

# Toward the comprehensive understanding of food chain length

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## Abstract

1. Food chain length (FCL), roughly defined by the number of trophic links, is one important aspect of biodiversity. However, studies on FCL are limited to simple food webs (e.g., only three or four species in a community) or simple hypotheses (i.e., what is a determinant of FCL?)
2. In this review, we propose research directions to comprehensively understand how multiple environmental factors affect FCL using food webs as complex as natural ones. To facilitate these research directions, we first introduce basic ideas of graph theory. Graph theory clarifies the requirements of food webs in the analysis of FCL and methods to calculate FCL.
3. We recommend using only directed acyclic graphs in studies of FCL because some definitions of FCL cannot be used in cyclic food webs. Within more than ten models that generate food webs as complex as in nature, a part of them generates only acyclic food webs. Such models include the (generalized) cascade model and the preferential prey model. In contrast, the (generalized) niche model and the nested hierarchy model can generate cyclic food webs, and they are not appropriate in the studies of FCL.
4. We then discuss how we can study the interdependent effects of the multiple environmental factors on FCL while using models that generate complex acyclic food webs. In addition, we propose research questions that would enrich our understanding of FCL.

Keywords: food chain length, food web, graph theory, theoretical ecology

# 1 Introduction

A central question in ecology is why many interacting species coexist in nature. Historically, researchers considered complex communities (i.e., communities with more species and/or more interactions) were more stable than simple ones (MacArthur, 1955). However, two theoretical studies in the 1970s show that it is not the case when random pairwise species interactions are assumed (Gardner and Ashby, 1970; May, 1972). Since then, ecologists have proposed and investigated mechanisms that allow high biodiversity in nature. Such mechanisms include, but are not limited to, non-random species interactions (Mougi and Kondoh, 2012), higher order (i.e., more than pairwise) interactions (Bairey et al., 2016), environmental fluctuations (Letten et al., 2018), and spatial structures (Tilman, 1994).

Biodiversity is a multidimensional entity characterized by horizontal and vertical axes (Wang and Brose, 2018). “Horizontal” biodiversity focuses on the coexistence of species competing for resources. For example, the competitive exclusion principle refers to the idea that species occupying the identical niche cannot coexist (Gause, 1934; Hardin, 1960). The modern coexistence theory (Chesson, 2000) has clarified that niche and fitness differences determine the coexistence of competing species (Letten et al., 2017; Godwin et al., 2020). In general, the number of competing species to coexist at equilibrium is restricted by the number of limiting factors (Levin, 1970): e.g., available resources, temperature, and predator. Meanwhile, our understanding of the “vertical” biodiversity lags behind the horizontal diversity in sense of the constraints. Vertical biodiversity comprises prey-predator interactions and considers species’ trophic levels in a food web, a network representing which species consume which species (Elton, 1927). Food chain length (FCL), roughly defined by the maximum number of trophic links from basal species to top predators (but see Section 4 for detailed definitions), is a summary statistics of the vertical biodiversity. Because of inefficient energy transfer from prey to predator (Pauly and Christensen, 1995), FCL cannot infinitely increase. Ecologists have investigated what generates the variations of FCL in nature. A critical problem is, however, that mathematical models and experiments in the studies of FCL analyzed only simpler food webs than those in nature. For example, some studies assume only food chains (Liao et al., 2016; Jonsson, 2017; Terui and Nishijima, 2019; Wang et al., 2021), although we can measure FCL in other food webs. In other studies, there are only three or four species in an experimental system (Diehl and Feissel, 2001; Doi and Hillebrand, 2019) or a mathematical model (Pimm and Lawton, 1977; Hastings, 1979; Takimoto et al., 2012; Ward and McCann, 2017). Polis (1991) investigated up to eight-species communities but analyzed the limited topology of food webs.

The lack of appropriate frameworks for complex food webs seems to lead to controversial debates on what controls FCL in natural systems. Three factors have been proposed as determinants of FCL: resource availability (Oksanen et al., 1981), disturbances in a community (Pimm and Lawton, 1977), and ecosystem sizes (Post et al., 2000a). Researchers have investigated whether each of the three restricts FCL or not, but several studies and meta-analyses show contradicting results (Briand and Cohen, 1987; Jake et al., 2007; Takimoto et al., 2008; McHugh et al., 2010; Sabo et al., 2009, 2010; Takimoto and Post, 2013). This contradiction may come from the fact that the three factors interdependently affect FCL (Post, 2002). For example, Ward and McCann (2017)

37 show that ecosystem size and resource availability affect the magnitudes that the other parameter changes FCL,  
38 respectively. Therefore, we need to consider in what condition resource availability, disturbances, and ecosystem  
39 sizes have dominant effects on FCL, rather than each of which is a general determinant.

40 In this review, we argue that some mathematical models (or algorithms) used in food webs studies can  
41 overcome the two problems in the studies on FCL. These models can generate food webs as complex as empirical  
42 ones, but they have not been used to investigate FCL. In section 2, we first introduce the terminology in graph  
43 theory. This helps us to clarify what kinds of characteristics a food web should satisfy in the analysis of FCL, and  
44 how to measure FCL. Section 3 reviews more than ten models that generate a variety of complex food webs,  
45 and we show which can be used for investigating how the three factors affect FCL. Section 4 shows various  
46 definitions of FCL and how to calculate them using algorithms in graph theory. In section 5, we discuss how to  
47 include the effects of resource availability, disturbances, and ecosystem sizes on FCL in food webs generated by  
48 models in Section 3. We also propose some research questions that could expand our understanding of FCL.

## 49 2 Requirements for food web as graph

50 In analyzing FCL, we first need to obtain a graph or network representing a food web. In a food web, each  
51 node represents species, and each edge (or arc) between a pair of species represents a prey-predator interaction.  
52 Because one of the pair is a prey species and the other is a predator species, the edge should have a direction  
53 from the prey to the predator: the food web should be a digraph (Bang-Jensen and Gutin, 2009). We also  
54 argue that the analysis of FCL requires acyclic food webs because some definitions of FCL are not applicable  
55 to cyclic food webs (see Section 4). A graph is called acyclic when it does not have any cycles (i.e., from node  
56  $x$ , we cannot go back to node  $x$  through finite edges).

57 A food web for analyzing FCL should be, therefore, a directed acyclic graph (DAG). Whether a food web  
58 is a DAG or not is investigated by a simple and linear-time algorithm (Cormen et al., 2009a; Erickson, 2019).  
59 We would like to emphasize that we do not argue that all food webs are acyclic in nature. For example, one of  
60 213 food webs (named WEB21) in Cohen’s database (Cohen, 2010) is cyclic. Another cyclic food web can be  
61 found in Fig. 5 of Polis (1991). However, some definitions of FCL are used only if a food web is a DAG while  
62 other definitions can be used in acyclic food webs and a part of cyclic food webs. For these reasons, we focus  
63 on acyclic food webs in this review.

