{X_b}{K} \right) - a_{bi} X_i - a_{bt} X_t \right], \tag{11}$$

$$\frac{dX_i}{dt} = X_i \left(e a_{bi} X_b - a_{it} X_t - d_i \right), \tag{12}$$

$$\frac{dX_t}{dt} = X_t \left[ea_{bt} X_b + ea_{it} X_i - d_t \right], \tag{13}$$

where the growth of bottom trophic group *b* is modelled by a logistic function with the maximum growth rate *r* and the carrying capacity *K*. a_{bi} , a_{bt} and a_{it} represent the attack rates of the intermediate trophic group *i* on *b*, of the top trophic group *t* on *b* and of *t* on *i* respectively. *e* is the conversion efficiency of *i* and *t*. d_i and d_t represent the death rates of *i* and *t* respectively.

To achieve different IGP food web structures with varying ISs resulting in different PFOLs, we ran the IGP model for a wide range of parameter values via randomly selecting the values for the parameters a_{bt} , a_{tt} , d_p , d_t separately from (0, 1) and K from (1, 10), while keeping r and e constant (1 and 0.3 respectively). Hence, we did not assume a priori that the inherent energetic constraints within each IGP model were fulfilled, but restricted the further analysis to the models with ecologically feasible combinations of parameters that ensured coexistence of the three trophic groups (see Appendix S1 for the coexistence conditions). In this way we generated 2,000 IGP models where the three groups coexisted, and calculated the equilibrium biomasses as the mean biomasses of the last 5,000 steps of a 10,000. This time interval ensured that all simulations reached stasis or regular oscillations to overcome any transients. By these means we obtained the full range of ecologically feasible IGP

models (within the interval set for the different model parameters), with a large variation in the biomass and flux distributions among the different IGP models. Then we derived the Jacobian matrix for each IGP model. To be consistent with the resilience quantification of the YRD food web, we also set the diagonal values at zero and calculated the Re(λ_{max}) as the measure of food web resilience. We also calculated the loop weight of the PFOL for each IGP model (based on Equation 5) and applied the reformulation (Equation 9) on the PFOL, calculating the P_i/B_i and P_t/B_t as $P_i/B_i = a_{it}X_t^* + d_i$ and $P_t/B_t = d_t$ respectively.

All simulations and calculations were performed using version 2019b of the MATLAB software.

3 | RESULTS

3.1 | Structure of the Yellow River Delta food web

First we characterized the properties of each trophic link in the YRD food web (Figure 1) in terms of the biomass ratio of predator to prey (B_j/B_i) , interaction strength (IS) of predator on prey (the per capita top-down effect, α_{ij}), IS of prey on predator (the per capita bottomup effect, α_{ij}) and the absolute value of the flux (Figure 2). We found that most B_j/B_i ratios were less than 1 (82%) but some trophic links had a much higher predator than prey biomass, that is, bivalves feeding on phytoplankton ($B_j/B_i = 45$), gastropods feeding on microphytobenthos (61) and crabs feeding on microphytobenthos (22). Fluxes decreased significantly with trophic positions (Spearman correlation = -0.9, p < 0.001).

The ISs of the YRD food web followed a log-normal distribution (Figure S2) with many weak (62% of 68 ISs, <2 year⁻¹) and only a few strong ISs (3% of 68 ISs, >20 year⁻¹) (Table S3). The average of the absolute values of the negative ISs (α_{ij} in Figure 2, 9 ± 16 year⁻¹) was higher than that of the positive ISs (α_{ij} in Figure 2, 2 ± 6 year⁻¹). The opposite was only found in three cases, that is, in the trophic links between phytoplankton and bivalves, microphytobenthos and gastropods, and microphytobenthos and crabs.

3.2 | YRD food web resilience as indicated by the maximum eigenvalue ($\text{Re}(\lambda_{max})$) of the Jacobian matrix

Resilience of the YRD food web was quantified by taking the real part of the maximum eigenvalue ($\text{Re}(\lambda_{max})$) of the Jacobian matrix (see Section 2). This value of $\text{Re}(\lambda_{max})$ was 0.2 year⁻¹. As the matrix has only zero values on the diagonal, it can be interpreted as the required strength of intraspecific interference (i.e. the diagonal values) to stabilize the matrix (Neutel et al., 2002). Following this interpretation, the value of 0.2 year⁻¹ can be judged as being low, as it is ca. 25 times lower than the average of the absolute values of nonzero off-ISs, positive and negative ISs, of the matrix which was 5 year⁻¹. Hence, the patterning of nonzero off-diagonal values in the Jacobian matrix led to a low value of $\text{Re}(\lambda_{max})$ indicating a high level of resilience.



