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LETTER

Will a large complex system be productive?

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Abstract
While the relationship between food web complexity and stability has been well documented, how complexity affects productivity remains elusive. In this study, we combine food web theory and a data set of 149 aquatic food webs to investigate the effect of complexity (i.e. species richness, connectance, and average interaction strength) on ecosystem productivity. We find that more complex ecosystems tend to be more productive, although different facets of complexity have contrasting effects. A higher species richness and/or average interaction strength increases productivity, whereas a higher connectance often decreases it. These patterns hold not only between realized complexity and productivity, but also characterize responses of productivity to simulated declines of complexity. Our model also predicts a negative association between productivity and stability along gradients of complexity. Empirical analyses support our predictions on positive complexity-productivity relationships and negative productivity-stability relationships. Our study provides a step forward towards reconciling ecosystem complexity, productivity and stability.

KEYWORDS
complexity, connectance, ecosystem productivity, food webs, interaction strength, species richness, stability

INTRODUCTION

Understanding the relationship between food web complexity and ecosystem functioning has been a long-standing theme in ecology. A first intuitive hypothesis was that more complex ecosystems are more stable (Elton, 1958; MacArthur, 1955). This was later challenged by May (1972) who used a random matrix approach to demonstrate that complexity generally impairs stability. In May's formulation, complexity was characterized by three facets, namely species richness, connectance, and average interaction strength between species, and stability was quantified by asymptotic resilience, namely the ability of an ecosystem to return to its original status after being disturbed (May, 1972). These contrasting perspectives sparked a long debate on complexity-stability relationships and stimulated decades of theoretical and empirical research (Donohue et al., 2016; Ives & Carpenter, 2007; McCann, 2000; Montoya et al., 2006). These studies provided important insights about when and how food web complexity impairs or enhances stability (Ives & Carpenter, 2007). But a related and equally important question, i.e. how food web complexity influences primary productivity—the fundamental function serving as the base of food webs, has been largely overlooked.

Indeed, one facet of complexity, that is species richness, has been extensively studied in the context of ecosystem productivity during the past three decades (Balvanera et al., 2006; Loreau et al., 2001; Tilman et al., 2014). Theoretical and empirical studies generally showed that higher species richness promotes biomass production. While early research focused on the effects of species richness in competitive systems (but see Naeem et al., 1994), particularly plant communities, later efforts embraced the complexity of food webs by integrating both horizontal (i.e. number of species within trophic levels) and vertical (i.e. number of trophic levels) diversity

(Albert et al., 2022; Buzhdygan et al., 2020; Duffy et al., 2007; Soliveres et al., 2016; Thébault & Loreau, 2003; Wang & Brose, 2018). While these studies reported generally positive biodiversity-ecosystem productivity relationships, their strengths vary considerably across trophic levels and ecosystems (Cardinale et al., 2006; Gruner et al., 2008; Katano et al., 2015; Maureaud et al., 2020; Rakowski et al., 2021; Schneider et al., 2016). One possible explanation for the variable biodiversity-productivity relationships in food webs is the structural complexity of multitrophic systems, as the topology and strengths of trophic interactions act together with species diversity in regulating ecosystem productivity (Ives et al., 2005; Maureaud et al., 2020; Thébault & Loreau, 2003; Wang et al., 2019; Wu et al., 2023).

Accumulating evidence has indicated that food web connectance and interaction strength play important roles in regulating ecosystem primary productivity (Finke & Denno, 2005; Poisot et al., 2013; Thébault & Loreau, 2003; Wang et al., 2019). One key mechanism underlying the biodiversity effect on primary productivity in food webs is trophic complementarity, which characterizes niche differentiations between species in both resource use and natural enemies (Albert et al., 2022; Loreau & Hector, 2001; Poisot et al., 2013; Rakowski et al., 2021). The effect of trophic complementarity was predicted to decrease with increasing connectance between trophic levels (Poisot et al., 2013); therefore, ecosystem productivity may be lower in more connected communities. However, connectance within trophic levels, e.g. intraguild predation links (IGP), has been shown to increase the biomass and productivity of basal species by weakening top-down controls and promoting the transformation of energy inflows into plant biomass (Wang et al., 2019). In addition, trophic interaction strength determines energy transfer rates between consumer and resource species, which can modulate productivity by altering the strengths of both complementarity effects within trophic levels and trophic cascade effects across trophic levels (Barnes et al., 2018; Brose & Hillebrand, 2016; Duffy et al., 2007; Reiss et al., 2009). Despite these growing insights on the functional roles of different network properties, how the three facets of complexity (i.e. species richness, connectance, and interaction strength) jointly regulate primary productivity remains elusive.

Both productivity and stability are ecosystem properties driven by species interaction and energetic dynamics; however, these two properties have usually been studied independently in the literature (but see Cardinale et al., 2013). Recent theoretical studies showed that ecosystem productivity and stability could either be simultaneously maximized or exhibit trade-offs (Montoya et al., 2019; Wang et al., 2021; Yen et al., 2016). Revealing the mechanisms underlying the positive and negative associations between productivity and stability is still in its infancy, especially in complex food webs. Given existing theories on the complexity-stability relationship (May, 1972), resolving the complexity-productivity relationship can shed light on the association between productivity and stability. Such insights will be particularly relevant to ecosystem management aiming to maximizing multiple benefits from ecosystems.

