Food web complexity modulates environmental impacts on food chain length

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Author contributions

S.S. and A.T. conceived the research, S.S. performed simulations, analyzed data, and wrote the first draft. All authors revise the manuscript.

Data availability

The data and codes used in this manuscript are available from the following repository:
https://github.com/ShotaSHIBASAKI/FCL_motif.

Conflict of interest

The authors declare no conflict of interest.

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Abstract

There have been long-standing debates on the determinants of the food chain length (FCL), a vertical dimension of biodiversity. Previous studies have proposed three environmental factors as putative controls of FCL: resource availability, disturbance, and ecosystem size. However, field studies using stable isotope approaches have produced inconsistent results, suggesting missing links between environmental drivers and FCL. Here, we hypothesized that species richness and motifs (i.e., 3-species subgraphs) modulated environmental effects on FCL. Empirical food webs and our mathematical model of N-species food webs showed that FCL positively correlated with species richness and the 3-species chain motif. Although species richness had a stronger effect on FCL than the chain motif, 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 the current inconsistency among FCL research may be a natural outcome of inherent food web complexity. Considering internal food web structure should deepen our understanding of how FCL changes over environments.

1 Introduction

Food webs have been of ecologist's interest for at least one hundred years (Elton, 1927). The food chain length (FCL) is a crucial aspect of food webs because FCL represents a vertical dimension of biodiversity (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 show, however, 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; McHugh et al., 2010; Sabo et al., 2009, 2010; Takimoto and Post, 2013), resulting in a long-lasting debate on the environmental determinants of FCL.

The controversy on the context dependency implies missing modulators between the environmental drivers and FCL (Fig. 1), and this potential shortcoming may be tied to the common approach in FCL research. Stable isotopes (Layman et al., 2012) have been used for decades 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) because they only require signatures from the "top" (i.e., top predator) and "bottom" (primary producers or consumers) of the food web; the difference between the two approximates the vertical structure of the food web while naturally accounting for the intrinsic complexity of predator-prey interactions (e.g., omnivory). While this simplification allowed us to investigate FCL across systems, it masks the internal food web processes that lead to the emergent relationships between FCL and environmental factors. 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). Such oversimplification limits variations of food web structures. Consequently, our ability to predict FCL in an N-species community is severely compromised. Uncovering the "missing modulator" that is unique to N-species communities should therefore help identify the underlying mechanisms that produce mixed results among empirical studies.

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. 1). Increasing species richness enhances FCL if an inserted species either occupies the higher trophic positions than resident species or increases trophic position of resident top predator(s) (Post and Takimoto, 2007) (but see SI 4 for the analysis of how "species richness" increases FCL in the random graph); however, decades of "diversity-stability" debates (McCann, 2000) 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 (Cirtwill and Wootton, 2022; Stouffer and Bascompte, 2010; Monteiro and Faria, 2016): the three-species chain, the omnivory, the apparent competition, and the exploitative (or direct) competition (see the right middle part of Fig. 1). Notably, these motifs differ in their FCL; the chain motif is longer than the two competition motifs, and the length of the omnivory motif is between the chain and the competition.

In this study, we investigate whether and how species richness 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 (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 non-linear relationship between species richness and FCL. This may explain the inconsistent patterns between the environmental drivers and FCL in previous studies.

2 Methods

2.1 Definitions of species, FCL, and trophic positions

In this study, we operationally use the term "species" as a node in food webs. In empirical food webs, each "species" 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). Each species in our simulations may be better interpreted as trophic species because our model focuses on trophic interactions and does not specify biological traits that define species' boundaries (e.g., reproductive isolation). "Species richness" in this manuscript, therefore, means just the number of nodes 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 *shor* 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. See the top panel of Fig. 1 as an example. We used these three definitions to analyze factors that consistently affect FCL. The main text, however, focuses on the results of FCL mean. See SI 2 for the results with the two rest 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 contains the presence and absence of prey-predator interactions

