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Food web complexity modulates environmental impacts on food chain length

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The determinants of food chain length (FCL), a crucial aspect of biodiversity due to its effects on ecosystem functioning, have long been debated. Previous studies proposed resource availability, disturbance, and ecosystem size as environmental drivers. However, studies using stable isotope approaches have shown inconsistent results, indicating missing links between environmental drivers and FCL. Here, we hypothesized that species richness and motifs (i.e. three-species subgraphs) modulated environmental effects on FCL. Combining empirical food webs with our N-species food web model, we found that FCL disproportionately changed at low species richness, with saturation at high species richness. This functional response was essential to the interdependent effects of disturbance and ecosystem size in our model. Disturbance more strongly regulated FCL in smaller ecosystems, where species richness was low. Similarly, increasing ecosystem size enhanced FCL under strong, but not weak, disturbance regimes. Our study suggests that internal food web structure should deepen our understanding of how FCL changes over environments.

Keywords: biodiversity, food web, mathematical modeling, motif, network analysis, trophic interactions

Introduction

Food webs have interested ecologists for at least 100 years (Elton 1927). The food chain length (FCL), which is defined as the maximum trophic position within a food web minus one (Post 2002), is a crucial aspect of food webs because FCL represents a vertical dimension of biodiversity (i.e. diversity over trophic levels, Wang and Brose 2018) and is associated with top–down effects, primary productions, and toxin contamination in predators (Kidd et al. 1995, Pace et al. 1999, Wang and Brose 2018). Three environmental factors are proposed as drivers of FCL: resource availability (Oksanen et al. 1981), disturbances (Pimm and Lawton 1977), and ecosystem sizes (Post et al. 2000). Previous studies, however, show inconsistent results on whether these three drivers change FCL (Briand and Cohen 1987, Jake et al. 2007, Takimoto et al. 2008, Doi et al. 2009, Sabo et al. 2009, 2010, McHugh et al. 2010,

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Takimoto and Post 2013), resulting in a long-lasting debate on the environmental determinants of FCL.

The ongoing debate regarding context dependency in FCL suggests the existence of missing modulators between environmental drivers and FCL. This potential shortcoming may be tied to the current common approach in FCL research, i.e. stable isotopes. Traditionally, empirical FCLs were assessed by measuring the feeding links connecting the basal and apex species within a food web (e.g. Briand and Cohen 1987); however, this method (the so-called 'connectance food web') is sensitive to issues arising from uneven and biased taxonomic resolutions within the food web nodes (Winemiller 2007, Pringle and Hutchinson 2020). The stable isotope approach elegantly addressed this problem by integrating trophic interactions in food webs (Layman et al. 2012); the stable isotope ratios of 'top' (i.e. top predator) and 'bottom'(primary producers or consumers) species approximates the vertical structure of the food web and the energy flow therein. Importantly, it naturally accounts for the inherent complexity of predator–prey interactions, such as omnivory. These distinctive features rendered stable isotopes a promising tool to quantify FCL in natural systems (Post et al. 2000, Post 2002, Jake et al. 2007, Layman et al. 2007, Takimoto et al. 2008, Sabo et al. 2010, Sullivan et al. 2015).

While we acknowledge the major advantage of stable isotopes in FCL research, however, it does not explicitly analyze the internal food web structure that may lead to the emergent relationships between FCL and environmental factors (Fig. 1). In addition, existing experiments and theoretical frameworks often oversimplify natural food webs, typically with three- to four-species communities (Pimm and Lawton 1977, Hastings 1979, Diehl and Feissel 2001, Takimoto et al. 2012, Ward and McCann 2017, Doi and Hillebrand 2019), or assuming only chain networks (Liao et al. 2016, Jonsson 2017, Terui and Nishijima 2019, Wang et al. 2021). Although there are a few noteworthy exceptions (Martinez and Lawton 1995, Neutel et al. 2007, Kondoh and Ninomiya 2009, Guo et al. 2023), it remains unclear how the internal structure of food webs alters the relationship between FCL and external environmental drivers. Here, we employ the classic 'connectance food web' approach to shed light on the role of food web structure in shaping the relationship between FCL and external environmental drivers.

A parallel line of research has documented how species richness and motifs, i.e. three-species subnetworks within a food web (Milo et al. 2002), alter the stability of food webs, which should be linked to the maintenance of long food chains. As such, a reasonable first step is to explore the processes through which these internal factors mediate the impacts of environmental controls on FCL (Fig. 1b–c). Increasing species richness enhances FCL if an inserted species either occupies a higher trophic position than resident species or increases the trophic position(s) of resident top predator(s) (Post and Takimoto 2007) (see the Supporting information for the analysis of how 'species richness' increases FCL in the random graph). Decades of "diversity–stability" debates (McCann 2000), however, revealed that random species assembly destabilizes food webs (Gardner and Ashby 1970, May 1972, Allesina and Tang 2012), and the non-randomness of assembly rules is the critical property of persistent food webs. Previous studies show that the following four motifs are dominant in empirical food webs (Stouffer et al. 2007, Borrelli 2015, Monteiro and Faria 2016) and relate to the persistence of food webs (Stouffer and Bascompte 2010, Monteiro and Faria 2016, Cirtwill and Wootton 2022): three-species chain, omnivory, apparent competition, and exploitative (or direct) competition (Fig. 1c). Notably, these motifs differ in their FCL; the chain motif is longer than the two competition motifs, and the

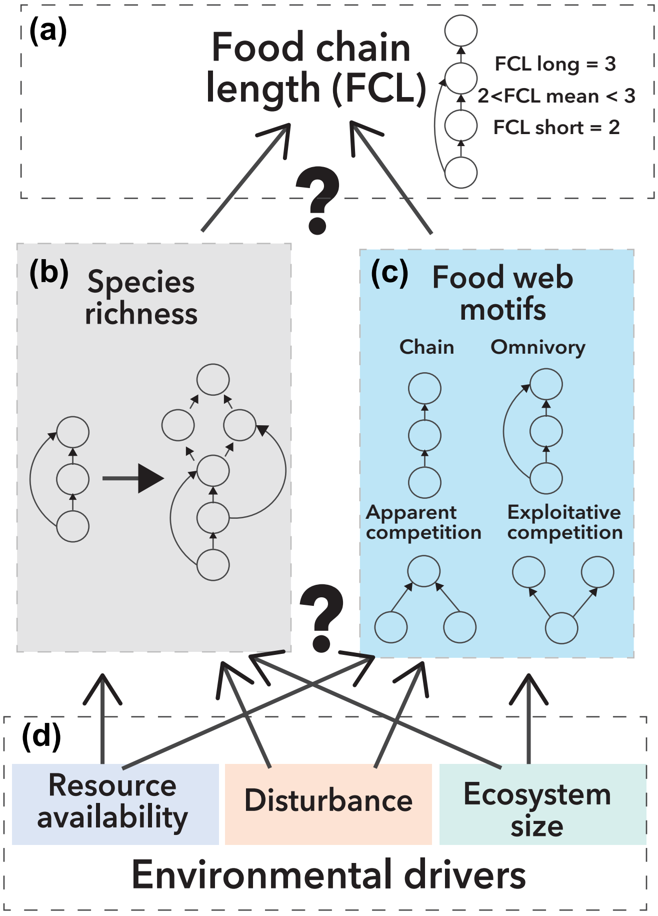

Figure 1. Schematic representations of research questions showing whether and how food chain length (FCL; a), species richness (b)), food web motifs (three-species chain, omnivory, apparent competition, and exploitative competition; (c), and the environmental drivers (resource availability, disturbance, and ecosystem size; (d) relate to one another . FCL is defined in three ways depending on how trophic positions are defined. If trophic levels are defined by one plus the longest-path length from basal species (FCL long), the FCL of the food web in (a) is three. If trophic positions are given by one plus the mean of the prey species' trophic positions (FCL mean), its FCL is between two and three. FCL short measures trophic positions as one plus the shortest-path length from basal species; FCL short of the top food web is two. In the main text, we focused on FCL mean. See the Supporting information for FCL definitions.

length of the omnivory motif is between the chain and the competition.

In this study, we investigate whether and how species richness (or, technically, 'operational species richness', defined in Subsection Definitions and terminologies) and food web motifs modulate the relationship between FCL and the three environmental drivers (i.e. resource availability, disturbances, and ecosystem sizes). We begin with the analysis of an empirical food web database (Cohen 2010) to assess the association between FCL and internal food web properties (operational species richness and food web motifs). With simulations of species-rich food webs, we further elaborated on how the association alters the relationship between the three environmental drivers and FCL. Our analysis suggests that species richness modulates environmental effects on FCL because of a nonlinear relationship between species richness and FCL. This may explain the inconsistent patterns between the environmental drivers and FCL in previous studies.

Material and methods

Definitions and terminologies

In this study, we refer to the number of nodes in a food web as 'operational species richness' because the number of nodes does not always correspond to the number of biological species (species richness). In empirical food webs, each node may include multiple biological species that share trophic status (i.e. trophic species) (Pringle and Hutchinson 2020) or are taxonomically close due to the limited resolutions. The issue of taxonomic resolution in food webs has been discussed in previous studies (Sugihara et al. 1997, Yodzis and Winemiller 1999). Alternatively, a single species can be subdivided into multiple nodes if the species has size- or stage-dependent trophic interactions. Individuals of such species should be assigned to different nodes to reflect their variations in diet (Cohen et al. 1993, Huxham et al. 1995); otherwise, information in a food web is lost (Luczkovich et al. 2003). The nodes in our simulations do not necessarily represent the biological species for the same reasons, and our model does not include the traits that define either species' boundaries (e.g. reproductive isolation) or size-dependent trophic interactions. We, therefore, use the term operational species richness in this manuscript. Similarly, 'species' in this manuscript refers to a unit of entity (i.e. node) in a food web.

We defined FCL as the maximum trophic position within a food web minus one (Post 2002). However, multiple definitions of trophic positions have been used in the literature. We used three of those defined in connectance (or binary) food webs: mean, short, and long trophic positions (hereafter, FCL mean, short, and long for corresponding FCLs). The mean trophic position is given by the mean trophic position of prey species plus one, while the short and long trophic positions are defined as the shortest- and longest-path length from the basal species plus one, respectively. These definitions can lead to different FCLs of the identical food web (e.g. Fig. 1a). We used these three definitions to analyze factors that consistently affect FCL. The main text, however, focuses on the results of FCL mean. See the Supporting information for the results with the two other definitions.