FIGURE 2 Biomass ratio (B_j/B_i) , interaction strengths $(\alpha_{ij} \text{ and } \alpha_{ji})$ and the flux (F_{ij}) for each trophic link in the food web of Yellow River Delta wetland. The vertical positions of prey *i* and predators *j* reflect their trophic positions

To further analyse this effect of the pattern of ISs on the resilience of the YRD food web, we applied four kinds of randomization to the empirical Jacobian matrix (see Section 2 and Figure S1). For randomization 1 and 2, we randomly permuted the pairs of nonzero off-diagonal ISs (randomization 1) and the ISs with the same signs (randomization 2) respectively (Figure S1). For both randomizations, the average values of $\operatorname{Re}(\lambda_{\max})$ were significantly higher than that of the empirical matrix, that is, $6 (\pm 5)$ year⁻¹ for randomization 1 (onesample $t_{(999)} = 39$, p < 0.001) and 8 (±6) year⁻¹ for randomization 2 (one-sample $t_{(999)} = 43$, p < 0.001). These values are respectively 29 and 37 times higher than that of the empirical matrix, which was 0.2 year⁻¹ (Figure 3). The maximum values of $\text{Re}(\lambda_{\text{max}})$ were 125 and 151 times higher than that of the empirical matrix ($\text{Re}(\lambda_{max}) = 26$ and 32 year⁻¹ respectively). Only one random matrix based on randomization 1 (Re(λ_{max}) = 0.08 year⁻¹) had a lower Re(λ_{max}) than that of the empirical matrix. For randomization 2, the minimum $Re(\lambda_{max})$ of the random matrices was still slightly higher than that of the empirical matrix. This all emphasizes that the placing of the ISs in the empirical matrix captures a pattern that is important to food web resilience.

To explore in more detail which IS permutations affected $\text{Re}(\lambda_{max})$ most, we did two other simpler randomizations which swapped only two pairs of ISs each time (randomization 3) or swapped only two ISs with same signs (both values positive or both values negative) each time (randomization 4) (Figure S1). Again we found that the randomized matrices had on average significantly higher values of $\text{Re}(\lambda_{max})$ indicating lower levels of resilience. For randomization



FIGURE 3 Food web resilience as quantified by the real part of the maximum eigenvalue, $\text{Re}(\lambda_{max})$, of randomized matrices based on randomization 1 (R1, randomly swapping pairs of ISs 1,000 times for each random food web), randomization 2 (R2, randomly swapping positive elements or negative elements 1,000 times for each random food webs), randomization 3 (R3, swapping only two pairs of ISs for each random food web) and randomization 4 (R4, only swapping two ISs with same signs for each random food web). The dashed blue line (value: 0.2 year⁻¹) marks the resilience of the food web of Yellow River Delta wetland

3 Re(λ_{max}) it was 1 ± 2 year⁻¹ (one-sample $t_{(560)} = 11, p < 0.001$) and for randomization 4 it was $0.8 \pm 2 \text{ year}^{-1}$ (one-sample $t_{(1,121)} = 12$, p < 0.001) (Figure 3). Although the swapping concerned only two pairs or two ISs. 82% of 561 random matrices based on randomization 3 and 73% of 1,122 random matrices had higher values of $\operatorname{Re}(\lambda_{\max})$ than the empirical matrix. Furthermore, the highest values of $\text{Re}(\lambda_{max})$ based on randomization 3 and 4 were 91 and 87 times higher than that of the empirical matrix ($\text{Re}(\lambda_{\text{max}}) = 19$ and 18 year⁻¹ respectively). These highest values were found when we swapped the pair of ISs between phytoplankton and shrimps with the pair of ISs between phytoplankton and bivalves for randomization 3, and swapped the positive IS of phytoplankton on shrimps with the positive IS of phytoplankton on bivalves for randomization 4. The minimum values of $\text{Re}(\lambda_{max})$ of random matrices based on randomization 3 and 4 were 0.06 and 0.09 year⁻¹, respectively, that is, lower than that of the empirical matrix.