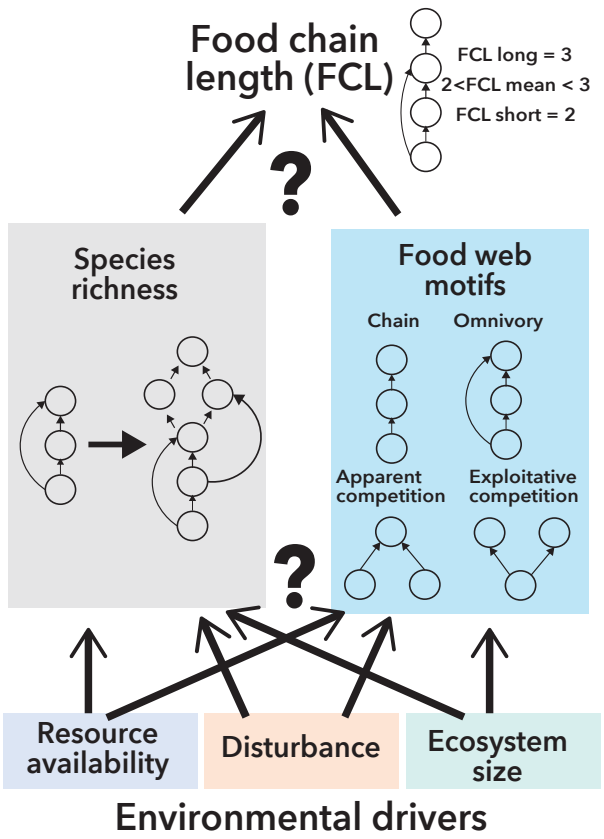

Figure 1: Schematic representations of research questions

We investigate whether and how species richness and food we motifs (3-species chain, omnivory, apparent competition, and exploitative competition) modulate the relationship between the environmental drivers (resource availability, disturbance, and ecosystem size) and food chain length (FCL). FCL is defined in three ways depending on how trophic positions are defined. If trophic levels are defined by the one plus the longest-path length from basal species (FCL long), FCL of the food web on the top panel 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 SI 2 in cases of the rest FCL definitions.

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 mutual predations). See also SI 1.1 for further details on FCL measures.

2.2 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 (Fig. S13). This enables us to calculate FCL, species richness, and the proportion of different three-species motifs in empirical food webs. Our analysis focuses 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). In addition, this result implies that most empirical food webs (203

out of 213) in this study are acyclic, where FCL long can be measured. See also SI 1.2 for more details.

A common issue in the database of Cohen (2010) are (1) the low taxonomic resolution and (2) binary prey-predator interactions. To address this typical issue in the food web database, we analyzed additional 11 food webs obtained from another database in SI 3, where higher taxonomic resolution and quantitative pre-predator information are available.

2.3 Mathematical model

2.3.1 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 enables 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 (Allesina et al., 2008; Caldarelli et al., 1998; Cattin et al., 2004; Cohen and Newman, 1985; Kondoh and Ninomiya, 2009; Rossberg et al., 2005, 2006; Stouffer et al., 2005, 2006; Williams and Martinez, 2000). 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 2.1, 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 pre-determines the number of basal species in a food web. Although (generalized) cascade models (Cohen and Newman, 1985; Stouffer et al., 2005) also generate acyclic food webs, we cannot fix the number of basal species in these models. The number of basal species may change FCL short and long because trophic positions are measured by the path length from basal species. Thirdly, the preferential prey model can generate N-species food chain. Finally, the modified preferential prey model generates food webs guven the definition of trophic positions (see below). 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. For these reasons, we used the preferential prey model to generate food webs.

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 larger than previous models (Pimm and Lawton, 1977; Hastings, 1979; Polis, 1991; Takimoto et al., 2012; Ward and McCann, 2017) yet computational costs of stochastic simulations (see below) 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 $l/N^2 \approx 0.11$, which is

the average connectance of empirical food webs (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 ($T \to 0$ represents species i consumes only species whose trophic positions are identical to species j, while $T \to \infty$ represents species i choose prey species regardless of prey's trophic positions). We set $T = 1$ in this study. 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.

2.3.2 Stochastic simulations of the ecological dynamics

Although the preferential prey model generates N-species food webs, the coexistence of N-species is not guaranteed. In other words, ecologically realized food webs would be subgraphs of the N-species food web. Hereafter, species richness and fractions of food web motifs in our simulations refer to those in realized food webs, not in 32-species food webs generated by the modified preferential prey model. 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.

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:

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

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 ($B + 1 \leq i \leq N$), on the other hand, the colonization rate depends on the presence of prey species:

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

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 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 maximum colonization rates (a_i and b_i) reflect the ecosystem size because species would migrate more frequently into a larger patch than a smaller one (i.e., the target effect).