In FCL mean, a trophic position of a predator species can reflect how much each prey species is eaten by the focal predator, although such information is not always available in empirical data. The other two definitions of FCL require only binary food webs, which contain the presence and absence of prey–predator interactions among species. FCL short can be measured in all food webs, while FCL long can be used only in acyclic food webs (e.g. food webs without cannibalism and mutual predations). See also the Supporting information for further details on FCL measures.

Empirical database

We analyzed 213 empirical food webs (from WEB1 to WEB213) in the database of Cohen (2010). This database contains adjacency matrices of food webs across many ecosystem classes (Supporting information). This enabled us to calculate FCL, species richness, and the proportion of different three-species motifs in empirical food webs. Our analysis focused on the following three-species motifs: chain, omnivory, apparent competition, and exploitative competition. We focused on these motifs because they were dominant in the empirical food webs, as reported in a previous study (Camacho et al. 2007). Most of the food webs (203 out of 213) in the database were acyclic; FCL long was measured only for acyclic food webs while FCL short and mean were measured in all food webs. See also the Supporting information for more details.

Common issues in the database of Cohen (2010) are 1) the low taxonomic resolution and 2) binary prey–predator interactions. To address these typical issues in the food web database, we analyzed additional 11 food webs (Christian and Luczkovich 1999, Angelini and Agostinho 2005, Bascompte et al. 2005, Angelini et al. 2006, 2010, 2013, Cruz-Escalona et al. 2007, Angelini and Vaz-Velho 2011, Torres et al. 2013) obtained from another database (Ortega et al. 2023) in the Supporting information, where higher taxonomic resolution and quantitative pre-predator information is available.

Mathematical model

Generating food webs

While the empirical database provides the important links among FCL, species richness, and motifs, it does not contain data for resource availability, disturbances, or ecosystem sizes. This limited our ability to understand how environmental factors control FCL through the internal structures of food webs. To complement this limitation, we simulated the community dynamics of an N-species food web model that enabled us to analyze how the environmental drivers affect FCL through species richness and food web motifs. In previous studies, multiple algorithms are proposed to produce

N-species food webs that mimic empirical food webs (Cohen and Newman 1985, Caldarelli et al. 1998, Williams and Martinez 2000, Cattin et al. 2004, Rossberg et al. 2005, 2006, Stouffer et al. 2005, 2006, Allesina et al. 2008, Kondoh and Ninomiya 2009). We used the modified preferential prey model (Johnson et al. 2014) for three reasons. First, this algorithm generates only acyclic food webs. As explained in section Definitions and terminologies, we can use only acyclic food webs when we measure FCL long. Although the original model in Johnson et al. (2014) allows cannibalism, we modified the model to preclude cannibalism from our simulated food webs. Second, this model explicitly predetermines the number of basal species in a food web. The predetermined number of basal species is necessary for our study because, without such a restriction, food webs may have limited variation in FCL due to the stochastic predominance of basal species. Although (generalized) cascade models (Cohen and Newman 1985, Stouffer et al. 2005) can generate acyclic food webs, this algorithm cannot fix the number of basal species in these models. Finally, the modified preferential prey model generates food webs given the definition of trophic positions. A similar model proposed by Kondoh and Ninomiya (2009) satisfies the conditions of acyclic models and the fixed number of basal species; however, this model cannot incorporate the difference in the definitions of trophic positions. We used the preferential prey model to generate food webs for these reasons.

In the preferential prey model, we first need to determine the maximum number of species N, the maximum number of basal species B, and the expected number of trophic links l. In this study, we set $(N, B, l) = (32, 4, 113)$ with the following rationale. $N = 32$ is sufficiently large to generate variations in realized operational species richness, yet the computational costs of stochastic simulations are reasonably small. $B = 4$ was used to avoid the entire loss of the basal species, which causes the global extinction of the food web. In addition, excessive numbers of basal species limit the observable variation in FCL because fewer species are expected to attain high trophic positions. In such cases, statistical analyses would be difficult. $l = 113$ was chosen to meet the connectance $l/N^2 \approx 0.11$, following statistics in Dunne et al. (2002).

Second, after setting parameters of (N, B, l), species $i = 1, \ldots, B$ are assigned as basal species with a trophic position of one. For each non-basal species $i = B + 1, \ldots, N$, its prey species are assigned as follows. Non-basal species i randomly chooses its first prey species from $j = 1, \ldots B, \ldots, i-1$. If species i has multiple prey species, additional prey species are stochastically assigned. Non-basal species i tends to choose additional prey species whose trophic positions are close to species i's initial prey (species j), but this tendency is tuned by parameter T ($T \longrightarrow 0$ represents species i consuming only species whose trophic positions are identical to species j, while $T \longrightarrow \infty$ represents species i choosing prey species regardless of the prey's trophic positions); see Johnson et al. (2014) for more details. We set $T = 1$ in the main text. In the original preferential prey model, species' trophic positions are determined by the mean of preys' trophic positions plus one. We extended this model to define species' trophic positions using the longest- or shortest-path length from the basal species. We sampled 30 food webs in each of the three definitions of the trophic positions to account for the stochasticity of the preferential prey model.

Stochastic simulations of the ecological dynamics

Although the preferential prey model generates N-species food webs, the coexistence of N-species is not guaranteed. The model provides initial static food webs, which are subsequently "pruned" into realized food webs of coexisting species (i.e. subgraphs of the N-species food web) considering ecological dynamics. Hereafter, species richness and fractions of food web motifs in our simulations refer to those in realized food webs, whose values vary greatly among simulation replicates. To obtain the realized food webs, we simulated the ecological dynamics by extending the theory of island biogeography (MacArthur and Wilson 1967). In the original theory of island biography, species colonization and extinction rates in a patch are constant. Gravel et al. (2011) extends this theory so that the colonization and extinction rates depend on the presence of prey and predator species in the patch, respectively. Saravia et al. (2022) showed that this modeling framework could reproduce the frequency of motifs and trophic positions that are statistically indistinguishable from empirical food webs. From this result, we assume that the extended theory of island biogeography model does not bias FCL and the food web motifs in realized food webs.

Our rationale for employing the theoretical framework of island biogeography is to make simulated results readily comparable to empirical food webs, which typically contain only the presence/absence information of constituent species. While previous studies implement population dynamics (Otto et al. 2007, Kondoh and Ninomiya 2009), implementing population dynamics did not alter the results in the main text (Supporting information).

In our model, we consider the presence ($P_i = 1$) and absence ($P_i = 0$) of species i in a single patch (i.e. 'island') with species migration from the external permanent species pool (i.e. "mainland"). The colonization–extinction process is defined by the following reactions:

$$P_i = 0 \xrightarrow{f_i(\vec{P})} P_i = 1 \tag{1a}$$

$$P_i = 1 \xrightarrow{g_i(\vec{P})} P_i = 0, \tag{1b}$$

where f_i is the colonization rate and g_i is the extinction rate. These rates depend on the presence of other species $\vec{P} = (P_1 \ldots, P_N)$ and environments. If species i is a basal species ($1 \leq i \leq B$), the colonization rate depends on the resource availability, the ecosystem size, and the presence of other basal species:

$$f_i(\vec{P}) = (1-P_i)a_i \exp\left(-\frac{\sum_{k=1}^{B} P_k}{R}\right), \quad i = 1,\dots,B, \tag{2}$$

where a_i is the maximum colonization rate of basal species i in the absence of other basal species (i.e. no competitors for resource), and R quantifies the resource availability in the patch. The resource availability R defines how rapidly the colonization rate decreases as the number of other basal species increases.

For non-basal species i ($B + 1 \le i \le N$), on the other hand, the colonization rate depends on the presence of prey species:

$$f_i(\vec{P}) = (1-P_i)b_i \frac{\rho_i^{h_1}}{\rho_i^{h_1} + K_i^{h_1}}, \quad i = B+1,\dots,N, \tag{3}$$

where b_i is the maximum colonization rate of non-basal species i, ρ_i is the number of species i's prey species in the patch, K_i gives the number of prey species that defines the half-max colonization rate, and h_1 is the Hill coefficient that determines the shape of the function. The ecosystem size in this model is realized by the maximum colonization rates (a_i and b_i) because species would migrate more frequently into a larger patch than a smaller one (i.e. the target effect). In Supporting information, we implemented alternative ecosystem size's effect as decreasing the extinction rate due to predation c_i, instead of increasing colonization rates (a_i and b_i). This idea can be justified when population abundances are fixed regardless of the system size. In such cases, population densities decrease over ecosystem size, resulting in lower encounter rates between prey and predators (Ward and McCann 2017). See the Supporting information qualitatively similar results to the main text with this implementation.

The extinction rate is composed of predation, lack of prey, and disturbances (e_i):

$$g_i(\vec{P}) = P_i\left(c_i \frac{q_i^{h_2}}{q_i^{h_2} + L_i^{h_2}} + d_i \frac{M_i^{h_3}}{M_i^{h_3} + \rho_i^{h_3}} + e_i\right), \tag{4}$$

where c_i and d_i represent maximum extinction rates of species i due to abundant predators and scarce prey, respectively; q_i is the number of species i's predator in the patch; L_i gives the number of predator species that defines the half-max extinction rate due to the predation pressure; M_i gives the number of prey species that defines the half-max extinction rate due to the lack of prey; and h_2 and h_3 are the Hill coefficients. For top predators, extinction due to predators never occurs ($c_i = 0$), while the basal species has $d_i = 0$ as they do not have any prey species. The default values and the descriptions of the parameters are listed in Table 1. In the main text, we focused on the effect of two environmental drivers: disturbance and ecosystem size. This is because our preliminary results (Supporting information) suggested that resource availability showed no correlations. Although species would differ in their parameter values (e.g. colonization rates a_i and b_i, and sensitivity to disturbance e_i) in nature, we fixed the parameter values across the species to focus on the effects of network structures of food webs. We replicated the simulations 20 times for each combination of a 32-species food web structure and a parameter set, because each replicate can realize different food webs depending on the colonization and extinction events. In total, we analyzed 30 food web structures × 20 replicates × 72 parameter sets (variations in a_i and e_i, see Table 1) = 43200 data in each definition of FCL.