3.3 | YRD food web resilience as indicated by the maximum weight of the trophic interaction loops

To get more insight in how and why the pattern of ISs was important to the resilience of the YRD food web, we analysed the structure of the YRD food web in terms of trophic interaction loops (Neutel et al., 2002, and see Section 2). The maximum loop weight is proposed as an indicator of the resilience of the food web. We identified 4,748 loops with a length from 3 to 8. A particular loop of length 3, that is, an omnivorous loop (Figure 1), consisting of phytoplankton, zooplankton and shrimps, was the heaviest (5 year⁻¹, Figure S2a). Among omnivorous loops, the mean and maximum values of the positive feedback omnivorous loops (PFOLs) were higher than those of the corresponding negative feedback omnivorous loops (Figure S2b).



FIGURE 4 Maximum loop weight of random food webs based on the four randomizations (R1–R4, details see Figure 3). The dashed blue line (value: 5 year⁻¹) marks the maximum loop weight of the food web of Yellow River Delta wetland

We repeated this loop analysis for the randomized Jacobian matrices. The average of the maximum loop weight of the random matrices based on randomization 1 and 2 was ca. 12 (\pm 5.0) year⁻¹ (Figure 4), that is approximately two times and significantly higher than that of the empirical matrix (both for randomization 1 and 2: one-sample $t_{(999)} = 39$, p < 0.001). Approximately 96% of the 1,000 matrices for randomization 1 and 2 had a higher maximum loop weight than the empirical matrix. The maximum and minimum values of the maximum loop weight in the random matrices based on randomization 1 and 2 were ca. 7 times higher and ca. 0.6 times lower than that of the empirical matrix respectively.

The average of the maximum loop weight values of matrices based on randomization 3 and 4 was also significantly higher than that of the empirical matrix (for randomization 3: one-sample $t_{(560)} = 4, p < 0.001$; for randomization 4: one-sample $t_{(1.121)} = 3$, p = 0.001). While, since only one (pair of) ISs was permuted, randomization 3 and 4 only partly altered the maximum loop weight (135 of 561 matrices (24%) for randomization 3 and 146 of 1,122 matrices (13%) for randomization 4). Eighty-one matrices for randomization 3 and 82 matrices for randomization 4 had a higher maximum loop weight than the maximum loop weight in the empirical matrix. The highest loop weights for randomization 3 and 4 were ca. 27 year⁻¹, that is, five times higher than that of the empirical matrix. The other 54 matrices for randomization 3 and 68 matrices for randomization 4 had a lower maximum loop weight than that of the empirical matrix, the lowest values being ca. 3 year⁻¹. Hence, decreases in maximum loop weight due to randomizations 3 and 4 were (slightly) less in number and (much) smaller than increases in maximum loop weight. Yet, it was frequently found that such swapping of only two (pairs) of ISs had a pronounced effect on maximum loop weight, and hence of YRD food web resilience.

3.4 | Example of the pattern of interaction strengths in positive feedback omnivorous loops to show how randomizations in interaction strengths decrease YRD food web resilience

As the loop with the maximum loop weight (PFOL_1, phytoplanktonshrimps-zooplankton-phytoplankton) indicates the resilience of the YRD food web, we took it as example together with the next heaviest loop (PFOL_2, phytoplankton-shrimps-bivalves-phytoplankton) to show the effects of the randomizations (Figure 5). In the empirical matrix, a PFOL includes two strong negative ISs and one weak positive IS (Figure 5a), that is, the PFOL 1 comprised the ISs of 0.2. -7 and -96 year⁻¹ leading to a weight of 5 year⁻¹ and the PFOL 2 comprised the ISs of 0.2, -10, and -4 year⁻¹ leading to a weight of 2 year⁻¹. When we did the randomization 3, that is, swapping the pair of ISs between phytoplankton and shrimps with the pair of ISs between phytoplankton and bivalves, it created a much higher weight: the PFOL_1 now comprised the ISs of 29, -7 and -96 year⁻¹ leading to a weight of 29 year⁻¹, and the PFOL 2 comprised the ISs of 29, -10 and -4 year⁻¹ leading to a weight of 10 year⁻¹, thus both caused ca. five times higher loop weights. Likewise, if we only swapped the two positive ISs, 0.2 year⁻¹ and 29 year⁻¹, the loop weights of the two PFOLs also increased by a factor of ca. 5 (Figure 5c). This shows that how the organization of the ISs in the YRD food web makes that the strong negative and strong positive ISs are not in the same