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 (SI 5) suggest that resource availability showed no correlations. Although species would differ in their parameter values 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 food web and a parameter set. In total, we analyzed 30 food webs $\times 20$ replicates $\times 72$ parameter sets $= 43200$ data in each definition of FCL.

The stochastic dynamics were implemented by Gillespie algorithm using GillespieSSA library (Pineda-Krch, 2008) version 0.6.2 in R version 4.2.1 (R Core Team, 2022). 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 $1,000$.

After removing species with no prey from the realized food webs at the end of the simulations, FCL was measured as SI 1.1 explains, and the fractions of 13 motifs were calculated using igraph library (Csardi and

Nepusz, 2006) version 1.3.5 in R. If all species go extinct, we regard FCL as -1 because FCL is zero when only basal species exist.

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	$\in \{0.25, 0.5, 0.75, \ldots, 2.0\}$	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	$\in \{0.1, 0.2, 0.3, \ldots, 0.9\}$	Extinction rate because of disturbances
h_j $(j = 1, 2, 3)$	1	Hill coefficients to determine the forms of functions.

2.4 Statistical analysis

In the regression analysis of how species richness and the fraction of the 3-species chain motif affects FCL (see Results), we assumed these two variables have either of the following three functional responses: linear, saturating, or quadratic. In total, we generated fifteen regression models: either species richness or the fraction of the chain motif, or both affect FCL in either of the three functional responses (i.e., $2 \times 3 + 3 \times 3 = 15$ models), respectively. The three functional forms are written as below:

$$\text{FCL} \sim ax - 1, \tag{5a}$$

$$\text{FCL} \sim a\{1 - \exp(-bx)\} - 1, \tag{5b}$$

$$\text{FCL} \sim -ax^2 + bx - 1 \tag{5c}$$

where x is either 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 species richness or chain (see Figs. S1 and S2). The constant terms of the three models are fixed as -1 given our definition of FCL (see Subsection 2.3.2). In the saturating functional response (Eq (5b)), parameter a controls how much x (i.e., either species richness or chain motifs) increases FCL because FCL converges to $a - 1$ in the limit of $x \to \infty$. In the quadratic function (Eq (5c)), the maximum increase of FCL by x is either $b^2/(4a)$ (if $b < 2a$) or $-a + b$ (otherwise).

We used nls() function with algorithm "port" in R to fit these models to the data from either the empirical database or our simulations of each definition of FCL, respectively. The lower boundaries of the coefficients were set zeros, 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). We chose the best models by calculating Akaike Information Criterion (AIC) of the regression models using AIC() function in R in each data. See Tables S3 - S8 for the ΔAIC and

Table 2 for the best models and the coefficient values.

The linear quantile regression analysis shown in Table 3 was performed by the quantreg package (Koenker, 2022) version 5.94 in R.

3 Results

3.1 Species richness non-linearly increases FCL

We first investigated whether species richness and food web motifs correlated with FCL to identify candidates for internal modulators. Species richness and three-species chain motif positively correlated with FCL in all three definitions (Figs. S1A-F). The two competition motifs (i.e., apparent competition and exploitative competition), on the other hand, negatively or non-significantly correlated with FCL (Figs. S1J-O). The correlations between FCL and the omnivory motif depended on the definition of trophic positions. Although omnivory increased FCL long (Figs. S1G), the correlation was weaker or non-significant with FCL mean (Figs. S1H) or short (Figs. S1I). These patterns were replicated in our simulated food webs (Fig. S2). The correlative analysis suggests that species richness and the chain motif may play key roles in modulating the environment–FCL relationships.

The functional forms between FCL and internal food web structures (species richness and motifs) determine how environments dictate FCL. From Figs. S1 and S2, we hypothesized three functional responses: linear, saturating, and quadratic functions. The best models (Table 2, see also Figs. S3 and S5 for FCL long and short, respectively) described the effect of species richness in the saturating functions both in empirical data and our simulations (Figs. 2A and B). This indicates that FCL changed disproportionately at low species richness with little changes at high species richness. The saturating functional response may be maintained in broad networks; it appeared in baseline models without species assembly (SI 4). In the meantime, linear or quadratic models were selected as the best models for describing the functional relationships between FCL and the fraction of the chain motifs (Figs. 2C and D).