The stochastic dynamics were implemented by Gillespie algorithm using the GillespieSSA library (Pineda-Krch 2008) ver. 0.6.2 in R ver. 4.2.1 (www.r-project.org). For each run of the simulations, all species are absent in the patch at the beginning: $\vec{P}(0) = \vec{0}$. We continued the simulations until time 1000. The master equation of the system describes the dynamics of the probability distribution of $\vec{P}$ as follows:

$$\frac{d\Pr(\vec{P})}{dt} = \sum_{i}^{N} \Pr[S_i(\vec{P})]\phi_i[S_i(\vec{P})] - \Pr(\vec{P})\sum_{i}^{N} \phi_i(\vec{P}), \tag{5}$$

where $\Pr(\vec{P})$ represents the probability density of presence–absence vector $\vec{P}$, S_i is an operator to switch the presence of species i to the absence and vice versa without changing other species' presence–absence

Table 1. Summary of parameters.

Symbol	Value	Description
N	32	Maximum number of species
B	4	Maximum number of basal species
l	113	Expected number of trophic links
a_i	∈ {0.25, 0.5, 0.75, …, 2.0}	Maximum colonization rate of basal species
R	4	Resource availability
b_i	a_i	Maximum colonization rate of non-basal species
K_i	1	Number of prey species giving the half-max colonization rate
c_i	0.3	Maximum extinction rate because of predation
L_i	2	Number of predator species giving the half-max extinction rate by predation
d_i	0 (basal) or 10 (non-basal)	Maximum extinction rate due to the lack of prey
M_i	0.05	Number of prey species giving the half-max extinction rate by lack of prey
e_i	∈ {0.1, 0.2, 0.3, …, 0.9}	Extinction rate because of disturbances
h_j (j = 1, 2, 3)	1	Hill coefficients to determine the forms of functions.

information, i.e. $S_i(\vec{P}) = (P_1 \ldots, P_{i-1}, 1 - P_i, P_{i+1,} \ldots, P_N)$, and $\phi_i(\vec{P}) = P_i f_i(\vec{P}) + (1 - P_i) g_i(\vec{P})$ represents the switching rate of species i from presence to absence and vice versa. Intuitively, the first term of Eq. 5 represents the rate at which the species composition becomes $\vec{P}$ and the second term indicates the rate at which species composition changes from $\vec{P}$.

After removing species with no prey from the realized food webs at the end of the simulations, FCL was measured (Supporting information), and the fractions of 13 motifs were calculated using the igraph library (Csardi and Nepusz 2006) ver. 1.3.5 in R. If all species go extinct, we regarded FCL as −1 because FCL is zero when only basal species exist.

Sensitivity analysis

While we fixed parameter values of (N, B, l, T) in the main text, these parameter values affect the structure of entire food webs. To ensure the robustness of the results in the main text, we ran additional 7200 simulations in which parameters were randomly sampled from the following sets with equal probability: $N \in \{16, 24, 32, 40, 48\}$, $B \in \{2, 4, 6, 8\}$, $l/N^2 \in \{0.9, 0.1, 0.11, 0.12, 0.13\}$, and $T \in \{0.1, 0.5, 1, 2, 10\}$. We varied the maximum operational species richness N within the range where the computational cost is not too huge. The range of the maximum number of basal species was chosen so that at least half of the species in a food web were non-basal species; otherwise, FCL would remain short. The range of connectance l/N was based on Dunne et al. (2002); the mean and standard deviations of connectance in empirical food webs were 0.11 and 0.09, respectively. The range of T was determined to generate a large variation of the entire food web structure following the results in Johnson et al. (2014). In this sensitivity analysis, we also randomly sampled the frequency of disturbance and ecosystem size while fixing resource availability and other parameter values (Table 1). These simulations allow us to validate 1) whether operational species richness and the fraction of chain motifs correlate with FCL, and 2) whether operational species richness modulates how environmental drivers affect FCL in diverse food web structures. The sensitivity analysis was performed in all three definitions of FCL.

Statistical analysis

Statistical analysis of empirical data

We used regression analysis to examine how operational species richness and the fraction of the three-species chain motif affect long, short, and mean FCLs (Results). We assumed these two variables had any of the following three functional forms: linear, saturating, or quadratic. These functional forms were determined from the scatter plots against FCL (Fig. 2–3); FCL positively correlates with the operational species richness and the fraction of the chain motifs, respectively. Because long FCL was not observed in communities with high operational species richness or with many chain motifs, the model selection included two non-linear functional forms, a saturating and a quadratic functional form. The saturating functional form indicates that FCL does not change at a high richness or a high fraction of the chain motif, while the quadratic form suggests that FCL can decrease there. We generated fifteen nonlinear models for each definition of FCL; i.e. either species richness or the fraction of the chain motif affects FCL in either of the three functional forms, respectively (2 × 3 = 6), or both of the two factors affect FCL in any of the three, respectively (3 × 3 = 9). The three functional forms are written as in Eq. 6a–c.

$$\mathrm{FCL} \sim ax - 1, \tag{6a}$$

$$\mathrm{FCL} \sim a\{1 - \exp(-bx)\} - 1, \tag{6b}$$

$$\mathrm{FCL} \sim -ax^2 + bx - 1 \tag{6c}$$

where x is either operational species richness or the fraction of the chain motifs in a food web, and coefficients a and b are assumed positive because of positive correlations between FCL and operational species richness or the fraction of chain motifs (Fig. 2–3). The constant terms of the three models are fixed as −1 given our definition of FCL. In the saturating functional form (Eq. 6b), parameter a controls how much x (i.e. either species richness or the fraction of chain motifs) increases FCL because FCL converges to $a - 1$ in the limit of $x \longrightarrow \infty$. In the quadratic function (Eq. 6c), the maximum increase of FCL by x is either $b^2/(4a)$ (if $b < 2a$) or $-a + b$ (otherwise).

We used the *nls()* function with algorithm "port" in R to fit these models to the data from the empirical database. The lower boundaries of the coefficients were set to zeros so that the linear and saturating functions were increasing functions and the quadratic function was concave), while the upper boundaries were either maximum FCL in the data plus one (for a in the saturating function) or 10 (for the other coefficients). The upper boundaries of the coefficients were justified as follows. For a in the saturating function, this upper boundary allowed the saturating function to fit the maximum FCL in the data: for the rest of the parameters, the upper boundaries were chosen so that the *nls()* function could search broad parameter ranges but it converged. We chose the best models by calculating Akaike information criterion (AIC) of the regression models using the *AIC()* function in R. See the Supporting information for the ΔAIC, and the best models and the coefficient values.

Statistical analysis of simulation data

We repeated a similar regression analysis for our simulation data. We grouped simulated data according to the 30 food web structures, which were used as random effects in nonlinear mixed effect models. We included the random effects in all coefficients in (Eq. 6a–c) because FCLs in different food webs may respond differently to changes in operational

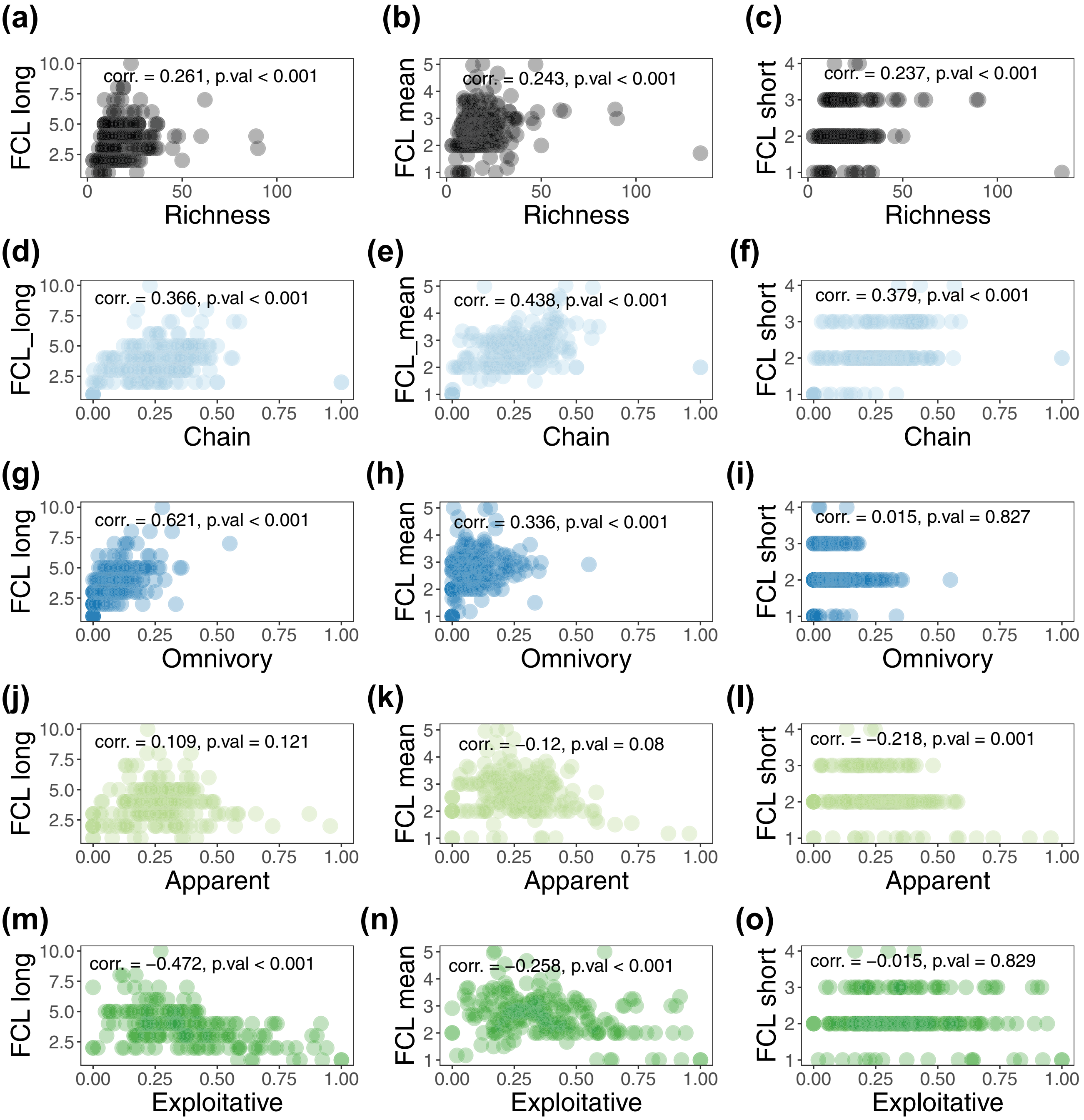

Figure 2. Correlations in empirical food webs. Spearman correlation coefficients between food chain length (FCL) and species richness (a–c) or the fractions of food web motifs (chain: (d–f), omnivory: (g–i), apparent competition: (j–l), and exploitative competition: (m–o)) in the empirical food webs are shown. The correlation results were obtained from the *cor()* function in R and we removed data of operational species richness < 3 because we cannot define the motifs there. We measured three types of FCL depending on how we define trophic positions. In the left column (FCL long), we define trophic positions as one plus the longest-path length from the basal species. In the center column (FCL mean), species' trophic levels are given by one plus mean of prey species' trophic positions. In the right column (FCL short), trophic positions are given by one plus the shortest-path length from the basal species. The p-value of the correlation test is also shown in each panel.