FIGURE 5 Interaction strengths in two positive feedback omnivorous loops, one loop (P–S–Z–P) is composed of phytoplankton (P), zooplankton (Z) and shrimps (S) and the other loop (P–S–B–P) is composed of phytoplankton, bivalves (B) and shrimps in (a) empirical YRD Jacobian matrix (the real part of maximum eigenvalue $\text{Re}(\lambda_{max}) = 0.2 \text{ year}^{-1}$), (b) randomized matrix based on randomization 3 (swapping the pair of ISs between P and S with the pair of ISs between P and B, $\text{Re}(\lambda_{max}) = 19 \text{ year}^{-1}$) and (c) randomized matrix based on randomization 4 (swapping the IS of P on S with the IS of P on B, $\text{Re}(\lambda_{max}) = 18 \text{ year}^{-1}$). Negative and positive interaction strengths are represented by red and green arrows respectively. The width of arrows is scaled to the absolute values of the interaction strengths. LW means loop weight

PFOL. This keeps loop weight low and food web resilience high. The example in Figure 5 is representative for all PFOLs in the YRD food web. By exploring all PFOLs in the YRD food web we found that the product of the negative ISs was negatively correlated with the value of the positive ISs (Figure 6a). That is, there is no loop where both the negative and positive ISs are high which would result in a really high loop weight.

To understand the biological mechanisms underlying this negative correlation between the ISs in PFOLs, we reformulated loop weight in terms of the energetic properties of the trophic groups in the loop, that is, by taking the two negative ISs as being proportional to the production to biomass ratios of intermediate and top groups (P_i/B_i and P_t/B_t respectively) and the positive IS being proportional to the product of the P_t/B_t and the top-bottom biomass ratio (B_t/B_b) (cf. Equations 6-8). We found that the term $\sqrt[3]{\frac{Pt}{B_i} \frac{Pi}{B_i} \frac{Pt}{B_i} \frac{Bt}{B_i}}$ derived by Equation (9) is highly correlated with the loop weight of the PFOLs (Figure 6b). We then checked the relationship between the term $\frac{Pt}{Bt}$. $\frac{Pi}{Bt}$ (referring to the product of the two negative ISs) and the term $\frac{Pt}{Bt}$. $\frac{Bt}{Bb}$ (referring to the positive IS), and we found a similar negative correlation between these two terms as with the ISs (Figure 6a,c).

3.5 | Resilience and the weight of the positive feedback omnivorous loop in an intraguild predation model

To investigate the generality of the observed negative correlations in ISs and energetic properties of trophic groups in the YRD food web, we ran a dynamical intraguild predation (IGP) model for a large variety



FIGURE 6 The 22 positive feedback omnivorous loops (PFOLs) in the empirical food web of the Yellow River Delta wetland (a-c) and 2000 PFOLs derived from 2000 intraguild predation models (d-f). (a, d) Relationships between the product of the two negative interaction strengths $(IS_{n1}^*IS_{n2})$ and the one positive interaction strength (IS_p) . (b, e) Relationships between the term $(P_t/B_t * P_t/B_t * P_t/B_t * B_t/B_b)^{(1/3)}$ derived by the energetic reformulation of loop weight (Equation 9) and the exact loop weight. *P/B* is the ratio of production to biomass. Subscripts *b*, *i* and *t* represent the bottom, intermediate and top trophic group in each loop respectively. (c, f) Relationships between the term $P_t/B_t * P_t/B_t (referring to the product of the two negative ISs)$ and the term $P_t/B_t * B_t/B_b$ (referring to the positive IS). The colour of each circle (i.e. each PFOL in a, c, d, f) reflects the loop weight. The different scales between a, c and d, f are due to the different absolute values of biomasses and fluxes between the empirical food web (see Tables S1 and S2) and simulated IGP models (see Figures S7, S8 and S9a)

of parameter values. From these runs we obtained 2,000 models in which the three trophic groups coexisted and exhibited a large variation in their ISs. Similar as in the YRD food web the product of the two negative ISs and the positive IS in the 2,000 PFOLs were negatively correlated (Figure 6d). Also consistent with the YRD food web, the term $\sqrt[3]{\frac{Pt}{Bt}\frac{Pi}{Bt}\frac{Pt}{Bt}}$ was closely correlated with the loop weights for the 2,000 PFOLs (Figure 6e). The terms $\frac{Pt}{Bt}$, $\frac{Pi}{Bt}$ and $\frac{Pt}{Bt}$, $\frac{Bt}{Bt}$ derived from the 2,000 PFOLs exhibiting a similar negative correlation (Figure 6f) as found for the YRD food web (Figure 6c). Their relationship is more scattered than the one in Figure 6d due to the influence of varying diet compositions which are not accounted for (Equation 10).