64 Ecologically speaking, a food web that is a DAG does not include cannibalism, mutual predation between  
65 a pair of species, or a cycle of predation composed of three or more species (Figs. 1A-C). The last condition  
66 indicates that we ignore decomposers (or “predation” by decomposers) in the analysis of FCL (Cohen and  
67 Newman, 1985). In addition, graph theory indicates that every directed acyclic food web should have one or  
68 more species that do not eat or are not eaten by any other species, respectively (Bang-Jensen and Gutin, 2009;  
69 Erickson, 2019): they are called basal species and top predators in ecology. These species are keys to calculating  
70 FCL in a given food web.

71 A topology of a food web composed of  $N$  species can be summarized in an  $N \times N$  adjacency matrix  $A = (a_{ij})$ .

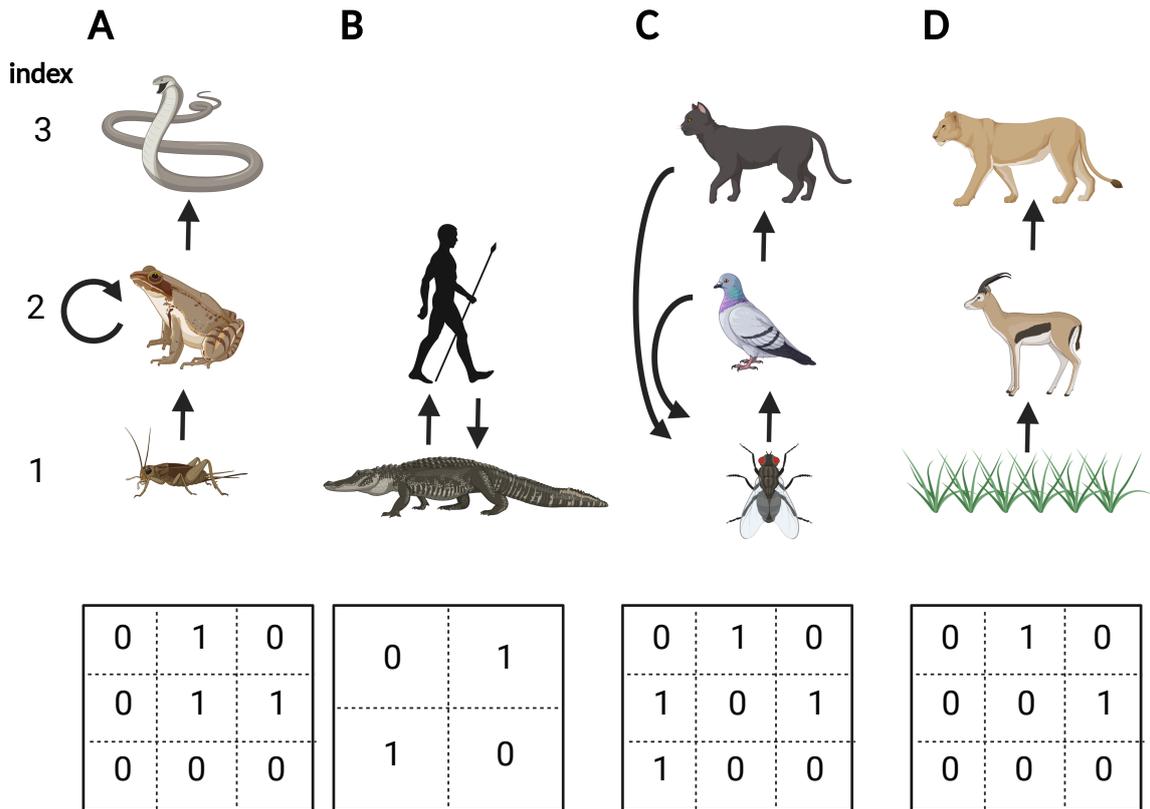


Figure 1: Examples of food web

In each panel, the top part represents a schematic food web and the bottom part shows a corresponding adjacency matrix. In panels from A to C, the food webs are cyclic because the frog performs cannibalism (A), the human and the alligator predate each other (B), and the decomposer fly is included (C). We do not focus on these food webs in this review. Panel D, on the other hand, represents a food chain and thus a DAG. Created with BioRender.com.

72 We use  $a_{ij} = 1$  when species  $i$  is eaten by species  $j$  while  $a_{ij} = 0$  indicates species  $j$  does not eat species  $i$ . An  
73 adjacency matrix is different from a species interaction matrix used in some theoretical studies of prey-predator  
74 dynamics (Lotka, 1910; Pimm and Lawton, 1977, 1978; Banerjee and Takeuchi, 2017; Mougi, 2022). A species  
75 interaction matrix shows how species affect the growth of others: an element of a species interaction matrix can  
76 be negative. In contrast, as explained above, an element of an adjacency matrix is either zero or one.

77 In general, an adjacency matrix of DAG should be a strictly upper triangular matrix ( $a_{ij} \geq 0$  if  $i < j$ ,  
78 otherwise  $a_{ij} = 0$ ) after ordering the species indices properly. A clear example of DAG is a food chain. This  
79 type of food web has a unique basal species and top predator, respectively, and each of the reset species has  
80 single prey and predator species, respectively. Mathematically, an adjacency matrix of a food chain is given as  
81 follows:

$$a_{ij} = \begin{cases} 1 & \text{if } j = i + 1 \quad (i, j = 1, \dots, N), \\ 0 & \text{otherwise.} \end{cases} \quad (1)$$

82 As shown by the bottom panel of Fig. 1D, an adjacency matrix of a food chain is strictly upper triangular.

83 An adjacency matrix also tells us the number of prey and predator species (called the in-degree and out-  
84 degree in graph theory) for each species. We denote  $D^-(i)$  and  $D^+(i)$  as the number of prey and predator  
85 species of focal species  $i$ , respectively. In a directed acyclic food web,

$$D^-(i) \equiv \sum_{j=1}^{i-1} a_{ji}, \quad (2)$$

$$D^+(i) \equiv \sum_{j=i+1}^N a_{ij} \quad (3)$$

86 after sorting the indexes of species so that the adjacency matrix is strictly upper-triangular. For example, basal  
87 species and top predators should satisfy  $D^-(i) = 0$  and  $D^+(i) = 0$ , respectively.

88 We assume that a  $N$ -species food web has no isolated species in this review. In other words, for  $i = 1, \dots, N$ ,  
89 species  $i$  should have at least one prey or predator species:

$$D^+(i) + D^-(i) \geq 1, \quad (i = 1, \dots, N). \quad (4)$$

90 As an isolated species does not have either prey or predator species, such species can be regarded as a basal  
91 species and a top predator at the same time. Then, an isolated species makes us underestimate FCL when we  
92 use a certain definition of FCL (see Section 4.3). This is why we assume no isolated species in this review. If  
93 such species exist in a food web, we remove them and redefine the number of species in the food web.