species richness and the fraction of chain motifs. We fitted the nonlinear mixed effect models to the data with the *nlme()* function in the nlme library (Pinheiro et al. 2023) ver. 3.1-162 in R. The best model was chosen by AIC (see the Supporting information for ΔAIC).

The linear quantile mixed models (Supporting information) were used to quantify how disturbance and ecosystem size affected FCL and species richness, using the *lqmm()* function in the lqmm library (Geraci and Bottai 2014) ver. 1.5.8 in R. We implemented the random effects of 30 entire

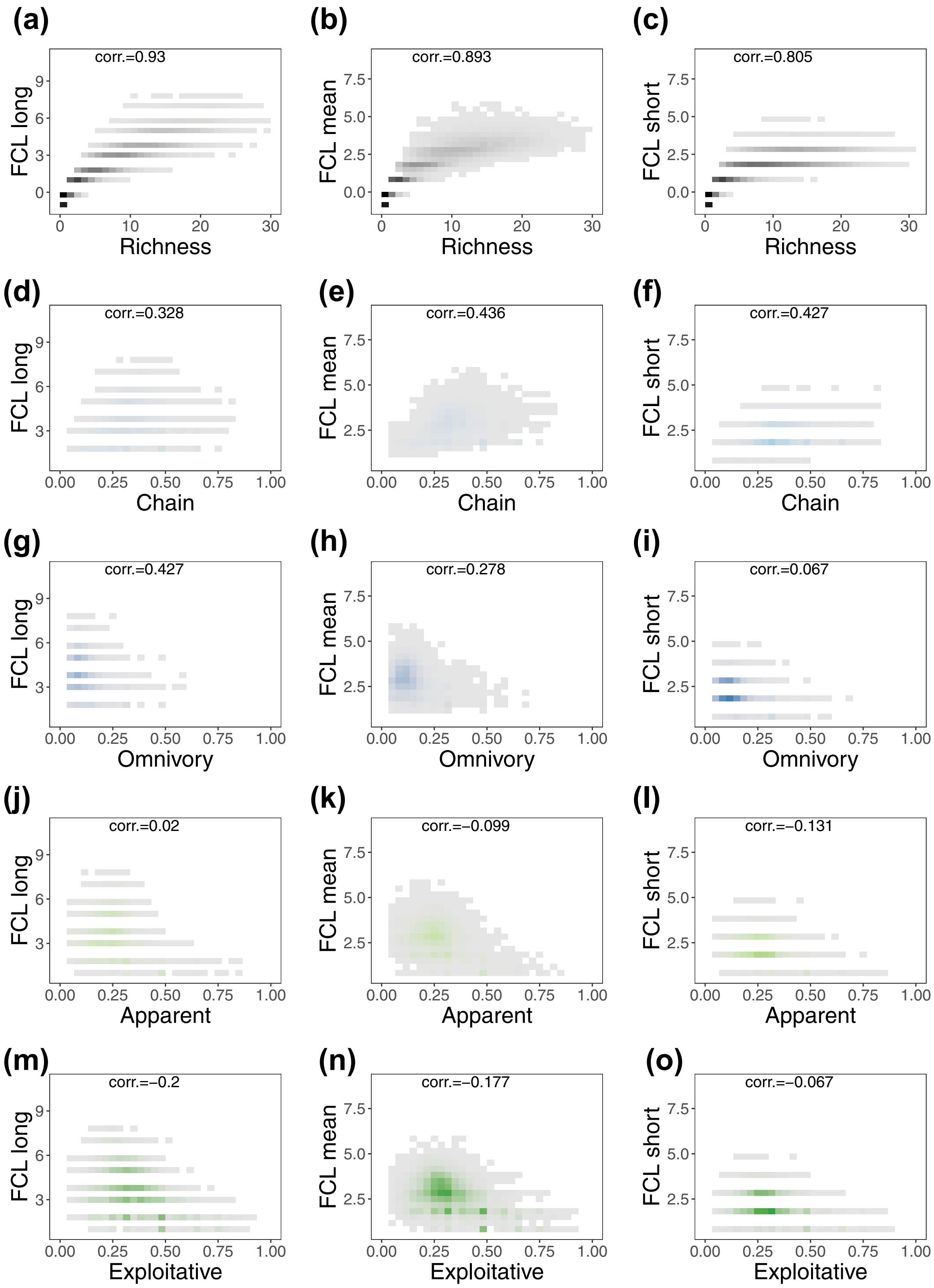

Figure 3. Correlations in food web simulations. As in Fig. 2, correlation plots between food chin length (FCL) and species richness or the fraction of food web motifs are shown. Because of the large number of simulation data, p-values are always small and omitted. The darker, bluer, or greener areas represent more data than gray areas. .

food web structures on the slopes and the coefficients of the models. This analysis was intended to see whether the effects of disturbance on FCL differed depending on ecosystem size, and vice versa. Wilcoxon signed-rank test was also used to compare the logarithm of slopes of the linear quantile mixed models over disturbance or ecosystem size.

Results

Operational species richness non-linearly increases FCL

We first investigated whether operational species richness and the fractions of different food web motifs correlated with FCL to identify candidates for internal modulators. Operational species richness and three-species chain motifs positively correlated with FCL in all three definitions (Fig. 2a–f). The two competition motifs (i.e. apparent competition and exploitative competition), on the other hand, were negatively or non-significantly correlated with FCL (Fig. 2j–o). The correlations between FCL and the omnivory motif depended on the definition of trophic positions. Although omnivory increased FCL long (Fig. 2g), the correlation was weaker or non-significant with FCL mean (Fig. 2h) or short (Fig. 2i). These patterns were replicated in our simulated food webs (Fig. 3). The correlative analysis suggested that operational species richness and the chain motif may play key roles in modulating the environment–FCL relationships. We proceeded with further analyses to see how they related to FCL and the potential environmental drivers.

The functional forms between FCL and internal food web structures (operational species richness and motifs) determine how environments dictate FCL. We compared three functional forms: linear, saturating, and quadratic functions (Fig. 2–3). The best models (see the Supporting information for FCL long and short, respectively) described the effect of operational species richness in the saturating functions both in empirical data and our simulations (Fig. 4a–b). This indicated that FCL changed disproportionately at low operational species richness, with little change at high operational species richness. This pattern did not change because of the difference in the entire food web structure; i.e. each 32-species food web in the simulations showed similar patterns over realized operational species richness (dashed lines in Fig. 4b). The saturating functional form may be maintained in broad networks; it appeared in baseline models without species assembly (Supporting information). Quadratic models were selected as the best models for describing the functional relationships between FCL (except for FCL short, see the Supporting information) and the fraction of the chain motifs (Fig. 4c–d).

The coefficients of best models (Supporting information) indicated that operational species richness had larger maximum effects on FCL than chain motif; i.e. the coefficient a in Eq. 6b for operational species richness ranged from 2.85 (empirical FCL short) to 6.61 (simulated FCL long), while the maximum increase in FCL due to the chain motifs ranged from 1.23 (simulated FCL short) to 2.15 (empirical FCL long). However, species richness increased FCL little at high species richness because of the saturating function. If a fraction of the chain motifs changes independently in operational species-rich food webs, the chain motifs may disproportionately influence FCL. To explore this possibility, we delved into how the fractions of the food web motifs changed over species richness. At high operational species richness, the fraction of the chain motif was lower than expected in random graphs where each interaction between species is realized with probability 0.11. The fractions of the chain motifs in the empirical and simulation food webs were lower than the expected value $\pm 2 \times$ expected standard deviation (ESD) in the random graphs (Fig. 4e–f). In the random graph, the expected fractions of the motifs were constant but their ESD decreased over operational species richness (see the Supporting information for mathematical details). These results imply that some regulation mechanisms hindered the persistence of chain motifs in species-rich food webs, limiting the motif effect on FCL. Therefore, we predict that key environmental drivers of FCL are those that change operational species richness from low to intermediate levels.

We repeated our analysis with empirical food webs at higher resolution (Supporting information). Although the amount of such food web data was small (11 food webs), operational species richness positively correlated with FCL, and the saturating functional form of operational species richness predicted empirical FCL.

Operational species richness modulates environmental effects on FCL

Our simulation shed light on how environmental factors – resource availability, disturbance, and ecosystem size – dictate FCL through changes in species richness. In the main text, we focused on the effects of disturbance and ecosystem size because our preliminary results suggested very weak correlations between resource availability and FCL (see the Supporting information for the analysis including resource availability). Figure 5a shows that the effect of disturbance was contingent on ecosystem size and vice versa. For example, disturbance strongly regulated FCL in small ecosystems, but such disturbance-induced regulation was weak in large ecosystems (Fig. 5c, Supporting information; one-sided Wilcoxon signed-rank test $p < 10^{-6}$, $T = 465$). Similarly, enlarging ecosystem size resulted in enhancing FCL under strong disturbance but such increase in FCL was smaller under weak disturbance (Fig. 5e, Supporting information; one-sided Wilcoxon signed-rank test $p < 10^{-6}$, $T = 465$). See the Supporting information for comparison of the slopes in the linear quantile mixed models.