In this study, we combine food web theory and a data set of 149 aquatic food webs to investigate how food web complexity affects primary productivity. Following May (1972), we characterize complexity by species richness, connectance, and average interaction strength. But different from May (1972) that evaluated the resilience of communities with hypothesized complexity, our analyses focus on the realized complexity (i.e. when the simulated food web reaches equilibrium), and metrics of species richness, connectance, and interaction strength always represent realized values unless otherwise specified. That said, because experimental studies on biodiversity-productivity relationships mostly used initial species richness and found that it had a better explanatory power than realized richness (Hagan et al., 2021; Stachová & Lepš, 2010), we also examine initial complexity and compare their effects with those of realized complexity. Furthermore, we investigate how productivity responds to simulated decline of food web complexity, that is artificially removing species or feeding links, or reducing interaction strengths. In addition, we test whether productivity and stability correlate with each other along gradients of complexity. We end with discussion about the implications and limitations of our results.

MATERIALS AND METHODS

Food web models

We model food web dynamics by multispecies consumer-resource interactions (Schneider et al., 2016; Wang et al., 2019). Specifically, the biomass dynamics of a plant species j (P_j) and animal species i (A_i) follow:

$$\frac{dP_j}{dt} = r_j G_j P_j - \sum_{i \in C_j} F_{ij} A_i - x_{pj} P_j \tag{1}$$

$$\frac{dA_i}{dt} = A_i \sum_{j \in R_i} e_{ij} F_{ij} - \sum_{l \in C_i} F_{li} A_l - x_{ai} A_i \tag{2}$$

where r_j is the maximal growth rate of plant species j, x_{pj} and x_{ai} are the mass-specific metabolic rates of plant j and animal i, respectively, and e_{ij} is the assimilation efficiency when species i consumes species j. R_i and C_i represent, respectively, sets of resources and consumers of species i.

The feeding rate of consumer i on resource j is determined by the functional response function (F_{ij}) (Schneider et al., 2016):

$$F_{ij} = \frac{\omega_{ij} a_{ij} Q_j^{1+q}}{1 + zA_i + \sum_{k \in R_i} \omega_{ik} h_{ik} a_{ik} Q_k^{1+q}} \qquad (3)$$

where Q_j is the biomass of resource j, and q is the Hill exponent that regulates the shape of functional response from type II ($q = 0$) to type III ($q = 1$) curves (Brose, 2008; Rall et al., 2008). ω_{ij} is the relative preference of consumer i on resource j, which is assumed to be same for all resources, that is $\omega_{ij} = 1/(\text{number of resources of consumer } i)$. h_{ij} and a_{ij} are the handing time and attack rate, respectively, when consumer i feeds on resource j. z is the strength of predator interference.

The nutrient-dependent growth rate of plant species j (G_j) is determined by the nutrient concentration N:

$$G_j = N / \left(K_j + N\right) \qquad (4)$$

where K_j represents the half-saturation density of plant species j. The dynamic change of nutrient concentration N follows:

$$\frac{dN}{dt} = D(T - N) - \sum_j r_j G_j P_j \qquad (5)$$

where D and T are nutrient turnover rate and supply concentration, respectively. Based on Equations (1–5), population dynamics within the food web are ultimately limited by a single nutrient. Ecosystem primary productivity can be defined as the overall growth rate or nutrient uptake rate of plants, that is $\sum_j r_j G_j P_j$, which equals the rate of nutrient replenishment (i.e. $D(T - N)$) at equilibrium.

Simulations

We used an allometric niche model to generate food web topology (Appendix S1) and simulated population dynamics following Equations (1–5). In total, 40,000 food webs were simulated. For each simulation, we first sampled a number of plant (from 5 to 20) and animal (from 10 to 80) species from pre-assigned niche ranges (i.e. intervals of body mass) and determined whether a feeding link existed for each pair of species based on their niche values (see Appendix S1). Given these feeding relationships, we simulated biomass dynamics specified in Equations (1–5), where parameters of plant species growth rates, consumer handling time and attack rates, metabolic rates of plant and animal species all depended on species' body mass (Table S1). Each food web was simulated for 10^6 steps to ensure that stationary states were reached, during which species with biomass less than 10^{-6} were considered as extinct.

At equilibrium, we recorded the realized species richness (S), realized connectance (C), and realized average interaction strength (σ) to represent the complexity of food webs. Specifically, species richness is the total number of species (i.e. S), and connectance (C) is defined as $C = L / S^2$, where L is the number of all feeding links. For each feeding link between consumer i and resource j, we define the interaction strength σ_{ij} as the mass-specific effect of species j on the growth rate of species i, that is $\sigma_{ij} = \left.\frac{\partial \frac{dB_i}{dt}}{\partial B_j}\right|_{\left(B_i^*, B_j^*\right)}$; similarly, $\sigma_{ji} = \left.\frac{\partial \frac{dB_j}{dt}}{\partial B_i}\right|_{\left(B_i^*, B_j^*\right)}$, where B_j is the biomass of species j and B_j^* denotes the equilibrium value. It is noted that these partial derivatives depend also on the equilibrium biomass of species other than i and j (see Equations (1) and (2)). This definition of interaction strength represents a linearization of our model that leads to an equivalent measure to May (1972). The average interaction strength is then calculated as the mean of absolute values of pairwise interaction strengths across all feeding links, that is $\sigma = \frac{1}{2L} \sum_{(i,\ j) \in \Omega} \left(|\sigma_{ij}| + |\sigma_{ji}| \right)$, where $\Omega = \{(i, j): i \textit{ consumes } j\}$ is the set of feeding links. Following May (1972), we also defined an overall complexity measure as the product of average interaction strength and square roots of both species richness and connectance ($\sigma\sqrt{SC}$). To compare with previous studies, we also calculated the species richness, connectance, and average interaction strength within or across three trophic groups: plants, herbivores (species that feed entirely on plants) and carnivores (species that feed entirely or partially on animals, including omnivores) (Figure S1; Wang et al., 2019).