The coefficients of best models indicated that species richness had larger maximum effects on FCL than chain motif;i.e., the coefficient a in Eq (5b) for species richness ranged from 2.85 to 6.76 while the maximum increase in FCL due to the chain motifs ranged from 1.42 to 3.06. However, species richness little increased FCL at high species richness because of the saturating function. If the fraction of chain motifs independently changes in species-rich food webs, the chain motifs may have a disproportionate influence on FCL. To explore this possibility, we delved into how the fractions of the food web motifs changed over species richness. At high species richness, the fraction of chain motif was lower than expected in random graphs (the expected value $\pm 2 \times$ expected standard deviation (ESD) in the random graphs) with no ecological rules in species assembly (Figs. 2E and F). In the random graph, the expected fractions of the motifs were constant but their ESD decreased over species richness (see SI 4 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 species richness from low to

intermediate levels.

In SI 3, we repeated our analysis with empirical food webs with higher resolution. Although the amount of such food web data was small (11 food webs), species richness positively correlated with FCL, and the saturating functional response of species richness predicted empirical FCL.

Table 2: Equations of the best models

Data	Equations
Empirical FCL long	$\mathrm{FCL} = 3.94 \times \{1 - \exp(-0.09 \times \mathrm{richness})\} - 7.3 \times \mathrm{chain}^2 + 9.45 \times \mathrm{chain} - 1$
Empirical FCL mean	$\mathrm{FCL} = 3.01 \times \{1 - \exp(-0.14 \times \mathrm{richness})\} - 2.82 \times \mathrm{chain}^2 + 4.92 \times \mathrm{chain} - 1$
Empirical FCL short	$\mathrm{FCL} = 2.85 \times \{1 - \exp(-0.19 \times \mathrm{richness})\} + 2.12 \times \mathrm{chain} - 1$
Simulated FCL long	$\mathrm{FCL} = 6.76 \times \{1 - \exp(-0.08 \times \mathrm{richness})\} - 1.58 \times \mathrm{chain}^2 + 3.13 \times \mathrm{chain} - 1$
Simulated FCL mean	$\mathrm{FCL} = 3.78 \times \{1 - \exp(-0.17 \times \mathrm{richness})\} - 1.00 \times \mathrm{chain}^2 + 2.53 \times \mathrm{chain} - 1$
Simulated FCL short	$\mathrm{FCL} = 2.95 \times \{1 - \exp(-0.25 \times \mathrm{richness})\} - 0.60 \times \mathrm{chain}^2 + 2.02 \times \mathrm{chain} - 1$

3.2 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 SI 5 for the analysis including resource availability). Consistent with the previous theory, small and frequently-disturbed ecosystems were unable to maintain long food chains (Fig. 3A). However, our theoretical prediction is unique because the effect of disturbance/ecosystem size was contingent on each other. For example, disturbance strongly regulated FCL in small ecosystems, but such disturbance-induced regulation was not observed in large ecosystems (Fig. 3C, and first and second rows in Table 3). Similarly, enlarging ecosystem size resulted in enhancing FCL under strong disturbance but such increase in FCL was smaller under weak disturbance (Fig. 3E, and third and fourth rows in Table 3).

The non-linear FCL-richness association underlay the emergent dual regulation of FCL. As expected, species richness decreased over disturbance while increased over ecosystem size (Fig. 3B). In contrast to the pattern of FCL, disturbance regulated species richness regardless of the ecosystem size, and vice versa (Figs. 3 D and F). The decoupling of FCL and richness patterns over environmental gradients can be explained by the saturating form of the FCL-richness relationship. For example, when species richness exceeded 15, changes in species richness did not translate into FCL changes due to the saturating functional response. Thus, species richness modulated how disturbance and ecosystem size affected FCL. These patterns were consistent regardless of the definition of FCL (Fig. S4).

Table 3: Linear quantile regression of median FCL mean

Data	Coefficient of disturbance	Coefficient of ecosystem size
Disturbance $\in [0.1, 0.3] \mid$ ecosystem size $= 0.5$	-3.33 ± 0.45	N.A.
Disturbance $\in [0.1, 0.3] \mid$ ecosystem size $= 2.0$	-0.82 ± 0.17	N.A.
Ecosystem size $\in [1.5, 2.0] \mid$ disturbance $= 0.1$	N.A.	0.33 ± 0.07
Ecosystem size $\in [1.5, 2.0] \mid$ disturbance $= 0.8$	N.A.	1.00 ± 0.18

The coefficient values show mean $\pm$ standard error. See also Fig. 3.