### 94 **3 Models generating complex food webs**

95 Table 1 shows the models (or algorithms) we reviewed in this manuscript. These models were proposed to  
96 mimic complex natural food webs. We focus on two features of each algorithm: (i) whether an algorithm always  
97 generates DAG or not, and (ii) whether a food web is statically or dynamically generated. In this section, we  
98 classify a model as one that generates acyclic food webs even when the original model proposed in the literature  
99 allows cannibalism. This is because we can easily modify the algorithms so that cannibalism would not occur.  
100 As mentioned in the previous section, algorithms that generate DAG are appropriate in studies of FCL. In  
101 the static algorithms, adjacency matrices are generated by some simple rules, while the dynamic algorithms  
102 generate food webs through meta-community or evolutionary dynamics.

Table 1: List of algorithms generating food webs

Model and source	Acyclic	Static	Description
Random model	✓	✓	An adjacency matrix is randomly filled with a constant probability.
Cascade model ( <a href="#">Cohen and Newman, 1985</a> )	✓	✓	An upper-right part of an adjacency matrix is filled with a constant probability.
Generalized cascade model ( <a href="#">Stouffer et al., 2005</a> )	✓	✓	An upper-right part of an adjacency matrix is filled with predator-specific probabilities.
<a href="#">Kondoh and Ninomiya (2009)</a>	✓	✓	Pre-determine the number of basal species $B$ , but unable to generate food chains.
Preferential preying model ( <a href="#">Johnson et al., 2014</a> )	✓	✓	Pre-determine the number of basal species $B$ , and able to generate food chains.
Niche model ( <a href="#">Williams and Martinez, 2000</a> )	✓	✓	Prey-predator interactions are given by species' niche values.
Generalized niche model ( <a href="#">Stouffer et al., 2006</a> )	✓	✓	Mixture of the generalized cascade model and the niche model.
Nested hierarchy model ( <a href="#">Cattin et al., 2004</a> )	✓	✓	Introduce the phylogenetic constraint of niche.
Minimal potential niche model ( <a href="#">Allesina et al., 2008</a> )	✓ if $c = 0$	✓	Introduce forbidden links into the niche model.
Webworld model ( <a href="#">Caldarelli et al., 1998</a> )		✓	Evolution of food webs with explicit species features. Cycles can have a length of $\geq 3$ .
Speciation model ( <a href="#">Rossberg et al., 2005</a> )	✓ if $\lambda = 0$		Evolution of a food web based only on species' evolutionary rates.
Matching model ( <a href="#">Rossberg et al., 2006</a> )	✓ if $\lambda = 0$		Similar to the speciation model, but with explicit traits for prey-predator interactions.
<a href="#">Loeuille and Loreau (2005)</a>	✓ (in food web)		Competitions other than resource competition are implemented.
Expansions of the theory of island biogeography ( <a href="#">Gravel et al., 2011</a> ; <a href="#">Saravia et al., 2022</a> )	✓ (if a regional food web is acyclic)		A local food web is assembled by colonization and extinction, while the regional food web determines trophic interactions.
Expansions of the patch dynamics ( <a href="#">Pillai et al., 2010</a> ; <a href="#">Wang et al., 2021</a> )	✓ (only food chains)		Fractions of patches where focal species exist or focal interactions occur are modeled.

### 103 3.1 Static models

104 In the static models, a food web is generated with some stochastic processes. Because many studies of food  
105 webs analyze connectance  $C \equiv \sum_{i,j}^N a_{ij}/N^2$  (Dunne et al., 2002a,b; Rall et al., 2008), these models typically  
106 generate many food webs given connectance and then compare some statistical properties of empirical food  
107 webs and simulated ones.

#### 108 3.1.1 Random model

109 The *random model* is a null model. In this model, each element of  $N \times N$  adjacency matrix is one with  
110 the probability of connectance  $C$  (otherwise  $a_{ij}=0$ ). Obviously, this algorithm can generate cycles and is not  
111 appropriate for the analysis of FCL. In Cohen and Newman (1985), for example, about 82 % of webs generated  
112 by this algorithm were cyclic after tuning parameters from empirical data.

#### 113 3.1.2 Cascade models

114 A simple way to generate acyclic food webs was proposed by Cohen and Newman (1985). This model, called the  
115 *cascade model* (Fig. 2A), assumes ranks of species: a species with a lower rank never eats higher rank species  
116 while species with a higher rank can predate lower rank species with a constant probability. Such ranks may be  
117 given by body sizes (Warren and Lawton, 1987): predators tend to be larger than their prey species. Without  
118 loss of generality, we assume that the species indices are sorted following such ranks. Then, the probability that  
119 species  $j$  predate species  $i$  ( $a_{ij} = 1$ ) is given by the following equation:

$$\text{Prob}(a_{ij} = 1) = \begin{cases} 0 & (\text{if } i \geq j) \\ \frac{2C}{N(N-1)} & (\text{otherwise}) \end{cases} . \quad (5)$$

120 As the cascade model always generates a strictly upper triangular adjacency matrix, all food webs generated in  
121 this algorithm are DAGs and appropriate for analyzing FCL.

122 However, the cascade model has been challenged because the model does not fit the empirical data and/or  
123 the assumption of constant predation probability seems violated in nature (Solow, 1996; Williams and Martinez,  
124 2000; Neubert et al., 2000). To overcome this problem, Stouffer et al. (2005) proposed the *generalized cascade*  
125 *model*, where species  $i$  can eat lower rank species with species-specific probability  $x_i \in [0, 1]$  drawn from the  
126 beta or exponential distributions. Stouffer et al. (2005) also revealed that the generalized cascade model show  
127 probability distributions of numbers of preys, predators, and trophic links similar to the niche model, which  
128 fits these patterns of empirical data (Camacho et al., 2002a,b): see Section 3.1.4 for more details of the niche  
129 model.

#### 130 3.1.3 Models tuning the number of basal species

131 The random and the (generalized) cascade models do not determine the number of basal species. Because basal  
132 species are important to measure FCL, we may want to tune the number of basal species while generating only