For each simulated food web, we recorded three metrics of ecosystem functioning (Figure S1): (i) gross primary production as the total production rate of plant communities from the abiotic nutrient pool: $\sum_{i=1}^{m} r_i G_i P_i$, where m is the realized plant richness; (ii) net primary production as the difference between gross primary production and total plant metabolism: $\sum_{i=1}^{m} r_i G_i P_i - \sum_{i=1}^{m} x_{pi} P_i$. At equilibrium, this property equals the total feeding of animals on plant communities: $\sum_{i=1}^{n} A_i \sum_{j \in R_{pi}} F_{ij}$, where n is the realized animal richness and R_{pi} is the set of plant species consumed by animal species i; and (iii) total community biomass as the sum of biomass across all species. Because these three measures were highly correlated (Figure S2) and exhibited similar patterns with complexity, we presented only results on the net primary production in the main text. Following May (1972), we also measured ecosystem stability by asymptotic resilience, calculated as the dominant eigenvalue ($\lambda_{\max}$) of the community matrix J consisting of interaction strengths (i.e. $J_{ij} = \sigma_{ij}$ if $(\text{i}, \text{j}) \in \Omega$ and $J_{ij} = 0$ otherwise). To facilitate comparison with empirical data, we used the community matrix with diagonal elements set to zero ($J_{ii} = 0$; see Appendix S2 for details; see also Moore & de Ruiter, 2012; Jacquet et al., 2016). Thus, $\lambda_{\max}$ characterizes the strength of self-regulation (i.e. the value of J_{ii}) that is needed to stabilize each community (i.e. to make the dominant eigenvalue of the community matrix negative) (Gauzens et al., 2019; Moore & de Ruiter, 2012). Communities that require stronger self-regulation are considered less stable.

We used partial and multivariate regression models to test the relationships between productivity and different facets of realized complexity. For comparison, we also examined complexity-productivity relationships using initial values of complexity, that is initial species richness (S_0), initial connectance (C_0), and initial interaction strength. Because the calculation of initial interaction strength depends on species biomasses (the initial values of which were randomly assigned), we used the Hill exponent (q) to capture the initial interaction strength (Holling, 1959; Rall et al., 2008). A higher Hill exponent indicates weaker interaction strengths. Furthermore, we performed a structural equation model (SEM) to investigate how initial species richness, initial connectance, and the Hill exponent affected realized complexity (i.e. realized species richness, realized connectance, and realized average interaction strength), which, in turn, affected ecosystem productivity and stability. We fitted the SEM using package *lavaan* in R and evaluated the goodness of fit using the comparative fit index (CFI), root mean square error of approximation (RMSEA), and standardized root mean squared residuals (SRMR) (Hu & Bentler, 1999). Because statistical tests tended to return significant results (e.g. $p<0.05$) for large sample size (e.g. in our simulated data), we did not report p values for analyses using simulated data and focus on the strength of relationships (e.g. R^2 and path coefficients).

Lastly, to illustrate how ecosystem productivity responds to declines in food web complexity, we conducted numerical experiments by artificially removing species or feeding links, or weakening interaction strengths. In doing so, we first generated 300 food webs with 60 realized species at equilibrium given the Hill exponent $q=0.5$. We then simulated: (i) decline in species richness by randomly eliminating a fixed proportion of both plant and animal species (from 0 to 60% by 10%), (ii) decline in connectance by randomly eliminating a proportion of feeding links (from 0 to 60% by 10%), and (iii) decline in interaction strengths by increasing the Hill exponent (from 0.5 to 1 by 0.05). For each level of species and connectance decline, simulations were repeated 10 times, leading to in total 45,300 numerical experiments.

Empirical data

We collected data of 149 aquatic food webs based on Ecopath models (provided in the Github repository, see Data and Materials Availability), which covers open ocean, coastal lagoon, estuary and other ecosystem types (Colléter et al., 2015; Zheng et al., 2021). Within each food web, the biomass dynamics of species j satisfies:

$$B_j \times (P/B)_j \times EE_j = M_j + \sum_{i=1}^{n} B_i \times (Q/B)_i \times DC_{ij} \quad (6)$$

where $B_j\left(t/km^2\right)$ is the biomass of species j, and $(P/B)_j$ and $(Q/B)_i$ are the production/biomass ratio of species j and the consumption/biomass ratio of a consumer species i, respectively. EE_j is ecotrophic efficiency of species j measured as the fraction of resource production utilized, and DC_{ij} is the proportion of resource j in the diet of consumer i. M_j represents the total biomass loss due to natural death and fishery catch. Ecopath models provide all these parameters and thus offer a quantitative description on species interactions in food webs (Jacquet et al., 2016; Zheng et al., 2021). It should be noted, however, that some parameters lack empirical observations and are estimated based on the mass balance assumption in Ecopath models. Across the 149 food webs, values of B_j, $(P/B)_j$, $(Q/B)_i$, and DC_{ij} are often obtained from empirical observations, whereas those of EE_j are often estimated in Ecopath models. We also note that in Ecopath models, species with similar trophic functions are often lumped as 'trophic species', particularly plant species.