4 | DISCUSSION

Food webs in a variety of ecosystems have been found to maintain their stability and resilience via multiple but interrelated mechanisms. Such mechanisms include patterns of interaction strengths (ISs) derived from energetic flux pattern (de Ruiter et al., 1995), a few strong links embedded in a majority of weak links (McCann et al., 1998) and the avoidance of heavy trophic interaction loops (Neutel et al., 2007; Neutel & Thorne, 2014). Based on the empirical seagrass food web in the YRD wetland, we contribute to these findings by revealing a negative correlation between the negative and positive ISs preventing that positive feedback loops become heavy. This results in relatively low maximum eigenvalue of the Jacobian matrix, indicating a relatively high resilience of the YRD food web. Importantly, this study extends our understanding of food web resilience by accounting for the energetics at the trophic group and food web level, based on our reformulation expressing loop weight in terms of specific production rates (production to biomass ratios, P/B) and biomass ratios within the loop. We found also a negative correlation between the product of the P/B values of intermediate and top groups $\left(\frac{Pt}{Bt}, \frac{Pi}{Bt}\right)$, referring to the two negative ISs) and the product of the P/B value of the top groups and the biomass ratio of the top and bottom groups $\left(\frac{Pt}{Bt}, \frac{Bt}{Bh}\right)$ referring to the one positive IS) in the PFOLs. The intraguild predation modelling underpinned the generality of the results. The set of 2,000 models showed a similar negative correlation between the ISs together with the underlying energetic properties of component trophic groups.

The distribution of IS values in the YRD food web confirmed earlier findings in that they were skewed towards weak ones, that is, exhibiting a few strong interactions embedded within many weak interactions (Emmerson & Raffaelli, 2004; McCann et al., 1998). Some other previously studied food webs had a similar log-normal distribution of ISs as the one in YRD (Figure S3; Bascompte et al., 2005; Berlow et al., 2009). The ISs in the YRD food web also showed that the absolute value of the negative IS was much higher than that of the positive IS (Pimm & Lawton, 1977; de Ruiter et al., 1995).

Randomizations 1 and 2 of ISs in the empirical matrix showed much higher maximum eigenvalues ($\text{Re}(\lambda_{max})$) than the empirical matrix, which is in line with previous studies (Jacquet et al., 2016; Neutel et al., 2002; Tang et al., 2014; Yodzis, 1981). The linkage

between the pairing of the negative and positive ISs in the YRD food web did not play a substantial role, as the effect of randomization 2 breaking up this linkage was not greatly different from that of randomization 1. Thus, this finding does not confirm that of Tang et al. (2014), and we speculate that the ISs parametrized on the basis of body size information in Tang et al. (2014) may have captured different properties than the present ones derived from mass-balanced fluxes. The two new randomization tests (randomization 3 and 4) exchanging only two pairs or two elements in the empirical matrix showed that the permutations of ISs in the heavier loops have the most pronounced effect (Figure S4). This finding confirms that heavier loops are Achilles heels of food web stability and resilience (Mitchell & Neutel, 2012).

The application of the concept of maximum loop weight provided a way to better understand the biological processes important for food web stability and resilience (Neutel et al., 2007; Neutel & Thorne, 2014). We found that maximum loop weight in the YRD food web originated from the fact that in PFOLs strong negative interactions coincided with a weak positive interaction and vice versa: a strong positive IS was combined with weak negative ISs. The modelled energetically feasible IGP food webs confirmed the occurrence of this counteracting pattern of ISs and its dampening of loop weight (Figure 6c). It is this pattern that constrains the maximum eigenvalue Re(λ_{max}) of the Jacobian matrix and promotes food web resilience (Figure S5).