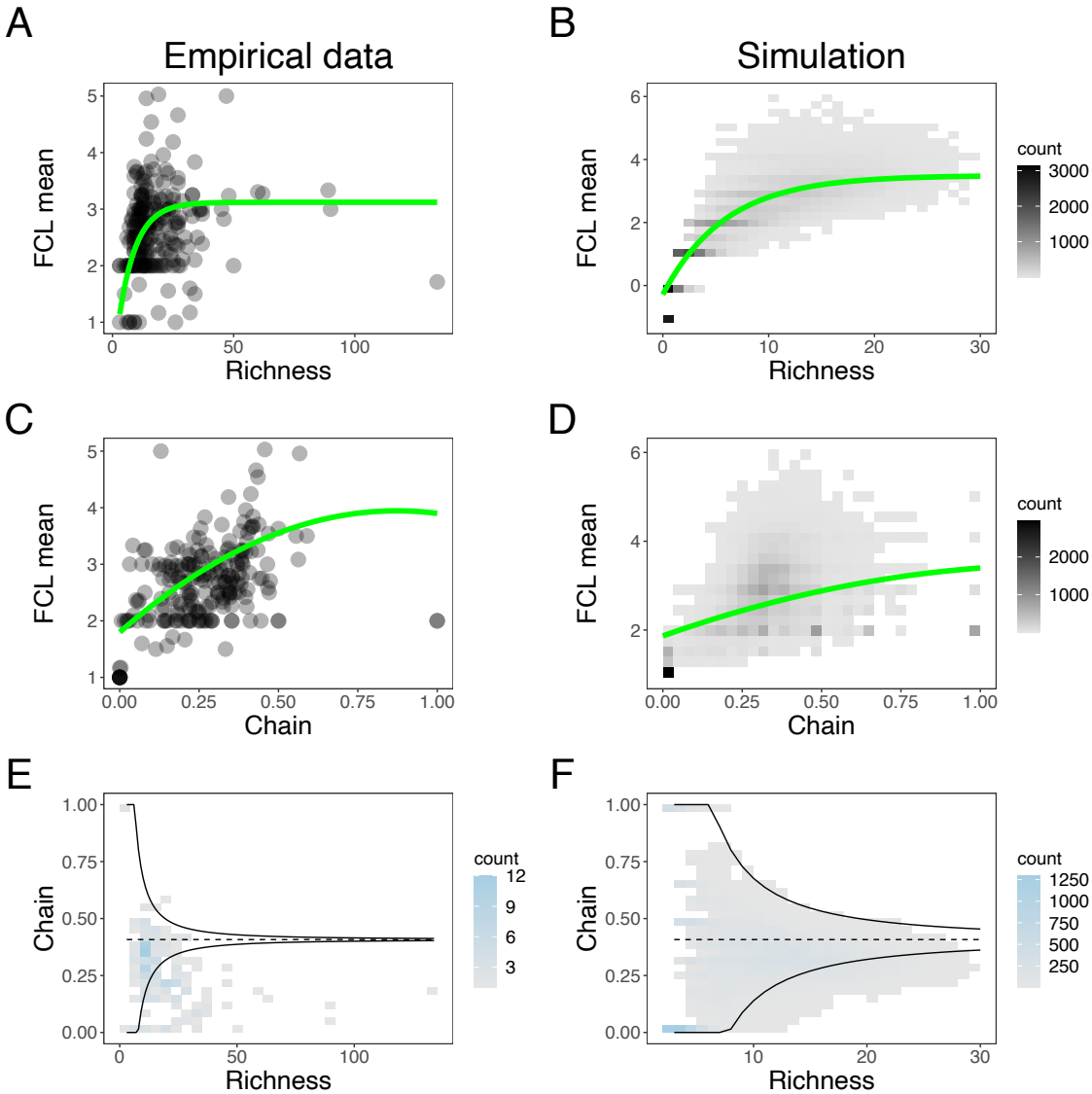

Figure 2: Species richness and the chain motifs relate to FCL

Relationships among species richness, the fraction of the three-species chain motifs, and FCL mean are shown (left: empirical data, right: our simulation data). A and B: species richness had saturating effects on FCL. The green curves represent the best models (Table 2) while fixing the fraction of the chain motif as the mean value. C and D: the fraction of the chain motif had quadratic effects on FCL. Similarly, the green curves represent the best models (Table 2) while fixing species richness as its mean value. E and F: The fractions of the chain motifs over 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 $\pm 2 \times$ ESD in the random graph. See SI 4 for more mathematical details.