For each Ecopath model, we calculated species richness, connectance, and the average interaction strength. As we cannot re-establish the exact underlying consumer-resource interactions, we calculated the interaction strength approximately by assuming linear functional responses in consumer-resource interactions (de Ruiter et al., 1995; Moore & de Ruiter, 2012; Schwarz et al., 2017). Under such assumptions, the interaction strength of consumer i on resource j is approximated by: $\sigma_{ji} = -\Psi_{ij}/B_i$, and that of resource j on consumer i is approximated by: $\sigma_{ij} = e_i\Psi_{ij}/B_j$, where $\Psi_{ij} = B_i \times (Q/B)_i \times DC_{ij}$ is the energy flux from resource j to consumer i, and $e_i = (P/B)_i/(Q/B)_i$ is the efficiency of biomass production of species i (Jacquet et al., 2016).

Similar as in our simulations, we estimated the net primary production by deriving the total herbivore feeding based on the concept of the integrated trophic level (Kato et al., 2018). Briefly, we first split each species across up to 100 trophic levels according to its diet composition; based on the information of energy input for each species, we then calculated the total herbivore feeding as the sum of energy input into each species weighted by their percentage as the second trophic level. We also quantified the stability for each Ecopath model by calculating the dominant eigenvalue of the corresponding community matrix. In doing so, we set the strength of intraspecific interactions as zero (i.e. $J_{ii}=0$) because they could not be estimated from Ecopath models (de Ruiter et al., 1995; Gauzens et al., 2019; Jacquet et al., 2016). Our results were robust if different values of J_{ii} (e.g. 0.1 or 1) were used (see Appendix S2 for details).

RESULTS

Simulation results

We first investigated how ecosystem productivity changed with realized complexity across simulated food webs. Results from partial regressions showed that productivity increased with total species richness and average interaction strength, but decreased with connectance (Figure 1a–c). The multivariate regression model including all three facets of complexity explained 79.3% of variation in productivity (Table S2). Productivity also increased with the overall complexity metric (i.e. $\sigma\sqrt{SC}$; Figure 1d), but this metric accounted for a much lower proportion of variation in productivity ($R^2=43\%$). In addition, across trophic levels, multivariate analyses showed that productivity increased with plant and carnivore richness, connectance between herbivores and carnivores, as well as the average interaction strengths between herbivores and carnivores and within carnivores (Table S3).

Moreover, productivity increased with the initial species richness and initial interaction strength (represented by a lower Hill exponent) but decreased with the initial connectance. The multivariate regression model including the initial values of three complexity facets accounted for 42.6% of variation in productivity, much lower than that from the model using the realized values of three complexity facets (i.e. 79.3%; see Table S2). The SEM showed that the initial complexity impacted productivity mainly through influencing the realized complexity (Figure 2). Specifically, the realized species richness increased with the initial species richness; the realized connectance increased with the initial connectance; the realized interaction strength decreased with the Hill exponent and the initial species richness and connectance. Overall, initial complexity affected productivity via indirect effects through the realized complexity, whereas its direct effects were negligible (Figure 2).

By simulating declines in food web complexity, our numerical experiments showed that ecosystem productivity decreased as species richness or average interaction strength was reduced, and it increased as connectance was reduced (Figure 3a–c). For example, productivity decreased on average by ~47% if 50% of both plant and animal species were removed, increased by ~62% if 50% of feeding links were removed, and decreased by ~12% if the Hill exponent increased from 0.5 to 1. Similar patterns held between productivity and the three facets of complexity at new equilibria following simulated declines in complexity (Figure 3d–f). These results were consistent with emergent relationships between realized complexity and productivity during community assembly (Figures 1 and 2).

Lastly, we investigated the relationship between productivity and stability as mediated by complexity. We found that stability decreased with species richness, connectance, as well as average interaction strength (Figure S3 and Table S2). Thus, ecosystems with higher overall complexity had lower stability (Figure S3d). Because productivity and stability exhibited opposite relationships with complexity, a negative productivity-stability relationship emerged across simulated food webs (Figure 4a). But partial regression analyses revealed only a weak negative relationship between productivity and stability after the effects of complexity were accounted for (Figure S4), indicating that the negative productivity-stability relationship was largely mediated by complexity.