The non-linear FCL–richness association underlay the emergent dual regulation of FCL. As expected, operational species richness decreased over disturbance while increasing over ecosystem size (Fig. 5b). In contrast to the FCL pattern, disturbance regulated operational species richness regardless of the ecosystem size, and vice versa (Fig. 5d, f). The decoupling

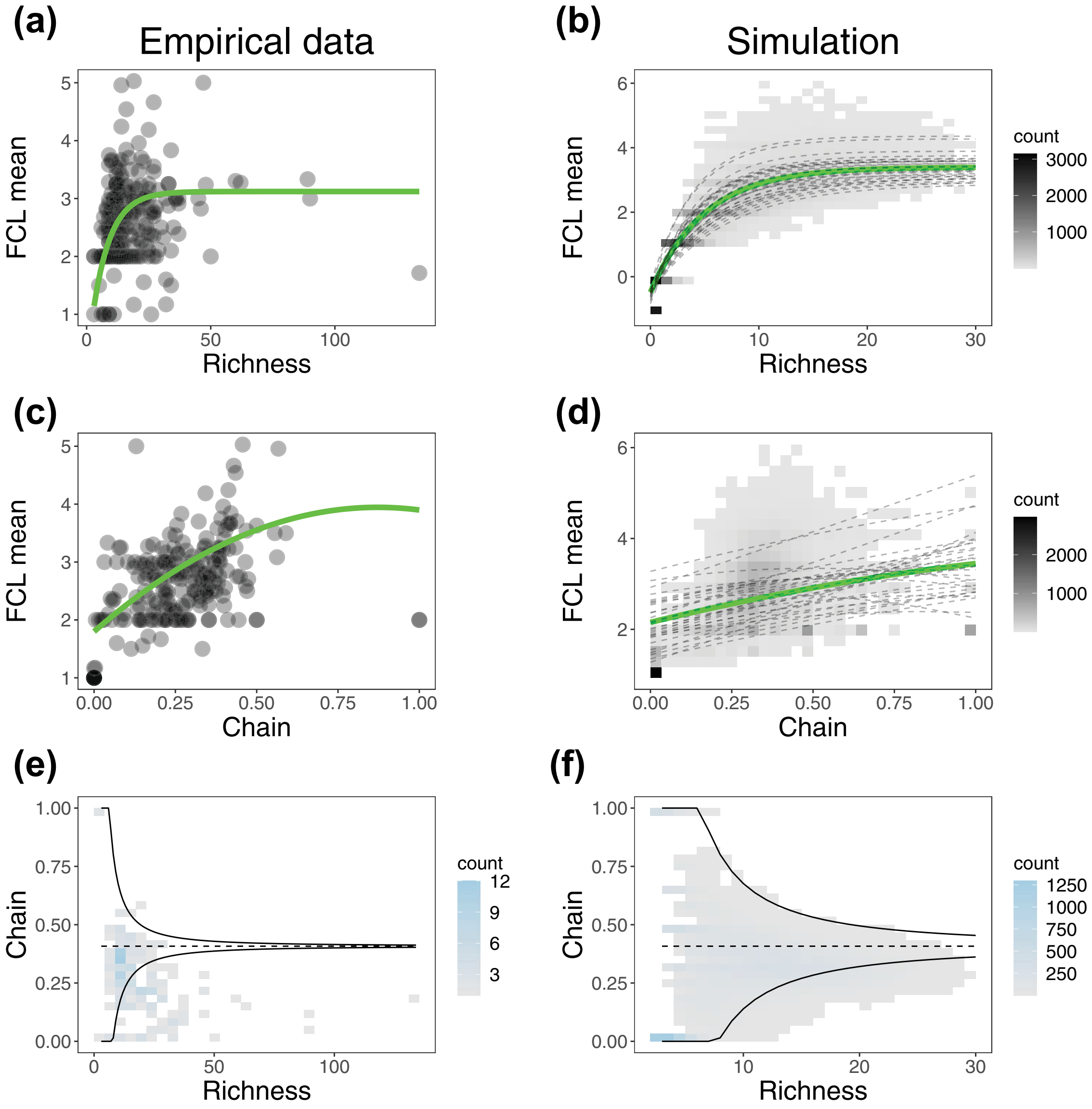

Figure 4. Species richness and the chain motifs relate to food chain length (FCL). Relationships among operational species richness, the fraction of the three-species chain motifs, and FCL mean are shown (left: empirical data, right: our simulation data). (a–b) Operational species richness had saturating effects on FCL. The green curves represent the best models (Supporting information) while fixing the fraction of the chain motif as the mean value. (c–d) The fraction of the chain motif had quadratic effects on FCL. Similarly, the green curves represent the best models (Supporting information) while fixing operational species richness as the mean value. Notably, the green curves in (b) and (d) represent only the fixed effects, and the black dashed lines include random effects. (e–f) The fractions of the chain motifs over operational species richness are shown. The dashed line represents the mean fraction of the chain motifs in the random graph, and the solid curves represent mean ± 2 × expected standard deviation (ESD) in the random graph. See the Supporting information for more mathematical details.

of FCL and richness patterns over environmental gradients can be explained by the saturating form of the FCL–richness relationship. For example, when operational species richness exceeded 15, changes in species richness did not translate into FCL changes due to the saturating functional form. Thus, operational species richness modulated how disturbance and ecosystem size affected FCL. These patterns were consistent regardless of the definition of FCL (Supporting information).

We also performed a sensitivity analysis to see whether our findings were robust against the variation of food web structure: the maximum operational species richness N, the maximum number of basal species B, expected connectance in N-species food web, and the pattern of omnivory T. FCL again positively correlated with operational species richness and the fraction of the chain motifs (Fig. 6a). Figure 6b–c compared the simulation data in the sensitivity analysis with the best model for these data suggested by ΔAIC (Supporting information): $\text{FCL} = 4.18 \times (1 - \exp(-0.14 \times \text{richness})) + 1.69 \times \text{chain} - 1$. The operational species richness still showed the saturating effect on FCL, and the estimated

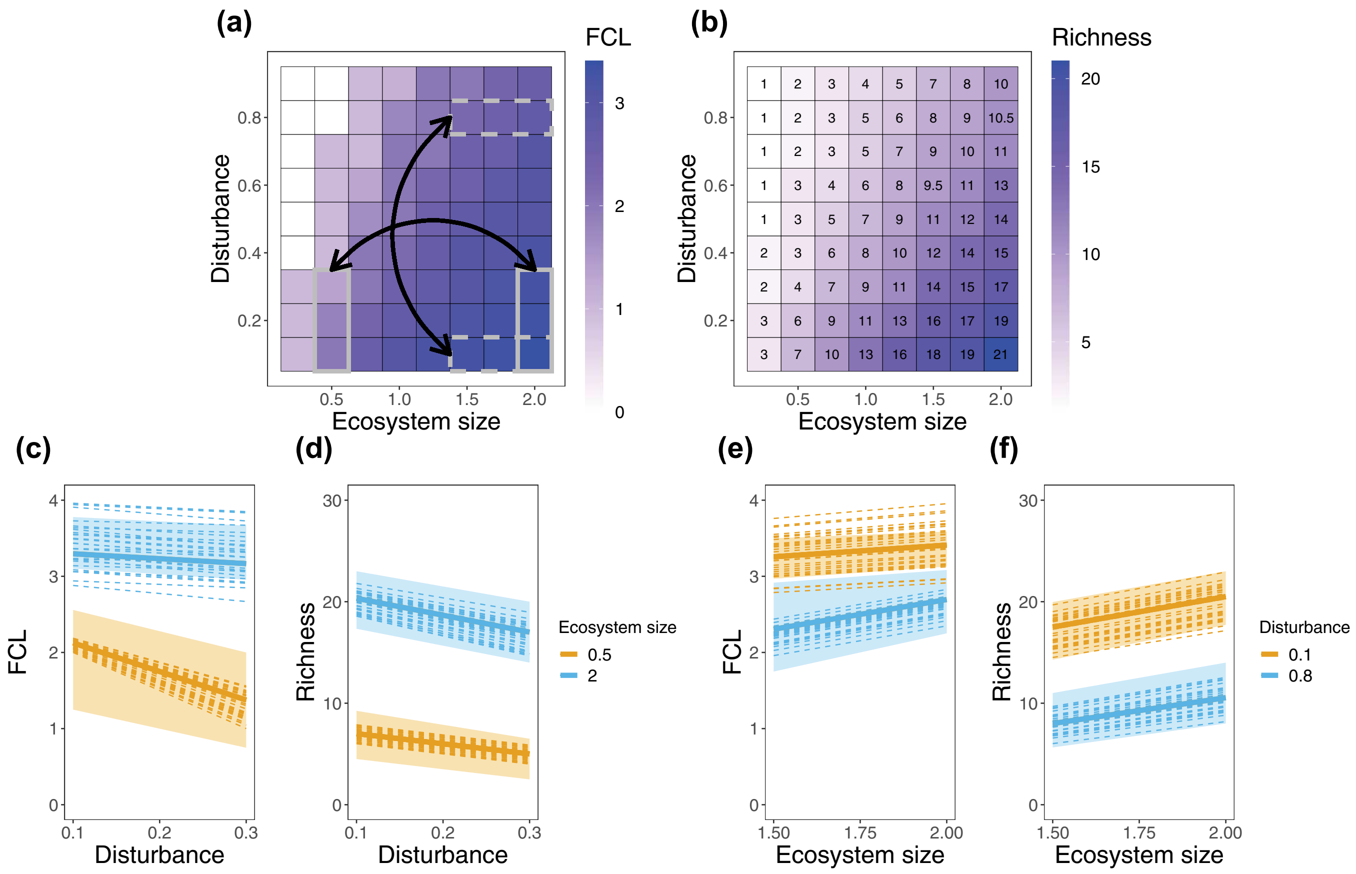

Figure 5. Species richness modulates environmental effects on food chain length (FCL). (a–b) Median values of FCL mean (a) and operational species richness (b) in our simulations over two environmental factors (disturbance and ecosystem size) are shown. On one hand, operational species richness consistently decreased over disturbance but increased over ecosystem size. On the other hand, the two environmental drivers had little effect on FCL at high operational species richness (>15), where disturbance is weak or ecosystem size is large. (c) Disturbance decreased FCL more in a smaller ecosystem (orange) than in a larger one (blue). These values correspond to the solid-line boxes in (a). (d) Disturbance decreased operational richness regardless of ecosystem size. (e) Ecosystem size increased FCL more under strong disturbances (blue) than weak ones (orange). These values correspond to the dashed-line boxes in (a). (f) Operational richness increased over ecosystem size regardless of the frequency of disturbances. In (c) – (f), the solid lines represent median values of the fixed effects, the dashed lines include the random effects of different 32-species food web structures, and the shaded areas show 25–75% quantile of the fixed effects. See the Supporting information for comparison of the slopes in the linear quantile mixed models.