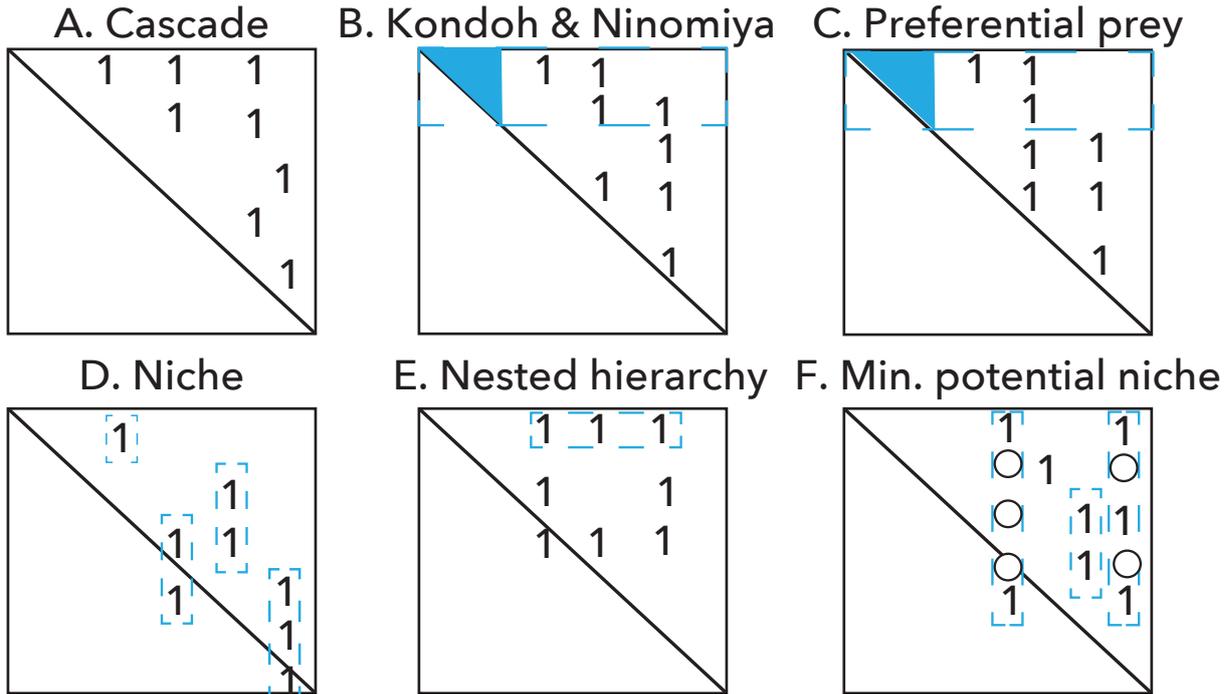


Figure 2: Schematic representations of static models' adjacency matrices

A: The (generalized) cascade model (Cohen and Newman, 1985) fills each upper element of the adjacency matrix with a certain probability. B: The model proposed by Kondoh and Ninomiya (2009) assumes that the basal species that do not predate any species (filled area) and that each non-basal species predate at least one basal species (the blue rectangle). C: The preferential prey model (Johnson et al., 2014) also assumes the basal species, but non-basal species may not predate basal species. D: The niche model (Williams and Martinez, 2000) assumes that each predator species has no gap in its prey's niche value (the blue rectangle). E: The nested hierarchy model assumes the phylogenetic constraints on the prey. As the three species predate species 1 (the blue rectangle), these species also share other prey species. F: The minimal potential niche model allows the gaps in the prey's niche value (the circles in the blue rectangles). A–C always generate strictly upper-triangle adjacency matrices (i.e., acyclic food webs), while it is not the case in D–F.

133 DAGs. Previous studies proposed two such models. One is proposed by [Kondoh and Ninomiya \(2009\)](#) but  
 134 this model cannot generate food chains. In their model (Fig. 2B), species  $i = 1, \dots, B$  are regarded as basal  
 135 species and they do not eat any species. The rest of the species (non-basal species,  $i = B + 1, \dots, N$ ) are sorted  
 136 following the ascending trophic ranks, and each of them randomly chooses one prey species from the basal  
 137 species. Then, the predetermined number of trophic links are added between species (except for between basal  
 138 species) so that higher rank species eat lower ones. This model always generated an acyclic food web because  
 139 lower-rank species never eat higher-rank ones. However, this model cannot generate a food chain because each  
 140 of non-basal species should eat at least one basal species. When  $N = 3$  and  $B = 1$ , for example, basal species 1  
 141 is always eaten by both species 2 and 3: we cannot generate a food chain where species 3 predate only species  
 142 2.

143 [Johnson et al. \(2014\)](#) proposed a similar algorithm called the *preferential prey model* (Fig. 2C), and this  
 144 model can generate food chains. In this model, species  $i = 1, \dots, B$  are first assigned as basal species. Then,  
 145 a single non-basal species ( $i = B + 1, \dots, N$  sorted according to the ascending trophic ranks) is sequentially  
 146 added to the food web. First, each non-basal species  $i$  is randomly awarded a single prey species from species  
 147  $i = 1, \dots, B, \dots, i - 1$ . Then, a certain number of prey species of species  $i$  is added. These additional prey  
 148 species are chosen depending on the difference in the trophic levels between the candidate prey species and the  
 149 species that is first chosen as species  $i$ 's prey. The generated food webs are acyclic because already existing  
 150 species cannot predate newly added species. In addition, this model can generate a food chain. When  $N = 3$   
 151 and  $B = 1$ , for example, species 2 should always eat species 1 while species 3 can predate only species 2 with  
 152 some probability, which cannot happen in the model of [Kondoh and Ninomiya \(2009\)](#).

### 153 3.1.4 Niche models

154 [Williams and Martinez \(2000\)](#) proposed the *niche model* (Fig. 2D), which shows more similar patterns to  
 155 empirical food webs than the random and cascade models. In the niche model, each species  $i$  has a niche  
 156 value  $n_i$ , and each species predate species whose niche values are in a certain range. This means that the  
 157 one-dimensional niche is assumed in the niche model. Species  $j$  is eaten by species  $i$  if  $n_j \in [c_i - r_i/2, c_i + r_i/2]$ ,  
 158 where  $r_i$  is the range of species  $i$ ' prey niche, and  $c_i$  is the center of the range. Although the center value is  
 159 assumed to be equal to or smaller than the focal species' niche value ( $c_i \leq n_i$ ), species  $i$  can predate those who  
 160 have larger niche values than species  $i$ . Therefore, food webs generated by the niche model can be cyclic.

161 Some mathematical analyses for the niche model have been done in a large community with a small con-  
 162 nectance ( $S \gg 1$  and  $C \ll 1$ ). [Camacho et al. \(2002a\)](#) show the probability distributions of the number of  
 163 prey species per species exponentially decays. On the other hand, the probability distribution of the number  
 164 of predators is constant until a certain threshold and exponentially decreases when the number of predators  
 165 exceeds the threshold. These patterns are observed in empirical food webs as well. ([Camacho et al., 2002b](#)).

166 The niche model was expanded by [Stouffer et al. \(2006\)](#). The *generalized niche model* is a mixture of the  
 167 niche model and the generalized cascade model to include "gaps" in an adjacency matrix (see Section 3.1.5 for a  
 168 more detailed explanation of the gaps). In this model, the range of prey' niche value  $r_i$  is shrunk by multiplying

169 with a parameter  $c \in [0, 1]$ . Although this decrease the number of species  $i$ 's prey species, additional prey  
170 species are chosen randomly from those which have lower ranks than species  $i$ . Therefore,  $c = 1$  corresponds to  
171 the niche model while  $c = 0$  corresponds to the generalized cascade model.