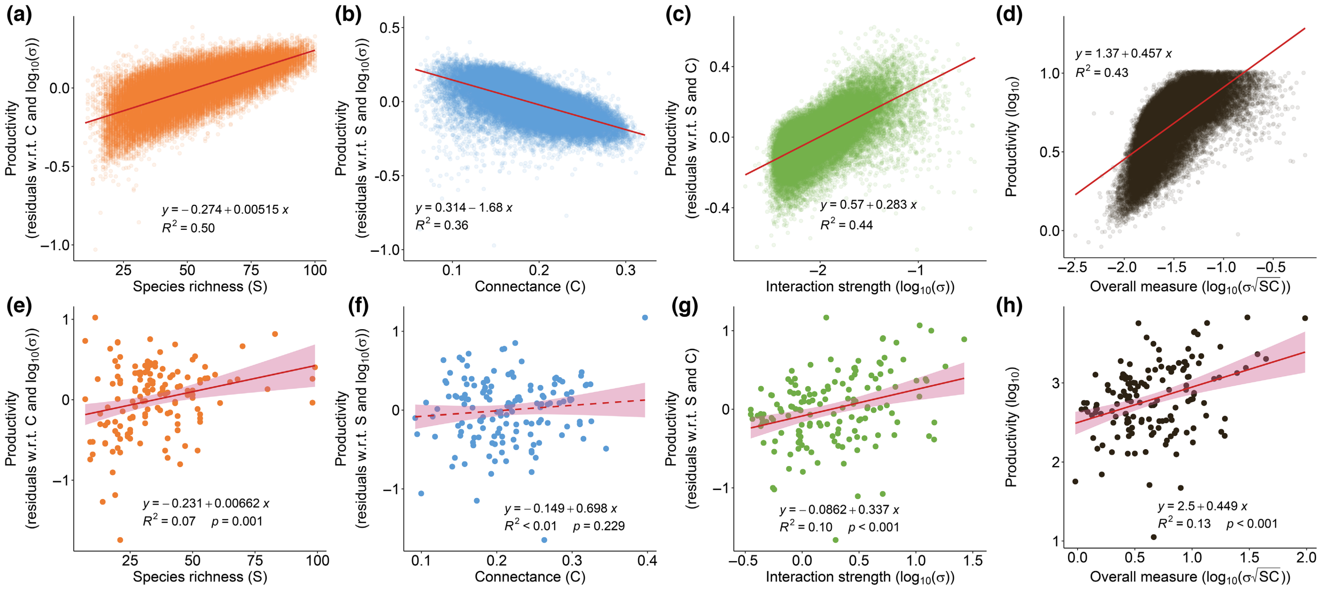

FIGURE 1 Relationships between ecosystem productivity and species richness (a, e), connectance (b, f), average interaction strength (c, g) and the overall complexity measure (d, h). (a–d) show results from 40,000 simulated food webs (see parameter values and units in Table S1), while (e–h) show results from empirical data of 149 aquatic food webs. In (a, e), the y-axis shows residuals of productivity with respect to (w.r.t) connectance and average interaction strength, thus the relationship represents partial regression between productivity and species richness. Similarly, (b, c, f, g) also represent partial regressions. Solid ($p<0.05$) and dashed ($p>0.05$) lines are fitted relationships from regression models. In (e–h), the shaded region shows the 95% confidence interval.

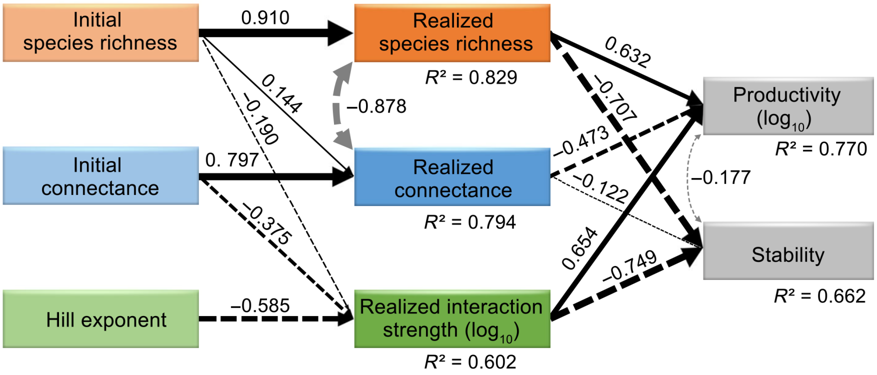

FIGURE 2 Structural equation model (SEM) showing how initial species richness and initial connectance, and the Hill exponent regulate realized complexity (i.e. realized species richness, realized connectance, and realized average interaction strength), and productivity and stability. Overall the model fits data well (CFI = 0.967, RMSEA = 0.162, SRMR = 0.054). Solid and dashed arrows represent positive and negative associations, respectively. Grey bidirectional arrows represent correlations between variables. Values associated with arrows represent standardized path coefficients. Paths with coefficients less than 0.03 are not shown. R^2 represents the proportion of variance explained for each dependent variable. Parameter values and units are same as in Figure 1.