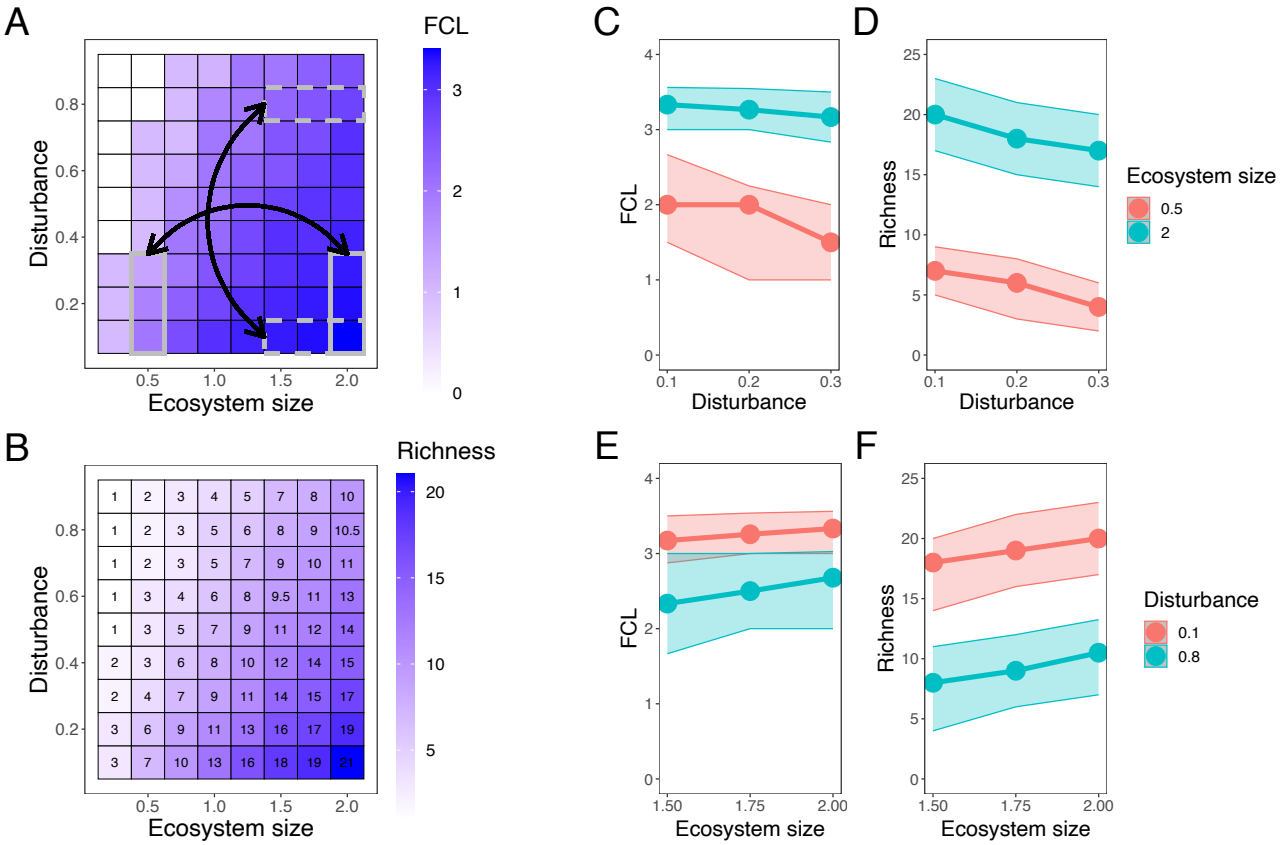

Figure 3: Species richness modulates environmental effect on FCL

A-B: Median values of FCL mean (A) and species richness (B) in our simulations over two environmental factors (disturbance and ecosystem size) are shown. On the one hand, species richness consistently decreased over disturbance but increased over ecosystem size; see also panels D and F. On the other hand, the two environmental drivers little affected FCL at high species richness (i.e., weak disturbance and large ecosystem size). The boxes in panel A represent FCL in panels C (the solid-line boxes) and E (the dashed-line boxes). C-F: Distributions of FCL (C and E) and species richness (D and F) are shown. The lines represent median values and the shaded areas show 25 % - 75% quantile. The environmental effects on FCL are clear when species richness was low (< 15); at high species richness, however, FCL was robust against the changes in the environments. C and D: Disturbance little changed FCL in a large ecosystem (cyan) while it decreased FCL in a smaller ecosystem (red). E and F: Ecosystem size little affected FCL under weak disturbance (red) while it increased FCL under strong disturbance (cyan). See Table 3 for the quantile regression analysis on panels C and E.