### 172 3.1.5 Nested hierarchical model

173 One pitfall of the niche model is that a predator species has no gap in its predation range. Suppose we have  
174 four species whose indices are given by the ascending order of the niche values. If species 4 predaes species 1  
175 and 3, species 2 is also eaten by species 4 in the niche model. As such a gap (e.g., species 4 predaes species 1  
176 and 3, but not 2) can happen in nature, [Cattin et al. \(2004\)](#) proposed the *nested hierarchical model* (Fig. 2E).  
177 They compared the number of properties of empirical food webs, ones generated by the niche model, and ones  
178 by the nested hierarchical model. The two models show similar patterns to the empirical data except that the  
179 niche model cannot predict the properties related to food webs' gaps while the nested hierarchy model can.

180 The key idea of this model is that if two predator species have a common prey species, they are likely to have  
181 other common prey species. This idea is justified by the assumption that such two predators are phylogenetically  
182 close. In the nested hierarchy model, we again assume that species indices are sorted according to the ascending  
183 order of their ranks. The number of prey species for each species is determined by a similar method that  
184 [Williams and Martinez \(2000\)](#) determines the range  $r_i$  of each species so that a species with a larger range in  
185 the niche model tends to have a larger number of prey species in the nested hierarchical model: read Method  
186 section of [Cattin et al. \(2004\)](#) for more details. Species  $i$  first randomly chooses a prey species  $j$  from lower  
187 rank ones ( $j \in [1, \dots, i - 1]$ ). Next, additional prey for species  $i$  is chosen in either of two ways. If prey species  
188  $j$  does not have any other predator species, species  $i$  again randomly chooses prey species from lower-rank ones.  
189 If prey species  $j$  has predators other than  $i$  (e.g., species  $k$ ), additional prey for species  $i$  are randomly chosen  
190 from prey species of species  $k$ . This implies a phylogenetic constraint. If species  $i$  needs more prey species,  
191 additional prey species are randomly chosen from the species with lower ranks. If the number of prey species is  
192 not enough yet, prey species are added from those with higher ranks than species  $i$ , which allows us to generate  
193 cyclic food webs.

194 The phylogenetic constraint can generate gaps in food webs. Suppose that species  $i$  first choose prey species  
195  $j$ , and species  $j$  has two predator species  $k$  and  $l$ . For the sake of simplicity, let us assume that species  $i$  needs  
196 two additional prey species, and species  $k$  and  $l$  have two other prey species, respectively:  $\{j - 2, j - 1, j\}$  as  
197 species  $k$ 's prey, and  $\{j - 4, j - 3j\}$  for species  $l$ 's prey. If species  $i$  chooses one prey from species  $k$ 's prey and  
198 the other from species  $l$ 's prey, the composed food web has a gap.

199 [Stouffer et al. \(2005\)](#) show some analytical results in the nested hierarchy model in a large community  
200 with small connectance ( $S \gg 1$  and  $C \ll 1$ ). First, the probability distribution of the number of prey in the  
201 nested hierarchy model is identical to the niche model. Second, the patterns of probability distributions of the  
202 number of predator species per species and the connectivity are similar to those generated by the niche model.  
203 Finally, the predation of species with higher rank occurs at eight percent. This implies that cyclic food webs  
204 are generated in eight percent or less in the nested hierarchy model in this case.

### 205 3.1.6 Minimal potential niche model

206 Instead of comparing summary statistics of empirical food webs and ones generated by the algorithms mentioned  
207 above, [Allesina et al. \(2008\)](#) proposed two measures to compare the performance of the models: (i) the minimum  
208 number of irreproducible connections, the edges that the focal algorithm cannot generate while reproducing a  
209 target empirical food web because of the algorithm’s assumptions, and (ii) the likelihood that a focal algorithm  
210 generates a chosen empirical food webs. In the calculation of the minimum number of irreproducible connections,  
211 an adjacency matrix of an empirical food web is decomposed into two matrices: a reproducible adjacency  
212 matrix containing edges that the focal algorithm can reproduce, and an irreproducible adjacency matrix that  
213 the algorithm cannot reproduce. Then, the likelihood of the model is given by the sum of the likelihood that  
214 the algorithm generates the reproducible adjacency matrix and the likelihood that the random model generates  
215 the irreproducible adjacency matrix. [Allesina et al. \(2008\)](#) show that the niche model has larger log-likelihoods  
216 than the cascade model and the nested hierarchy models, but the number of irreproducible connections of the  
217 niche model is also larger.

218 These results support the assumption of the niche model but suggest it is imperfect: prey species are likely  
219 to share some characteristics (i.e., the niche values) but the dimension of the niche would be more than one.  
220 Then, [Allesina et al. \(2008\)](#) expanded the niche model and proposed the *minimal potential niche model* (Fig.  
221 2F). In this model, each species has a one-dimensional niche value and a potential range of prey’s niche. Instead  
222 of predating all species whose niche values fall in this range, a fraction of species in the range is not eaten by  
223 the focal predator species. This fraction, called a fraction of forbidden links, represents the average fraction  
224 of species that fall in dimension 1 of the predator’s niche (i.e., the niche value in the model) but not in other  
225 dimensions which is not explicitly defined in the model. The generated food webs have gaps as in the nested  
226 hierarchy model, but [Allesina et al. \(2008\)](#) report that the likelihood of the minimal potential prey model is  
227 larger than the niche model and nested hierarchical model. However, the minimal potential prey model generates  
228 cyclic food webs because the potential range of the prey niche can exceed the predators’ niche value.

## 229 3.2 Dynamic models

230 In the dynamical model, a food web changes its topology over time. These models simulate macro-evolutionary  
231 or meta-community dynamics. In the macro-evolutionary models, a new species has prey and predator species  
232 similar, but not identical, to the ancestral species. An adjacency model in these cases is a function of species’  
233 traits that evolve over time. Although we can simulate how properties of food webs evolve over time, none of  
234 the following models compares these temporal features with empirical data over time. This would be because  
235 empirical food web data over a long time are unavailable. Instead, these models measure the properties of  
236 generated food webs after a long run and then compare them with empirical data and static models. In meta-  
237 community models, on the other hand, regional food webs (hereafter called metawebs) are assumed. Then,  
238 researchers investigate what kinds of food webs are realized in a local community. A local food web is assembled  
239 by stochastic colonization and extinction of each species. The realized food web in the local community is given

240 by a subset of a metaweb. This indicates that acyclic metawebs generate only acyclic local food webs.

### 241 3.2.1 Webworld model

242 [Caldarelli et al. \(1998\)](#) proposed the *Webworld model* to generate food webs over the evolutionary dynamics. In  
243 this model, each species has a certain number of features, and these features determine which of a pair species  
244 is a prey or a predator (i.e., no mutual predation is assumed). Suppose we have two species (species  $i$  and  $j$ ).  
245 The features of the two species give us scores  $S_{ij}$  and  $S_{ji}$ . If  $S_{ij} > 0$ , species  $i$  predate species  $j$ , but species  $i$   
246 does not predate if  $S_{ij} = 0$ . Because of an assumption in the calculation of  $S_{ij}$ ,  $S_{ji} = 0$  if  $S_{ij} > 0$ . However, this  
247 does not exclude the possibility that cyclic predation whose length is three or larger is generated. Therefore,  
248 this model can generate cyclic food webs.