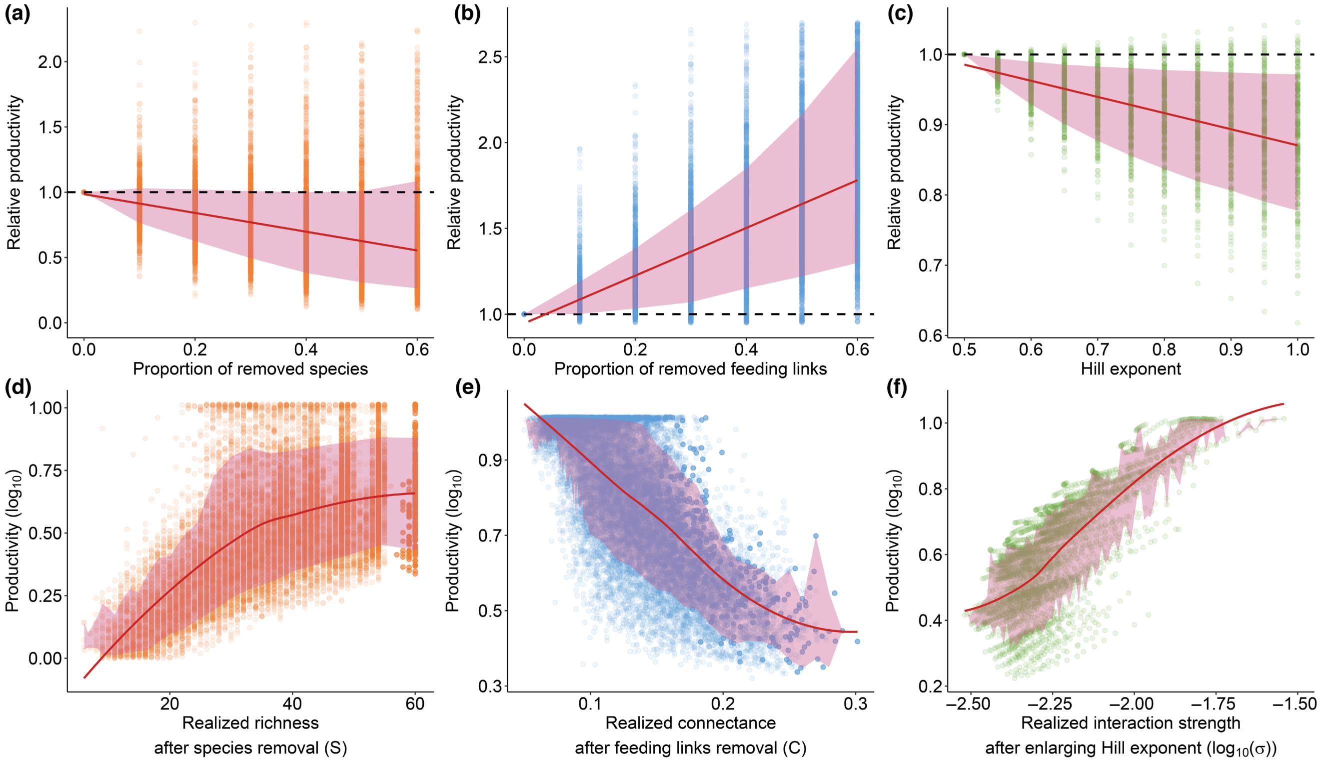

FIGURE 3 Numerical experiments illustrating the response of ecosystem productivity to simulated declines in species richness (a, d), connectance (b, e) and interaction strength (c, f). (a–c) show changes in the relative productivity following manipulated reductions in species richness, connectance and interaction strength, respectively. Here, the relative productivity denotes the ratio of productivity when manipulated food webs reach new equilibria to that before manipulation. (d–f) show the relationships between productivity and the realized complexity measure when the communities reach new equilibria following declines in complexity. The red lines represent the loess smothers across simulated food webs along gradients of simulated declines (a–c) or realized complexity (d–f), and the shaded regions show values between 10% and 90% quantiles. Parameter values and units are same as in Figure 1.

Empirical results

Based on the 149 aquatic food webs, partial regression analyses showed that productivity was weakly positively correlated with total species richness ($R^2 = 0.07$, $p = 0.001$) and average interaction strength ($R^2 = 0.10$, $p < 0.001$), whereas it exhibited no relation with connectance ($R^2 < 0.01$, $p = 0.229$) (Figure 1e-g). Also, ecosystems with higher overall complexity were more productive ($R^2 = 0.13$, $p < 0.001$; Figure 1h). However, the three facets of complexity explained a much lower proportion of variation in productivity across empirical food webs

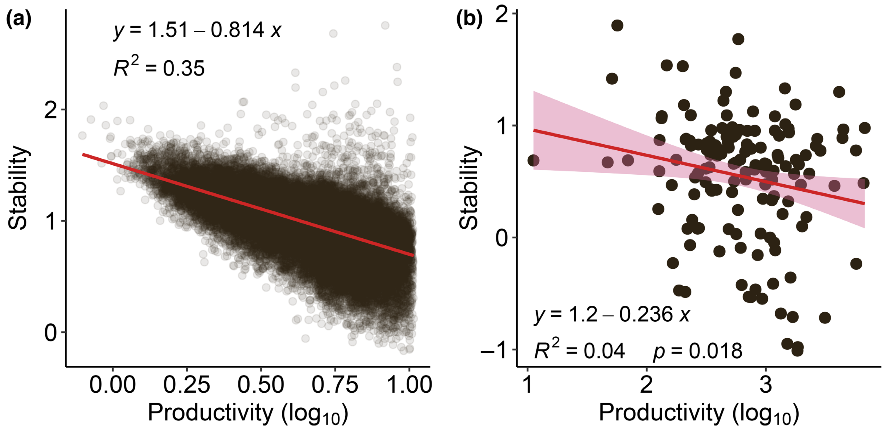

FIGURE 4 Relationships between productivity and stability across 40,000 simulated food webs (a) and 149 aquatic food webs (b). Stability is measured as $\log_{10}(1 / Re(\lambda_{\max}))$, where $Re(\lambda_{\max})$ is the real part of the dominant eigenvalue of community matrix. $Re(\lambda_{\max})$ characterizes the strength of self-regulation that is needed to stabilize each community, thus communities with larger $Re(\lambda_{\max})$ are considered less stable (see details in Appendix S2). The lines are fitted relationships from linear regression models. In (a), parameter values and units are same as in Figure 1. In (b), the shaded region shows the 95% confidence interval.