The negative correlation between the negative and positive ISs originated from the energetic properties of the trophic groups and mass-balanced constraints. In the ecologically feasible IGP models, the fluxes F_{hi} (from the bottom to the intermediate trophic group) and F_{it} (from the intermediate to the top trophic group) (Figure S6) were both negatively correlated with the flux F_{ht} (from the bottom to top trophic group) (Figure S7). This is because the production of the bottom trophic group P_{μ} has to be shared between the two consumers (Holt & Polis, 1997). Furthermore, relatively high values of F_{bi} and F_{it} occurred when the biomass of the bottom trophic group B_{h} was close to the half of its carrying capacity (Figure S8), implying that P_b is high. This implies that when relatively high values of F_{hi} and F_{it} facilitate high negative ISs (being F_{hi}/B_i and F_{it}/B_t , Equation 3), the positive IS (being eF_{ht}/B_h , Equation 4) cannot be relatively high as well given the high value of B_{b} . The IGP modelling also showed a negative correlation between the two negative ISs (Figure S9b). This is because although the fluxes F_{bi} and F_{it} are positively correlated, B_i and B_t are negatively correlated due to the competition between the intermediate and the top trophic group for P_h (Figure S9a). B_t is high when it preys predominately directly on the lowest trophic level reducing F_{hi} . Likewise, there is a negative correlation between P_t/B_t and P_i/B_i (Figure S10a, Rooney et al., 2008), which influence the two negative ISs respectively. Moreover, there is also a negative correlation between P_t/B_t and B_t/B_h limiting the value of the positive IS in the loop, as the product of the two values refers to the positive IS (Figure S10b). Obviously, from a mathematical perspective, low values of B_t enhance P_t/B_t but reduce B_t/B_h , and vice versa.

Furthermore, from the perspective of energetic feasibility, if the top level is metabolically highly active, that is P_t/B_t is high, a substantial amount of food is required to sustain a certain amount of B_t . This imposes an upper limit on B_t given that the overall primary production, P_b , is limited. A high value of P_b , in turn, is only feasible if B_b is sufficiently high, reducing B_t/B_b . Hence, P_t/B_t and B_t/B_b cannot be maximized at the same time.

The reformulation of loop weight also revealed why the loop comprising phytoplankton, zooplankton and shrimps had the maximum loop weight in the YRD food web. This is because zooplankton and shrimps have higher *P/B* values than the other consumers (Table S1), leading to high values of the two negative ISs (Rooney et al., 2006). In addition, the biomass of phytoplankton is not substantially higher than that of shrimps (Table S1), leading to a relatively high biomass ratio, and hence a relative strong positive IS. Therefore, in this loop the dampening effect of the positive interaction was weak and led to the relative high loop weight. Besides, zooplankton only relies on phytoplankton production (i.e. $f_{bi} = 1$ in Equation 10), which also contributes to the high weight.

Recent studies have indicated the possible important role of rare species, that is, species with a low biomass, in community stability (Arnoldi et al., 2019; Säterberg et al., 2019). In particular the study (Säterberg et al., 2019) showed that perturbations of rare species may have large effects on stability. This result seems congruent with our finding in randomizations 3 and 4, since it was indeed the permutations of ISs between rare species (i.e. phytoplankton and shrimps) and abundant species (i.e. bivalves) that had the greatest effect (Figure 5).

Our analyses of omnivorous loops with three trophic groups in terms of the new reformulation of loop weight can also be extended to longer feedback loops. This is because the ISs among trophic groups are inherently a function of *P/B* and biomass ratios (Equations 6–8). Longer feedback loops, for example, loops with four trophic groups (see Appendix S2), are subject to similar energetic constraints in omnivorous loops and even more mass-balanced constraints due to more complex trophic interactions.

Knowledge of patterns and processes underlying resilience of food webs is important to understand how species-rich communities can withstand environmental disturbance. Our study contributes to this understanding by revealing mechanisms underlying resilience of an empirical food web. The results show that food web resilience is conserved by the organization of interaction strengths in the food web, which is determined by energetic properties of the component trophic groups and mass-balanced constraints forming the energetic build-up of the food web. In particular, the results reveal how energetic constraints at the trophic group and food web level enhance food web resilience by dampening the strength of destabilizing positive feedback loops.

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AUTHORS' CONTRIBUTIONS

P.C.d.R. and X.L. conceived the ideas and designed the methodology; X.L., W.Y. and U.G. prepared the data; X.L. performed the model in close cooperation with P.C.d.R.; X.L. analysed the data under the joint supervision of P.C.d.R., U.G. and W.Y. The manuscript was written by X.L. and valuable inputs from all authors. All authors gave their final approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/ 10.5061/dryad.brv15dv92 (Li, Yang, Gaedke, et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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