249 The food web evolves because of speciation. When speciation happens, a new species mimic the features of  
250 its ancestral species, but randomly loses one feature and obtains a new feature. Then, the new species is likely  
251 to have prey species similar to those of the ancestral species, but not necessarily identical. This depends on  
252 how the newly obtained and lost features affect the scores of the new species against the other species. The  
253 new species may suddenly go extinct and/or remove other species because of resource competition. Although  
254 this model is simple, [Caldarelli et al. \(1998\)](#) could not tune the parameter values to fit the empirical food webs  
255 available at that time.

### 256 3.2.2 Speciation and Matching models

257 Another dynamical model generating food webs over the evolutionary time scale is the *speciation* model ([Ross-  
258 berg et al., 2005](#)). In this model, each species has an evolutionary rate. This parameter determines the focal  
259 species' speciation rate, extinction rate, and body size. In [Rossberg et al. \(2005\)](#), a faster evolutionary rate  
260 indicates a smaller body size. As in the cascade model, potential predator (prey) species of a focal species  
261 are those which have larger (smaller) body sizes than the focal species, but the parameter loopness  $\lambda \in [0, 1]$   
262 controls the violation of this constrain: larger  $\lambda$  means that a species is more likely to predate other species  
263 whose body sizes are larger. Therefore, this model can generate cyclic food webs when  $\lambda > 0$ .

264 When a new species  $i$  joins the community, the speciation model determines the prey and predator species  
265 of species  $i$  as follows. First, species that are potential prey (predator) species of both species  $i$  and its ancestral  
266 species  $j$  are regarded as species  $i$ 's prey (predator). Next, new potential prey (predator) species of  $i$  (i.e.,  
267 potential prey or predator species of species  $i$ , but not those of  $j$ ) are assigned as prey (predator) species  
268 with a certain probability. Then, each potential prey (predator) species is pooled with a certain probability  
269 called the recombination probability. If pooled species are already assigned as species  $i$ 's prey (predator), the  
270 trophic interactions are removed. Finally, the pooled prey (predator) species are (re-)assigned as species  $i$ 's  
271 prey (predators) with a certain probability.

272 [Rossberg et al. \(2005\)](#) calculated the goodness of fit of the speciation model to seven empirical data. The  
273 goodness of fit was calculated based on 12 statistics. Comparing the goodness of fit of the niche model and the  
274 nested hierarchy model, the speciation model is the closest to the empirical data.

275 While the speciation model does not explicitly define species traits related to trophic interactions, the  
276 following study (Rossberg et al., 2006) includes foraging and vulnerability traits. These traits are given by  
277 binary sequences and determine whether one species predate another or not. This model, called the *matching*  
278 *model*, also considers the speciation and species' body sizes, The body sizes restrict prey-predator interactions.  
279 As in the speciation model, the matching model assumes that species cannot predate ones whose body sizes are  
280 larger, and this relation is violated when the loopness  $\lambda > 0$ . Species  $i$  predate its potential prey  $j$  if the match  
281 between  $i$ ' foraging traits and  $j$ 's vulnerability traits exceeds a threshold. When speciation occurs, the new  
282 species mimic its ancestral species foraging traits, vulnerability traits, and body size, but they slightly change.

283 The matching model was also compared with the niche model and nested model. Rossberg et al. (2006)  
284 shows that the matching model is favored over the niche model in 12 out of 17 empirical food webs and over  
285 the nested hierarchy model in 16 out of them.

### 286 3.2.3 Model incorporating interference competition

287 While the above models can include exploitative competition (two or more predator species sharing prey in-  
288 directly interact via resource competition), the model proposed by Loeuille and Loreau (2005) can include  
289 interference competition (e.g., the two predator species directly interact with each other). In this model, each  
290 species is assigned a body size, and speciation changes only the body size. Without loss of generality, species  
291 indices are sorted in the ascending order of the body sizes. As in the cascade model, species  $i$  predate species  
292  $j$  if and only if species  $i$  has a larger body size. However, the consumption rates depend on the difference in  
293 the body sizes, and an optimal body size is assumed to exist: the rationale is that energy gain should increase  
294 over the prey's body size (i.e., decrease over the difference in the body sizes), but the predator's attack is less  
295 likely to succeed when the prey has a body size closer to the predator. In addition, interference competition  
296 occurs between two species if the difference in their body sizes is enough small. Therefore, if we focus on the  
297 prey-predator interactions, the food webs generated in this model are always acyclic. However, if we include  
298 interference interactions in the food webs, the networks can be cyclic. Loeuille and Loreau (2005) also show the  
299 fitting of this model to some empirical food webs is better than the fitting of the niche model.

### 300 3.2.4 Expansion of the theory of island biogeography

301 In the theory of island biogeography (TIB) (MacArthur and Wilson, 1967), a local community (called an island)  
302 is modeled by two processes: colonization from a source of species (called mainland), and stochastic extinction  
303 in the local community. In the classic case, the colonization and extinction rates are not species-specific, and  
304 thus the species richness at equilibrium is determined by the balance of the colonization and extinction rates.

305 Gravel et al. (2011) expand TIB so that trophic interactions affect colonization and extinction rates: col-  
306 onization and extinction rates of predator species depend on the presence and absence of prey species. The  
307 authors also show that this extended TIB generates communities more similar to empirical data than the classic  
308 TIB in the sense of species richness, the number of trophic links, and the connectance in a local community.  
309 Saravia et al. (2022) also built a similar model while introducing the secondary extinction of non-basal species.

310 Because this model does not include local community dynamics, a local food web generated by the model may  
311 not be stable. However, the generated food webs were not very different from empirical food webs.

### 312 **3.2.5 Expansion of patch dynamics models**

313 Another framework for meta-community dynamics is patch dynamics. In its classical framework, the dynamics  
314 of fractions of patches occupied by species of interest are analyzed. Typically, the coexistence of competitive  
315 species is analyzed, and their colonization rates are determined by fractions of open patches and patches where  
316 inferior competitors occupy (Tilman, 1994; Yamauchi et al., 2021). A natural extension of this framework to  
317 food webs is analyzed by Wang et al. (2021). In their model, the colonization rates of predator species are  
318 determined by a fraction of patches where the focal predator does not exist but its prey species exist. Their  
319 model assumes, however, that a metaweb is a food chain. Alternatively, Pillai et al. (2010) proposed the patch  
320 dynamics for the fractions of patches where a focal trophic interaction is realized. However, Pillai et al. (2010)  
321 and the following study (Pillai et al., 2011) allow only food chains in local communities by assuming competitive  
322 exclusion of predator species that share prey species. This may be because the authors are interested in the  
323 realized regional food webs (i.e., food webs generated by merging local food webs). Even though, one could  
324 estimate local food webs and analyze FCL from the fractions of the trophic interactions in this model.