(empirical: 17.9% vs. simulation: 79.3%; Table S2). Across trophic levels, multivariate analyses showed that productivity increased with carnivore richness and the average interaction strengths within carnivores (Table S3).

Besides, stability weakly decreased with species richness ($R^2=0.06$, $p=0.001$), average interaction strength ($R^2=0.08$, $p<0.001$), and the overall complexity measure ($R^2=0.11$, $p<0.001$), but it did not change with connectance ($R^2=0.01$, $p=0.144$) (Figure S3). Due to their contrasting relationships with complexity, productivity and stability showed a negative relationship across empirical food webs ($R^2=0.04$, $p=0.018$; Figure 4b). Again, after controlling for the effects of complexity, the relationship between productivity and stability became non-significant ($R^2<0.01$, $p=0.593$; Figure S4).

DISCUSSION

Understanding the relationship between structural complexity, productivity and stability of ecosystems is a central goal of food web research. While the effect of food web complexity on at least some measures of stability (e.g. asymptotic resilience) has been well documented (Allesina & Tang, 2012; Jacquet et al., 2016; May, 1972), its effect on productivity remains poorly resolved. By combining food web theory and empirical data, our analyses shed new light on the functional implications of food web complexity. Overall, more complex ecosystems tend to be more productive. This positive relationship could be understood intuitively from the principle of energy balance, that is more complex communities display higher energy loss due to metabolism and inefficient feeding processes and thereby requires higher energy input (see Appendix S3 for analytic investigations). That said, whereas a larger species richness and average interaction strength increase productivity across simulated food webs, a higher connectance tends to decrease it. These patterns hold not only between realized complexity and productivity during community assembly (Figures 1 and 2; see also Appendix S3), but also characterize the responses of ecosystem productivity to simulated declines of food web complexity (Figure 3). That is, artificial reduction in species richness or interaction strength decreases productivity, while reduction in connectance increases it. These findings offer a unified perspective on the role of food web complexity in ecosystem functioning.

Our results show that ecosystem productivity increases with the overall species richness, as well as plant and carnivore richness. These results corroborate recent studies showing positive relationships between productivity and species richness across trophic groups in food webs (Cardinale et al., 2006; Lefcheck et al., 2015; Schneider et al., 2016; Schuldt et al., 2018; Wang & Brose, 2018). The positive effect of species richness on primary productivity may be attributed mainly to enhanced trophic complementarity between plant species as animal species richness increases (Albert et al., 2022). In particular, a richer carnivore community not only exerts stronger suppression over herbivores and thereby releases the plant community (Schneider et al., 2016), but also creates more heterogeneous or asymmetric top-down trophic niches for lower trophic levels and contributes to weakening niche overlaps between plant species (Poisot et al., 2013; Wang & Brose, 2018). It is worth noting that our model and data both show a weak association between herbivore richness and productivity (Figure S5), which may be understood from the balance of positive effects by promoting trophic complementarity and negative effects from top-down controls of herbivores over plant biomass production (Gamfeldt et al., 2005).

In contrast to the overall complexity, connectance shows a negative relationship with productivity across simulated food webs and non-significant relationship in empirical data. Our additional simulations using various food web topologies and parameterizations further show that the relationship between connectance and productivity is more variable, in terms of both strengths and directions (Table S4). Such variable effects of food web connectance on productivity may be understood from the contrasting effects of connectance within and across trophic levels suggested by previous studies, for example negative effect of connectance between plants and herbivores (Poisot et al., 2013) and positive effects of connectance between herbivores and carnivores (Schneider et al., 2016) and connectance within the carnivore group (Wang et al., 2019). By simulating tri-trophic food web models using same parameters as our main simulations (i.e. Table S1), we confirmed that primary productivity increased with the connectance between herbivores and carnivores but decreased with the connectance between plants and herbivores (Figure S6). Additionally, based on the principle of energy balance, our analytical investigations also indicate that connectance could be associated with productivity in multiple pathways, such that the net effect of connectance reflects combined effects of the number, trophic distribution, and average efficiency of feeding links (see Appendix S3 for details). For example, although a higher connectance indicates more feeding links that require a higher productivity, it is also associated with a higher average assimilation efficiency that contributes to reducing total energetic requirement and hence productivity (Figure S7; Appendix S3). These contrasting linkages indicate that the effect of connectance depends on the topology of feeding links, which likely explains the variation and relatively weak strengths of connectance-productivity relationships in simulated and empirical data (Figure 1; Table S4).