parameter values indicated that the operational species richness had a larger maximum effect on FCL than the fraction of the chain motifs. The patterns of FCL and operational species richness across the environmental drivers (Fig. 6d–e, respectively) were similar to Fig. 5a–b; the effect of the disturbance on FCL was contingent on the ecosystem size, and vice versa. Such consistency also appeared in the two other definitions of FCL (Supporting information). Therefore, operational species richness is a robust modulator between the environmental drivers and FCL.

Discussion

Our mechanistic exploration highlighted the innate complexity of FCL responses to environmental drivers, offering a potential explanation for the mixed results in previous studies (Sabo et al. 2009, 2010, Takimoto and Post 2013, Warfe et al. 2013, Young et al. 2013). In particular, the effects of ecosystem size and disturbance were contingent on each other. While previous studies (Sabo et al. 2010, Pomeranz et al. 2023) suggest the context-dependent effects through the relationships among potential environmental drivers, our theory does not require such relationships. Instead, the context dependency in our model arose from the nonlinear relationship between FCL and operational species richness (Fig. 4b, 5a–b). This nonlinear pattern is confirmed by empirical food web data (Fig. 4a), and is consistent with previous studies (Martinez and Lawton 1995, Vander Zanden et al. 1999). Hence, our results suggest the prevalence of 'apparent' interactions between multiple environmental drivers, implying that the observed contingency may be a natural outcome of

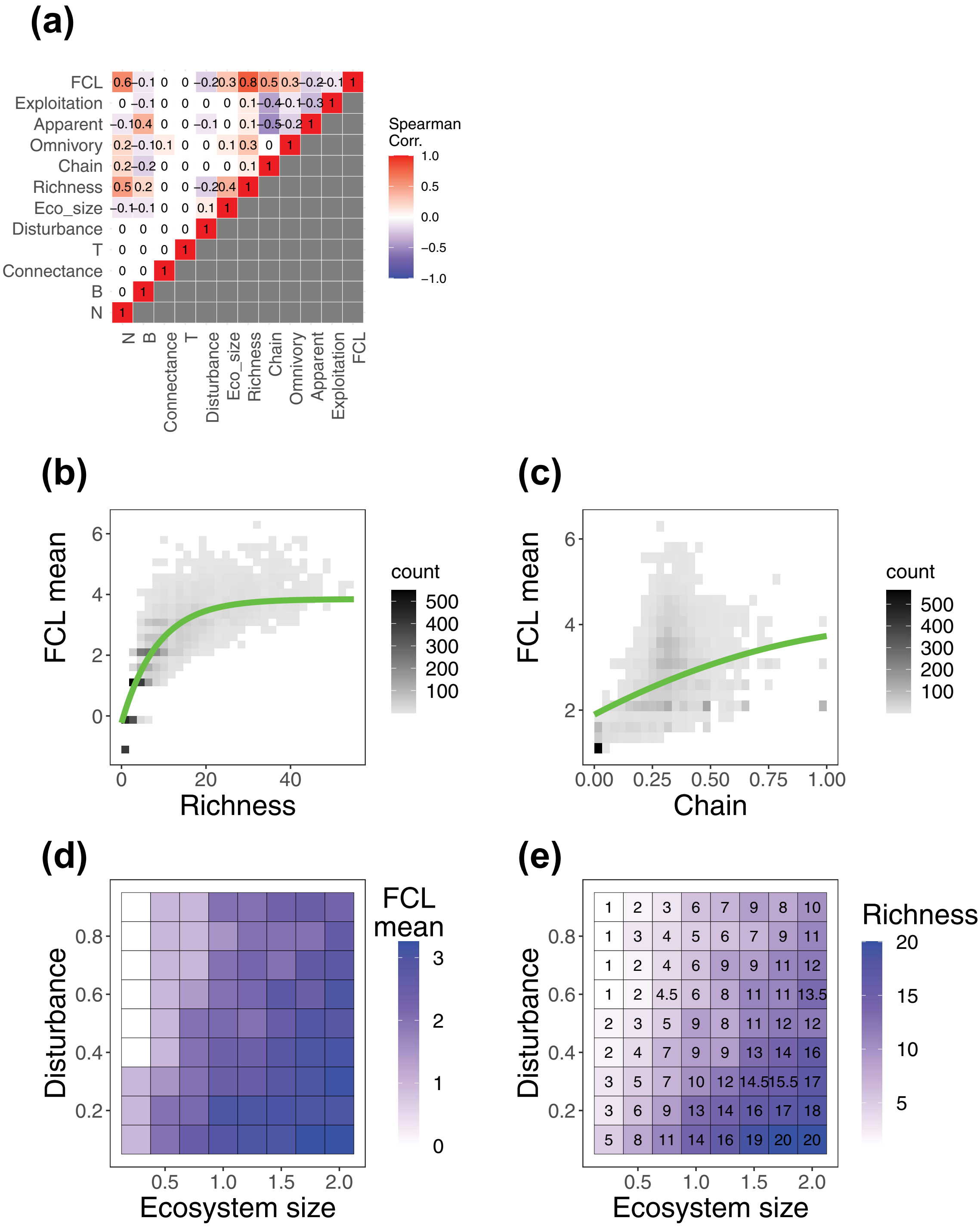

Figure 6. Sensitivity analysis in food chain length (FCL) mean. The summary of the sensitivity analysis is shown. (a) Spearman correlation coefficients between the sampled parameters and realized network metrics are shown. Here, 'Eco_size' represents ecosystem size. FCL positively correlates with operational species richness and the fraction of chain motifs in realized food webs. (b–c) Operational species richness and the fraction of chain motifs are fitted to the saturating and quadratic functions, respectively. The green curves represent the best model in the sensitivity analysis (Supporting information): $\text{FCL} = 4.18 \times (1 - \exp(-0.14 \times \text{richness})) + 1.69 \times \text{chain} - 1$. In (b) we fixed the fraction of chain motifs as its mean value, while we used mean richness in (c). (d–e) Median FCL and operational species richness over two environmental drivers (disturbance and ecosystem size) are shown.

complex food webs. The gradient of operational species richness across environments would be key to resolving inconsistencies in previous FCL studies.

The lack of resource effects (see the Supporting information for information on including resource availability in the main text model, and for an alternative model) seems counterintuitive because some previous studies report the importance of resource availability (Post and Takimoto 2007, Doi et al. 2009, Kondoh and Ninomiya 2009, Takimoto and Post 2013, Ward and McCann 2017, Terui and Nishijima 2019). This mismatch may be attributable to the difference in the number of operational species considered. Some of the above studies analyzed simple systems composed of three or four species (Post and Takimoto 2007, Doi et al. 2009, Ward and McCann 2017, Terui and Nishijima 2019) unlike our theoretical model (32 species). These studies suggest that FCLs lengthen with increasing resource availability at lower ranges (Post and Takimoto 2007, Ward and McCann 2017, Terui and Nishijima 2019), although excessive productivity may shorten FCL if intraguild predation exists (Post and Takimoto 2007, Ward and McCann 2017). It is possible that this prediction is only applicable to simplified food webs with a few species. Another, but not mutually exclusive explanation is that the effect of resource availability could be simply weaker than other environmental drivers. Although Kondoh and Ninomiya (2009) analyzed the effect of resource availability in *N*-species communities, their model does not include ecological processes driven by ecosystem size and disturbance. Our model complemented these components (see the Supporting information for the abundance-based model), finding the lack of noticeable effects of resource availability. These differences may account for the contrasting results of resource availability between our study and studies of other researchers.

Like any theoretical research, our results must be viewed with some caution. First, they might be a unique attribute of the particular food web model we employed. However, we are confident that this is not the case. The saturating effect on FCL appeared regardless of the assembly rules we considered, including random graphs and cascade models (Cohen and Newman 1985, Supporting information). Thus, this saturating response of FCL to operational species richness may apply to a broad range of networks. While we did not consider food web models that produce cyclic food webs (e.g. the niche model Williams and Martinez 2000), it is difficult to envision that cycles qualitatively alter our results because the saturating effect appeared even in random graphs. In support of this view, the saturating function accurately predicted FCL in more recent food web data with the higher taxonomic resolution and cyclic food webs (Supporting information). These addressed the potential limitation of Cohen's larger database, i.e. inaccurate estimates of trophic positions due to the low taxonomic resolution. This fact suggests the robustness and generality of our findings, since the non-linear relationship was responsible for the contingent effects of environmental drivers on FCL. Second, we did not account for variations in species' traits other than their trophic positions in a food web. In nature, species may differ in their colonization rates, sensitivities to disturbances, or competitive abilities. Nevertheless, we could reproduce empirical patterns of how FCL changes over the gradients of food web structures. Hence, introducing more complexity to our model will unlikely overturn our conclusions.