## 325 **4 Definitions and algorithms for FCL**

326 In this section, we review a variety of definitions of FCL, and how to calculate FCL using algorithms in graph  
327 theory. In the following definitions, FCL is defined by the length of some walks or paths from basal species.  
328 Before moving to the review of FCL, we define a walk and a path.

329 A walk from node  $x$  to node  $y$  is a set of sequential edges that starts from  $x$ , through some other nodes, and  
330 arrives at  $y$ . A walk may visit a node multiple times. A path from  $x$  to  $y$  is a special walk from  $x$  to  $y$  that a  
331 node is not visited multiple times (Bang-Jensen and Gutin, 2009). The length of a walk or a path is given by  
332 the number of sequential edges.

333 A  $N$ -species food chain has FCL of  $N - 1$  in any definitions except for the empirical definition (Section 4.5)  
334 because there is a unique path from the basal species to the top predator. However, a definition of FCL can  
335 change its value in a non-chain food web because there can be multiple walks or paths. For this reason, we  
336 cannot quantitatively compare the results of studies using different definitions of FCL, although we would be  
337 able to qualitatively compare how FCL changes.

### 338 **4.1 Shortest-length approaches**

339 In Caldarelli et al. (1998), a trophic level of each species is defined by one plus the length of the shortest path  
340 from a basal species. Because FCL is given by the maximum trophic level minus one (Post, 2002), FCL here  
341 is defined by the maximum shortest path length from a basal species in a food web. One advantage of this  
342 definition is that we can use this definition in cyclic food webs if we have basal species. This is because the

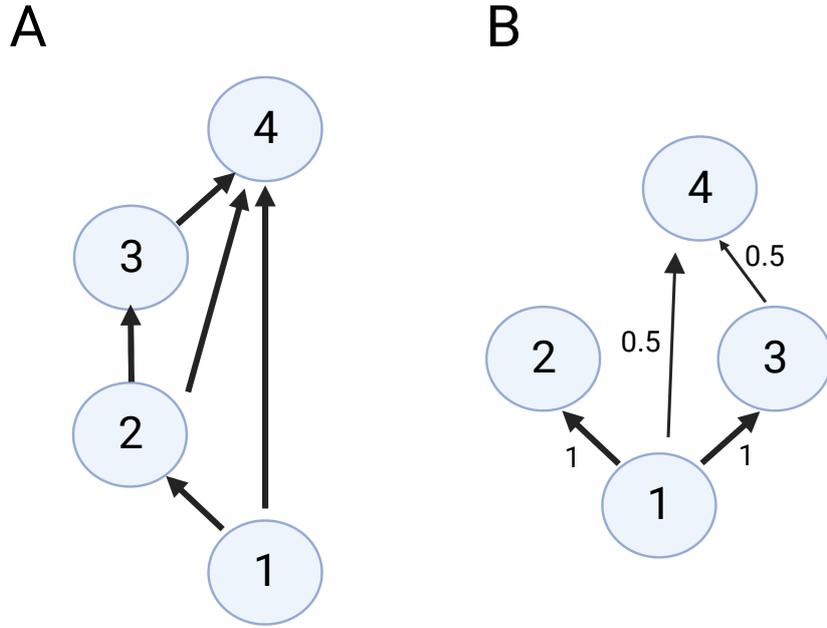


Figure 3: Examples food webs for FCL analysis

Schematic representations of food webs that are useful to understand each definition of FCL. Each circle represents species, and values on the edges in panel B are weights  $w_{ij}$  of predation. A: When FCL is defined by the maximum shortest path (Section 4.1), the top predator, species 4, does not determine FCL. The shortest path from species 1 (the basal species) to species 4 is one, while the shortest path from species 1 to species 3 is two. Therefore, FCL is determined by non-top predator 3 if we define FCL as the maximum shortest path in a food web. B: This food web clarifies that FCL based on the mean path length (Section 4.3) differs from that based on the prey’s mean trophic level (Section 4.4). In this food web, we have two top predators (species 2 and 4), and we have two paths from species 1 (the basal species) to species 4. The mean length of paths from the basal species to either of the top predators is  $(1 + 1 + 2)/3 = 1.33$ . When we calculate the trophic levels based on the prey’s mean trophic level, species 2 is level 2 and species 4 is level  $1 + (1 + 2)/2 = 2.5$ . Then, the FCL based on the prey’s mean trophic levels is  $\max\{2, 2.5\} - 1 = 1.5$ . Created with BioRender.com.

343 shortest paths should not include cycles by definition. The disadvantage of this definition is, on the other hand,  
 344 that the top predators do not always determine FCL. Suppose we have a four-species food web: species 1 is a  
 345 basal species, species 2 predaes species 1, species 3 predaes species 2, and species 4 predaes all other species  
 346 (Fig. 3A). In this example, species 4 is the top predator (as no species predaes species 4) but its trophic level  
 347 is two since species 4 predaes the basal species. In contrast, the FCL is two because the maximum shortest  
 348 path in this food web is given by the path from species 1 to species 3, which is not a top predator.

349 In graph theory, this definition of FCL is identical to the diameter of a food web (Estrada, 2013). To calculate  
 350 the diameter, we first need to measure the (directed) *distance* between two species in a focal food web: the  
 351 distance  $d(x, y)$  is the shortest path from species  $x$  to species  $y$ . The diameter of a food web is, then, given by  
 352 the longest distance between two species in the food web. The diameter, or FCL in this definition, of a food web  
 353 is easily obtained. Given a food web, we first collect basal species such that  $D^-(i) = 0$  for  $i = 1, \dots, N$ . Then,  
 354 we solve the single-source shortest path problem for each basal species, which calculates the shortest path from  
 355 a given basal species to all other species. The single-source shortest path problem is solved by the Breadth-first  
 356 search algorithm whose computational complexity is  $\mathcal{O}(N + \sum_{i,j} A_{ij})$  (Cormen et al., 2009a). Finally, the FCL

357 is given by  $-1$  plus the maximum shortest path across all basal species. Because the number of basal species is  
358 smaller than  $N$ , the total computational complexity for FCL in this definition is  $\mathcal{O}(N^2 + N \sum_{i,j} A_{ij})$

359 A similar, but identical, to the above definition was used in [Kondoh and Ninomiya \(2009\)](#). Here, the authors  
360 defined FCL as the shortest path from a basal species to a top predator. With this definition, the top predator,  
361 species 4, in Fig. 3A gives the FCL of one. We can calculate FCL in a similar way to the above algorithm:  
362 we calculate the shortest path from each basal species to each top predator using the Breadth-first search, and  
363 then we look for the minimum shortest path over pairs of basal species and top predators. We need to keep  
364 in mind that top predators may not be defined in a part of cyclic food webs (e.g., where “top predators” are  
365 predated by decomposers).