The average interaction strength of trophic interactions is also important for ecosystem functioning (Barnes et al., 2018; de Ruiter et al., 1995; Reiss et al., 2009). Stronger interaction strength indicates faster energy flows across trophic levels. Although fast energy flows may induce stronger top-down controls and cause instability in consumer-resource dynamics (Katano et al., 2015; McCann, 2012; Wang et al., 2019), theoretical analyses showed that weak trophic interactions could mute the unstable potential of strong interactions (McCann, 2012). If an ecosystem does achieve a higher average interaction strength, the ecosystem then needs to be more efficient in biomass production so as to compensate the fast energy flow and turnover (Wang & Brose, 2018; see Appendix S3). This explains the positive association between productivity and realized interaction strength in our model and data, and is line with observations that food webs with stronger interactions and energy flows show a higher productivity compared to those with weaker interactions, e.g. aquatic versus terrestrial food webs (Cebrian & Lartigue, 2004), pelagic versus benthic food webs (Rooney et al., 2006).

Our simulations also show that, while both initial and realized values of complexity facets explain ecosystem productivity, the realized values have a much higher explanatory power than the initial ones (Table S2). This pattern contrasts to findings from plant biodiversity experiments where initial species richness predicts biomass production better than realized richness (Hagan et al., 2021), but corroborates results from food web models in which the realized vertical diversity (i.e. the maximum trophic level) outperforms the initial one in predicting primary productivity (Wang & Brose, 2018). One possible explanation is that the realized complexity carries over signatures of not only initial structural complexity but also trophic interactions that reshape network structure, both of which are important processes underlying ecosystem energetics and productivity (DeBruyn et al., 2007).

The contrasting effects of ecosystem complexity on productivity and stability lead to a negative productivity-stability relationship, as revealed in both simulations and data. In the present study, stability is measured by asymptotic resilience that characterizes the long-term recovery rate of ecosystems when they are perturbed. Our models, based on community assembly, largely confirm May's prediction on complexity-stability relationships for random communities (May, 1972). In line with the negative productivity-stability relationship revealed here, recent theoretical work shows the possibility of negative associations between productivity and stability using different measures of stability, for example temporal invariability, resistance, recovery rate, and robustness (Wang et al., 2021; Yen et al., 2016). These studies, however, also showed that productivity could exhibit positive relationships with stability under certain conditions (Wang et al., 2021). Given that stability is a multidimensional concept and that its different dimensions may exhibit either synergy or trade-offs (Domínguez-García et al., 2019; Donohue et al., 2013), clarifying the circumstances under which productivity exhibits positive or negative relationships with different dimensions of stability is an important task that is of both scientific and practical relevance.

Lastly, we addressed two limitations of our empirical analyses. First, while Ecopath models provide an opportunity to estimate species interaction strengths and test our model predictions, these data consist of not only observed information but also estimated parameters according to the mass balance principle (Walters et al., 1997). This can induce uncertainty in the estimates of average interaction strength and may bias the quantification of stability (but see Barabás & Allesina, 2015). Also, by lumping species with similar trophic functions, Ecopath models often exhibit low taxonomic resolution, which may bias the estimation of species richness and connectance. Second, while the three facets of complexity explain the majority of variation in productivity across simulated food webs, they have a much lower explanatory power in empirical data. Our additional simulations suggest that the weak empirical relationship between complexity and productivity may be partially explained by the topology of Ecopath models and the approximate approach we used to calculate interaction strengths (Appendix S4). To improve the estimation of interaction strengths in empirical food webs, future research may use the time dynamic version of Ecopath, that is the Ecosim model, when available (Christensen et al., 2005). Additionally, the variation in productivity not accounted for by complexity may also be attributed to covariates not considered in our study, for example environmental conditions (e.g. temperature or nutrient conditions) or structural properties not captured by the three facets of complexity (e.g. modularity and nestedness; Thébault & Fontaine, 2010).

CONCLUSION

Anthropogenic environmental changes are reshaping food web complexity by altering species richness (Essington et al., 2006; Estes et al., 2011), connectivity (Bartley et al., 2019; Valiente-Banuet et al., 2014), and interaction strengths (Traill et al., 2010; Tylianakis et al., 2008), calling for an advanced theory to predict the functional consequences of changes in complexity. Our study contributes to such a theory by illustrating the link between complexity and primary productivity in modelled and empirical food webs. Importantly, we show that the complexity-productivity relationships hold not only for realized complexity but also for manipulated complexity, for example both initial food web complexity at the beginning of community assembly and simulated declines in complexity starting from equilibrium food webs. These results extend the biodiversity-ecosystem functioning research by highlighting the functional roles of not only species diversity, but also the structure and strengths of trophic interactions. The three facets of complexity thus provide useful predictors for ecosystem productivity, which extends the classic complexity-stability paradigm. Combined, our study highlights the roles of complementary effects within trophic levels and interactions across trophic levels in ecosystem functioning, which provides a flexible theoretical framework to derive mechanistic insights into the relationship between complexity, productivity and stability.

AUTHOR CONTRIBUTIONS

SW conceived the idea; SN performed the research and analysed the model, with help from SW and DG; M.Luo derived the analytic solutions; SN and JZ analysed data; SN and SW wrote the first draft of the manuscript; M.Loreau and DG contributed to revision.

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CONFLICT OF INTEREST STATEMENT

Authors declare that they have no competing interests.

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DATA AVAILABILITY STATEMENT

MATLAB code for simulation and empirical data have been deposited in GitHub (https://github.com/NieShp/Complexity-Productivity-Stability.git).

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SUPPORTING INFORMATION

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