Our findings may also provide important insights into the stability–diversity debate (McCann 2000). "May's paradox" of community stability has sparked a discussion of how complex webs of interacting species are maintained despite their inherent instability (Gardner and Ashby 1970, May 1972, Allesina and Tang 2012), and previous studies suggest that the non-random species interaction is the key factor promoting stable coexistence (Thébault and Fontaine 2010, Mougi and Kondoh 2012, García-Callejas et al. 2023). The present study suggests another non-randomness related to community stability: expanding the "ertical" dimension of biodiversity (Wang and Brose 2018), or increasing FCL, is more likely to lead to community collapse than increasing "horizontal" biodiversity or adding species to the already-occupied trophic positions. The chain motif is distinctive because species within the chain motif occupy broader trophic positions than others (Supporting information). Increasing chain motifs means that species occupy open and higher trophic positions, resulting in longer FCL. However, Fig. 4e–f indicates that chain motifs were unlikely to be prevalent in species-rich communities; instead, colonized species likely occupied trophic positions similar to resident species, forming competitive motifs with the saturating increase in FCL (Fig. 4a–d). It is reasonable to observe the saturating effect of operational species richness on FCL (Fig. 4). This finding may open up an opportunity to link the ongoing diversity–stability debate to FCL research.

Our findings do not mean to downplay the role of stable isotopes in FCL research; instead, they suggest the importance of combining multiple methods to gain deeper insights. Although stable isotopes are applicable to a variety of natural systems, they treat internal food web structure as a 'black box'. Emerging molecular techniques, such as (meta-)barcoding of environmental DNA, can investigate the food web structure (Taberlet et al. 2018, Pringle and Hutchinson 2020). Recent studies use such techniques to assess species' diet (Deagle et al. 2009), to reconstruct food web structure (D'Alessandro and Mariani 2021), or to estimate interspecific interaction strength (Ushio et al. 2023). These analyses have the potential to unveil detailed internal food web structures, including species richness and fractions of food web motifs.

In conclusion, this manuscript sheds light on the role of internal food web structure in producing the context-dependency of FCL controls. Uncovering food web structure in nature may prove challenging. However, recent technological advancements have created opportunities to address this issue. In this regard, our theoretical framework serves as a conceptual foundation for future studies that utilize emerging methodologies to investigate food webs: how operational species richness and, to a lesser extent, food web motifs modulate the associations between FCL and environmental drivers.

By incorporating the intrinsic complexity of food webs into FCL research, we can potentially resolve contradictory results observed in various ecosystems.

Speculation

Recently, Guo et al. (2023) show alternative nonlinear patterns of how FCL changes across the three environmental drivers; while FCL increases over ecosystem size, it oscillates over resource availability and disturbance. This complex pattern comes from the colonization–competition tradeoff of basal species in their model. The diversity of basal species shows zig-zag patterns across the environmental gradients, leading to oscillating patterns of non-basal species and FCL. Although our patterns of FCL across the environments differ from those in Guo et al. (2023), species richness in Guo et al. (2023) seems to increase FCL in a saturating form because changes in richness affect FCL little when FCL is long; see Supporting information in Guo et al. (2023). We speculate that species richness robustly affects FCL in a saturating form, but that how environments affect species richness depends on the biological details (e.g. colonization–competition tradeoffs). If this is the case, the patterns of FCL across environments can be diverse; however, the changes in species richness can explain the patterns. This could be a future research direction.

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Author contributions

Shota Shibasaki: Conceptualization (equal); Formal analysis (lead); Investigation (equal); Methodology (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Akira Terui:** Conceptualization (equal); Funding acquisition (lead); Supervision (lead); Writing – review and editing (equal).

Data availability statement

Data are available from the Zenodo repository https://zenodo.org/records/10473889 (Shibasaki 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

References

Allesina, S. and Tang, S. 2012. Stability criteria for complex ecosystems. – Nature 483: 205–208.

Allesina, S., Alonso, D. and Pascual, M. 2008. A general model for food web structure. – Science 320: 658–661.

Angelini, R. and Agostinho, A. A. 2005. Food web model of the Upper Paraná River floodplain: description and aggregation effects. – Ecol. Modell. 181: 109–121.

Angelini, R. and Vaz-Velho, F. 2011. Estructura del ecosistema y análisis trófico de desembarques pesqueros en Angola. – Sci. Marina 75: 309–319.

Angelini, R., Agostinho, A. A. and Gomes, L. C. 2006. Modeling energy flow in a large Neotropical reservoir: a tool to evaluate fishing and stability. – Neotrop. Ichthyol. 4: 253–260.

Angelini, R., Alóisio, G. R. and Carvalho, A. R. 2010. Mixed food web control and stability in a Cerrado river (Brazil). – Pan Am. J. Aquat. Sci. 5: 421–431.

Angelini, R., de Morais, R. J., Catella, A. C., Resende, E. K. and Libralato, S. 2013. Aquatic food webs of the oxbow lakes in the Pantanal: a new site for fisheries guaranteed by alternated control? – Ecol. Modell. 253: 82–96.

Bascompte, J., Melián, C. J. and Sala, E. 2005. Interaction strength combinations and the overfishing of a marine food web. – Proc. Natl Acad. Sci. USA 102: 5443–5447.

Borrelli, J. J. 2015. Selection against instability: stable subgraphs are most frequent in empirical food webs. – Oikos 124: 1583–1588.

Briand, F. and Cohen, J. E. 1987. Environmental correlates of food chain length. – Science 238: 956–960.

Caldarelli, G., Higgs, P. G. and McKane, A. J. 1998. Modelling coevolution in multispecies communities. – J. Theor. Biol. 193: 345–358.

Camacho, J., Stouffer, D. B. and Amaral, L. A. 2007. Quantitative analysis of the local structure of food webs. – J. Theor. Biol. 246: 260–268.

Cattin, M. F., Bersier, L. F., Banasek-Richter, C., Baltensperger, R. and Gabriel, J. P. 2004. Phylogenetic constraints and adaptation explain food-web structure. – Nature 427: 835–839.

Christian, R. R. and Luczkovich, J. J. 1999. Organizing and understanding a winter's seagrass foodweb network through effective trophic levels. – Ecol. Modell. 117: 99–124.

Cirtwill, A. R. and Wootton, K. L. 2022. Stable motifs delay species loss in simulated food webs. – Oikos 2022: e09436.

Cohen, J. 2010. ECOWeB: ecologists' cooperative web bank. Ver. 1.1. – https://digitalcommons.rockefeller.edu/cohen_joel_laboratory/1. Machine-readable database of food webs. The Rockefeller University.

Cohen, J. E. and Newman, C. M. 1985. A stochastic theory of community food webs. I. Models and aggregated data. – Proc. R. Soc. B 224: 421–448.

Cohen, J. E. et al. 1993. Improving food webs. – Ecology 74: 252–258.

Cruz-Escalona, V. H., Arreguín-Sánchez, F. and Zetina-Rejón, M. 2007. Analysis of the ecosystem structure of Laguna Alvarado, western Gulf of Mexico, by means of a mass balance model. – Estuarine Coast. Shelf Sci. 72: 155–167.

Csardi, G. and Nepusz, T. 2006. The igraph software package for complex network research. – InterJ. Complex Syst. https://cran.r-project.org/web/packages/igraph/citation.html.

D'Alessandro, S. and Mariani, S. 2021. Sifting environmental DNA metabarcoding data sets for rapid reconstruction of marine food webs. – Fish Fish. 22: 822–833.

Deagle, B. E., Kirkwood, R. and Jarman, S. N. 2009. Analysis of Australian fur seal diet by pyrosequencing prey DNA in faeces. – Mol. Ecol. 18: 2022–2038.

Diehl, S. and Feissel, M. 2001. Intraguild prey suffer from enrichment of their resources: a microcosm experiment with ciliates. – Ecology 82: 2977–2983.

Doi, H. and Hillebrand, H. 2019. Historical contingency and productivity effects on food-chain length. – Commun. Biol. 2: 40.

Doi, H., Chang, K.-H., Ando, T., Ninomiya, I., Imai, H. and Nakano, S.-I. 2009. Resource availability and ecosystem size predict food-chain length in pond ecosystems. – Oikos 118: 138–144.

Dunne, J. A., Williams, R. J. and Martinez, N. D. 2002. Food-web structure and network theory: the role of connectance and size. – Proc. Natl Acad. Sci. USA 99: 12917–12922.

Elton, C. S. 1927. Animal ecology. – Macmillan.

García-Callejas, D., Godoy, O., Buche, L., Hurtado, M., Lanuza, J. B., Allen-Perkins, A. and Bartomeus, I. 2023. Non-random interactions within and across guilds shape the potential to coexist in multi-trophic ecological communities. – Ecol. Lett. 26: 831–842.

Gardner, M. R. and Ashby, W. R. 1970. Connectance of large dynamic (cybernetic) systems: critical values for stability. – Nature 228: 784–784.

Geraci, M. and Bottai, M. 2014. Linear quantile mixed models. – Stat. Comput. 24: 461–479.

Gravel, D., Massol, F., Canard, E., Mouillot, D. and Mouquet, N. 2011. Trophic theory of island biogeography. – Ecol. Lett. 14: 1010–1016.

Guo, G., Barabás, G., Takimoto, G., Bearup, D., Fagan, W. F., Chen, D. and Liao, J. 2023. Towards a mechanistic understanding of variation in aquatic food chain length. – Ecol. Lett. 26: 1926–1939.

Hastings, H. M. and Conrad, M. 1979. Length and evolutionary stability of food chains. – Nature 282: 838–839.

Huxham, M., Raffaelli, D. and Pike, A. 1995. Parasites and food web patterns. – J. Anim. Ecol. 64: 168–176.

Jake, M., Zanden, V. and Fetzer, W. W. 2007. Global patterns of aquatic food chain length. – Oikos 116: 1378–1388.

Johnson, S., Domínguez-García, V., Donetti, L. and Muñoz, M. A. 2014. Trophic coherence determines food-web stability. – Proc. Natl Acad. Sci. USA 111: 17923–17928.

Jonsson, T. 2017. Conditions for Eltonian pyramids in Lotka–Volterra food chains. – Sci. Rep. 7: 10912.

Kidd, K. A., Schindler, D. W., Muir, D. C. G., Lockhart, W. L. and Hesslein, R. H. 1995. High concentrations of toxaphene in fishes from a subarctic lake. – Science 269: 240–242.

Kondoh, M. and Ninomiya, K. 2009. Food-chain length and adaptive foraging. – Proc. R. Soc. B 276: 3113–3121.