4 Discussion

Our mechanistic exploration highlighted the innate complexity of FCL responses to environmental drivers, offering the potential explanation for the mixed results in previous studies (Sabo et al., 2009, 2010; Takimoto and Post, 2013). In particular, the effects of ecosystem size and disturbance were contingent on each other; this context-dependency emerged as a result of the non-linear relationship between FCL and species richness (Figs. 3A and B, and S11), a pattern that we confirmed with empirical food web data. A three-species metacommunity model also predicts interactive effects of ecosystem size and disturbance (Terui and Nishijima, 2019). However, the present study is unique because our model predicted a similar FCL response within a local habitat by considering realistic N-species food webs. In other words, this alternative mechanism arose purely from the internal food web attributes. Therefore, the long-lasting puzzle of FCL controls may be a natural outcome of complex food webs.

The mutual dependence of ecosystem size and disturbance in regulating FCL may help reconcile the inconsistent results in previous studies. In Sabo et al. (2009), seven studies show negative correlations between FCL and disturbance, while six show non-significant correlations. Similarly, a meta-analysis revealed that ecosystem size effects are highly variable among studies (Takimoto and Post, 2013). More recent studies reported non-significant effects of ecosystem size in aquatic (Warfe et al., 2013) and terrestrial ecosystems (Young et al., 2013). Our simulation suggests that mixed results may naturally emerge from the interactive nature of multiple environmental drivers. For example, FCLs in small and large ecosystems may show distinctive responses to disturbance gradients due to their difference in vulnerability to a disturbance (Fig. 3C). Similarly, the FCL response to ecosystem size gradients may differ under strong or weak disturbance regimes (Fig. 3E). While it is increasingly recognized that FCLs are determined by multiple environmental drivers, empirical FCL research often treats them as "independent" factors. In light of our model predictions, the reported variation in disturbance and ecosystem size effects (Takimoto and Post, 2013) may be better addressed by considering their reciprocal contingency.

The lack of resource effects may seem counterintuitive (Fig. S11) 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). However, the comparison of our model with previous studies suggests that population abundance is critical in observing the effects of resource availability on FCL. For instance, Kondoh and Ninomiya (2009) analyzed acyclic N-species food webs as we did, but their model implemented the dynamics of population abundances. Unlike our presence-absence model, Kondoh and Ninomiya (2009) showed a positive association between FCL and resource availability. Although our stochastic model was designed to allow for direct comparisons with available empirical food web data, future studies may better incorporate species abundances to capture the importance of resource availability.

Like any theoretical research, our results must be viewed with some caution. First, our results might be a unique attribute of the 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 graph

and cascade models (Cohen and Newman, 1985) (see SI 4). Thus, this saturating response of FCL to 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 (SI 3), which 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 "vertical" 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. This may explain why the effect of species richness was saturated at high levels (Fig. 2). Among the food web motifs, the chain motif is distinctive because species within the chain motif occupy broader trophic positions than others (see Fig. S14 and Table S9). Increasing chain motifs means that species occupy open and higher trophic positions, resulting in longer FCL. However, Figs. 2E and F indicate 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 (Figs. 2 A-D). Although current methods in FCL research (e.g., stable isotopes) treat internal food web structure as a "black box," emergent techniques, such the diet meta-barcoding (see recent review by Pringle and Hutchinson (2020)), enable us to yield highly-resolved predator-prey interactions in the field. Leveraging such recent technological advancement may provide means to test our hypothesis and will help synthesize FCL research and the diversity-stability debate.

In conclusion, this manuscript shed light on species richness as a hidden but main modulator between the environmental drivers and FCL. Our analysis indicates that species richness and, to a lesser extent, three-species chain motifs are internal modulators in food webs. Because of their differences in functional responses, the effect of species richness is dominant. The non-linear effect of species richness on FCL generates the contingent effects of the environmental drivers, which would explain the inconsistent results on FCL in previous studies. The less dominant effect of the chain motif may suggest that expanding the vertical dimension of diversity may destabilize

food webs more than the horizontal dimension. Future studies, therefore, need to assess how environmental conditions affect the internal properties of food webs as well as FCL.

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