Layman, C. A., Quattrochi, J. P., Peyer, C. M. and Allgeier, J. E. 2007. Niche width collapse in a resilient top predator following ecosystem fragmentation. – Ecol. Lett. 10: 937–944.

Layman, C. A., Araujo, M. S., Boucek, R., Hammerschlag-Peyer, C. M., Harrison, E., Jud, Z. R., Matich, P., Rosenblatt, A. E., Vaudo, J. J., Yeager, L. A., Post, D. M. and Bearhop, S. 2012. Applying stable isotopes to examine food-web structure: an overview of analytical tools. – Biol. Rev. 87: 545–562.

Liao, J., Chen, J., Ying, Z., Hiebeler, D. E. and Nijs, I. 2016. An extended patch-dynamic framework for food chains in fragmented landscapes. – Sci. Rep. 6: 33100.

Luczkovich, J. J., Borgatti, S. P., Johnson, J. C. and Everett, M. G. 2003. Defining and measuring trophic role similarity in food webs using regular equivalence. – J. Theor. Biol. 220: 303–321.

MacArthur, R. H. and Wilson, E. O. 1967. The theory of island biogeography. – Princeton Univ. Press.

Martinez, N. D. and Lawton, J. H. 1995. Scale and food-web structure: from local to global. – Oikos 73: 148–154.

May, R. M. 1972. Will a large complex system be stable? – Nature 238: 413–414.

McCann, K. S. 2000. The diversity–stability debate. – Nature 405: 228–233.

McHugh, P. A., McIntosh, A. R. and Jellyman, P. G. 2010. Dual influences of ecosystem size and disturbance on food chain length in streams. – Ecol. Lett. 13: 881–890.

Milo, R., Shen-Orr, S., Itzkovitz, S., Kashtan, N., Chklovskii, D. and Alon, U. 2002. Network motifs: simple building blocks of complex networks. – Science 298: 824–827.

Monteiro, A. B. and Faria, L. D. B. 2016. The interplay between population stability and food-web topology predicts the occurrence of motifs in complex food-webs. – J. Theor. Biol. 409: 165–171.

Mougi, A. and Kondoh, M. 2012. Diversity of interaction types and ecological community stability. – Science 337: 349–351.

Neutel, A. M., Heesterbeek, J. A. P., van de Koppel, J., Hoenderboom, G., Vos, A., Kaldeway, C., Berendse, F. and de Ruiter, P. C. 2007. Reconciling complexity with stability in naturally assembling food webs. – Nature 449: 599–602.

Oksanen, L., Fretwell, S. D., Arruda, J. and Niemela, P. 1981. Exploitation ecosystems in gradients of primary productivity. – Am. Nat. 118: 240–261.

Ortega, R., Vindigni, A., Fortuna, M. A. and Bascompte, J., accessed 18 Apr. 2023. Web of life: ecological networks databases. – https://www.web-of-life.es/map.php?type=7.

Otto, S. B., Rall, B. C. and Brose, U. 2007. Allometric degree distributions facilitate food-web stability. – Nature 450: 1226–1229.

Pace, M. L., Cole, J. J., Carpenter, S. R. and Kitchell, J. F. 1999. Trophic cascades revealed in diverse ecosystems. – Trends Ecol. Evol. 14: 483–488.

Pimm, S. L. and Lawton, J. H. 1977. Number of trophic levels in ecological communities. – Nature 268: 329–331.

Pineda-Krch, M. 2008. GillespieSSA: implementing the stochastic simulation algorithm in R. – J. Stat. Softw. 25: 1–18.

Pinheiro, J., Bates, D. and R Core Team. 2023. nlme: linear and nonlinear mixed effects models. – R package ver. 3.1-162, https://CRAN.R-project.org/package=nlme.

Pomeranz, J. P. F., Finlay, J. C. and Terui, A. 2023. Ecosystem size and complexity as extrinsic drivers of food chain length in branching ecosystems. – Ecosphere 14: e4648.

Post, D. M. 2002. The long and short of food-chain length. – Trends Ecol. Evol. 17: 269–277.

Post, D. M. and Takimoto, G. 2007. Proximate structural mechanisms for variation in food-chain length. – Oikos 116: 775–782.

Post, D. M., Pace, M. L. and Hairston, N. G. 2000. Ecosystem size determines food-chain length in lakes. – Nature 405: 1047–1049.

Pringle, R. M. and Hutchinson, M. C. 2020. Resolving food-web structure. – Annu. Rev. Ecol. Evol. Syst. 51: 55–80.

Rossberg, A. G., Matsuda, H., Amemiya, T. and Itoh, K. 2005. An explanatory model for food-web structure and evolution. – Ecol. Compl. 2: 312–321.

Rossberg, A. G., Matsuda, H., Amemiya, T. and Itoh, K. 2006. Food webs: experts consuming families of experts. – J. Theor. Biol. 241: 552–563.

Sabo, J. L., Finlay, J. C. and Post, D. M. 2009. Food chains in freshwaters. – Ann. N. Y. Acad. Sci. 1162: 187–220.

Sabo, J. L., Finlay, J. C., Kennedy, T. and Post, D. M. 2010. The role of discharge variation in scaling of drainage area and food chain length in rivers. – Science 330: 965–967.

Saravia, L. A., Marina, T. I., Kristensen, N. P., De Troch, M. and Momo, F. R. 2022. Ecological network assembly: how the regional metaweb influences local food webs. – J. Anim. Ecol. 91: 630–642.

Shibasaki, S., 2024. ShotaSHIBASAKI/FCL_motif: New release after acceptance (Version ver1). – Zenodo, https://zenodo.org/records/10473889.

Stouffer, D. B. and Bascompte, J. 2010. Understanding food-web persistence from local to global scales. – Ecol. Lett. 13: 154–161.

Stouffer, D. B., Camacho, J., Guimerà, R., Ng, C. A. and Nunes Amaral, L. A. 2005. Quantitative patterns in the structure of model and empirical food webs. – Ecology 86: 1301–1311.

Stouffer, D. B., Camacho, J. and Amaral, L. A. N. 2006. A robust measure of food web intervality. – Proc. Natl Acad. Sci. USA 103: 19015–19020.

Stouffer, D. B., Camacho, J., Jiang, W. and Amaral, L. A. 2007. Evidence for the existence of a robust pattern of prey selection in food webs. – Proc. R. Soc. B 274: 1931–1940.

Sugihara, G., Bersier, L. F. and Schoenly, K. 1997. Effects of taxonomic and trophic aggregation on food web properties. – Oecologia 112: 272–284.

Sullivan, S. M. P., Hossler, K. and Cianfrani, C. M. 2015. Ecosystem structure emerges as a strong determinant of food-chain length in linked stream riparian ecosystems. – Ecosystems 18: 1356–1372.

Taberlet, P., Bonin, A., Zinger, L. and Coissac, E. 2018. Diet analysis. – In: Environmental DNA: for biodiversity research and monitoring, vol. 1. Oxford Univ. Press, pp. 131–139.

Takimoto, G. and Post, D. M. 2013. Environmental determinants of food-chain length: a meta-analysis. – Ecol. Res. 28: 675–681.

Takimoto, G., Spiller, D. A. and Post, D. M. 2008. Ecosystem size, but not disturbance, determines food-chain length on islands of the Bahamas. – Ecology 89: 3001–3007.

Takimoto, G., Post, D. M., Spiller, D. A. and Holt, R. D. 2012. Effects of productivity, disturbance, and ecosystem size on food-chain length: insights from a metacommunity model of intraguild predation. – Ecol. Res. 27: 481–493.

Terui, A. and Nishijima, S. 2019. Spatial disturbance synchrony alters the association of food chain length and ecosystem size. – Ecol. Res. 34: 864–871.

Thébault, E. and Fontaine, C. 2010. Stability of ecological communities and the architecture of mutualistic and trophic networks. – Science 329: 853–856.

Torres, M. Á., Coll, M., Heymans, J. J., Christensen, V. and Sobrino, I. 2013. Food-web structure of and fishing impacts on the Gulf of Cadiz ecosystem (south-western Spain). – Ecol. Modell. 265: 26–44.

Ushio, M., Sado, T., Fukuchi, T., Sasano, S., Masuda, R., Osada, Y. and Miya, M. 2023. Temperature sensitivity of the interspecific interaction strength of coastal marine fish communities. – eLife 12: RP85795.

Vander Zanden, M. J., Shuter, B. J., Lester, N. and Rasmussen, J. B. 1999. Patterns of food chain length in lakes: a stable isotope study. – Am. Nat. 154: 406–416.

Wang, S. and Brose, U. 2018. Biodiversity and ecosystem functioning in food webs: the vertical diversity hypothesis. – Ecol. Lett. 21: 9–20.

Wang, S., Brose, U., van Nouhuys, S., Holt, R. D. and Loreau, M. 2021. Metapopulation capacity determines food chain length in fragmented landscapes. – Proc. Natl Acad. Sci. USA 118: e2102733118.

Ward, C. L. and McCann, K. S. 2017. A mechanistic theory for aquatic food chain length. – Nat. Commun. 8: 2028.

Warfe, D. M., Jardine, T. D., Pettit, N. E., Hamilton, S. K., Pusey, B. J., Bunn, S. E., Davies, P. M. and Douglas, M. M. 2013. Productivity, disturbance and ecosystem size have no influence on food chain length in seasonally connected rivers. – PLoS One 8: e66240.

Williams, R. J. and Martinez, N. D. 2000. Simple rules yield complex food webs. – Nature 404: 180–183.

Winemiller, K. O. 2007. Interplay between scale, resolution, life history and food web properties. – In: Rooney, N., McCann, K. S. and Noakes, D. L. G. (eds), From energetics to ecosystems: the dynamics and structure of ecological systems. Springer Netherlands, pp. 101–126.

Yodzis, P. and Winemiller, K. O. 1999. In search of operational trophospecies in a tropical aquatic food web. – Oikos 87: 327–340.

Young, H. S., Mccauley, D. J., Dunbar, R. B., Hutson, M. S., Ter-Kuile, A. M. and Dirzo, R. 2013. The roles of productivity and ecosystem size in determining food chain length in tropical terrestrial ecosystems. – Ecology 94: 692–701.