## 366 4.2 Longest-length approach

367 Alternatively, we can define FCL as the length of the longest walk from a basal species in a food web ([Briand  
368 and Cohen, 1987](#); [Cohen and Newman, 1991](#); [Kondoh and Ninomiya, 2009](#); [Calcagno et al., 2011](#); [Sommer et al.,  
369 2018](#)). An advantage of this definition is that non-top predator species cannot have the longest path from a basal  
370 species because non-top predators should have species that predate the focal non-top predators. The longest  
371 walks or paths to the predators of the non-top predators are longer than that of the focal non-top predators.  
372 However, this definition cannot be used in a cyclic food web: the length of a walk in such a food web can be  
373 infinite as visited nodes are not necessarily distinct in a walk.

374 Hereafter, we assume an acyclic food web while considering this definition of FCL. Then, a walk is identical  
375 to a path, and FCL is given by the length of the longest path. Although the longest-path analysis is, in general,  
376 NP-complete ([Cormen et al., 2009b](#)), we can easily and quickly obtain it in a directed acyclic graph. The idea  
377 is that we consider a graph whose topology is identical to an original graph but the weights of all edges are  
378 multiplied by  $-1$  ([Bang-Jensen and Gutin, 2009](#)). The shortest path in this new graph corresponds to the  
379 longest path in the original graph.

## 380 4.3 Mean-length approach

381 [Briand and Cohen \(1987\)](#) and [Sabo et al. \(2009\)](#) also considered FCL as the mean length of a walk from a basal  
382 species to a top predator within a food web. Again, we assume an acyclic food web here: FCL can be infinite  
383 in cyclic food webs (see Section 4.2). Then, we define FCL as the mean length of paths from a basal species to  
384 a top predator within a food web. One advantage of this definition is that we can incorporate the information  
385 of all top predators and basal species in a food web. In the rest definitions of FCL, on the other hand, FCL  
386 is given by a certain pair of species because we consider the maximum or minimum length of paths or trophic  
387 levels. To our best knowledge, however, there is no algorithm that calculates this FCL efficiently.

#### 388 4.4 Prey’s mean trophic level approach

389 Another definition of FCL is based on the trophic levels given by mean trophic levels of prey species (Diehl  
 390 and Feissel, 2001; Post and Takimoto, 2007; Kondoh and Ninomiya, 2009; Takimoto et al., 2012). Notably, this  
 391 definition is not identical to the mean-length approach (Fig. 3B). Once all species’ trophic levels are obtained,  
 392 FCL is given by the maximum trophic level minus one. This definition can reflect how much each prey is eaten  
 393 by a focal predator species while FCL based on the shortest or the longest walks or paths cannot. However, we  
 394 cannot use this FCL in cyclic food webs because we cannot define trophic levels in cyclic food webs.

395 Suppose that a fraction of species  $i$  in non-basal species  $j$ ’s prey is  $w_{ij}$ :

$$\begin{aligned} w_{ij} &> 0 && \text{if } a_{ij} = 1 \\ w_{ij} &= 0 && \text{if } a_{ij} = 0, \end{aligned} \tag{6}$$

396 and

$$\sum_{i=1}^N w_{ij} = 1. \tag{7}$$

397 Then, species  $j$ ’s trophic level  $\tau_j$  is given the mean trophic level of prey species plus one:

$$\tau_j = 1 + \sum_{i=1}^N \tau_i w_{ij}. \tag{8}$$

398 We cannot define each species’ trophic level in cyclic food webs because of a circular problem. For example,  
 399 if two species mutually predate each other, one species’ trophic level depends on the trophic level of the other  
 400 species, whose trophic level depends on the first species’ trophic level. Therefore, we can use this definition of  
 401 FCL only in acyclic food webs.

402 Hereafter, we assume an acyclic food web, and the species indices are assigned so that the adjacency matrix  
 403 is a strictly upper triangular matrix when we use this definition of FCL. FCL of this definition can be obtained  
 404 as follows. First, we collect basal species from a food web. Next, we assign trophic levels of species that predate  
 405 only basal species. Then, we recursively assign trophic levels to species that predate species whose trophic  
 406 levels are already assigned. The computational complexity of this process is  $\mathcal{O}(N^2)$  because  $N \times N$  adjacency  
 407 matrix tells us which species predate which. We repeat this process at most  $N$  times to assign all species’  
 408 trophic levels because at least one new species’ trophic level is assigned in each step; the total computational  
 409 complexity is  $\mathcal{O}(N^3)$  in this definition of FCL. After assigning all species’ trophic levels, we can calculate FCL  
 410 as the maximum trophic level minus 1 (Post, 2002). As in the definition in Section 4.1, top predators do not  
 411 always determine FCL; for example, species 4 in Fig. 3A can have a lower trophic level than species 3 when  
 412 species 4 most frequently predate species 1 than other prey species.

## 4.5 Empirical approach

A typical definition of FCL in empirical studies is given by the trophic positions of species estimated by stable isotope  $\delta^{15}N$ . (Post et al., 2000b; Takimoto et al., 2008; Jake et al., 2007; Sabo et al., 2010; Sullivan et al., 2015; Ward and McCann, 2017; Doi and Hillebrand, 2019). The assimilation of stable isotopes represents the mass or energy flows in a food web. Then, FCL is defined by

$$\text{FCL} \equiv \frac{(\max_i \delta^{15}N_i - \delta^{15}N_{\text{base}})}{\delta N} + \lambda_{\text{base}} \quad (9)$$

where  $\delta^{15}N_i$  corresponds to  $\delta^{15}N$  of a top predator (we choose one whose  $\delta^{15}N$  within all top predator species),  $\delta^{15}N_{\text{base}}$  is  $\delta^{15}N$  of baseline species,  $\delta N$  is the average enrichment of  $\delta^{15}N$  per trophic level (typically  $\delta N = 3.4$ ) (Post et al., 2000b), and  $\lambda_{\text{base}}$  is a constant value depending on the trophic position of the baseline species. In empirical studies, researchers tend to use the trophic position of baseline species (e.g.,  $\lambda_{\text{base}} = 2$  for primary consumers). However, if we convert the maximum trophic position into FCL following (Post, 2002),  $\lambda_{\text{base}}$  should be the baseline species' trophic level minus 1.

One advantage of this definition is that we do not need an entire food web. We need only a top predator and a baseline species, which is not necessarily a basal species (e.g., we can use primary consumers as baseline species). In addition, this definition allows cyclic food webs.

## 5 Discussion

FCL is an important summary statistics of biodiversity in nature, and ecologists have investigated what determines FCL. However, the studies on FCL have been very simple in two points. First, theoretical models and laboratory experiments analyzed only food webs simpler than natural food webs. Second, many studies have tested simple hypotheses: whether each of resource availability, disturbances, and ecosystem sizes affect FCL or not. Since FCL in natural communities is likely to be determined by these three factors in a complex way, we need a comprehensive theory that integrates the three hypothetical controls of FCL. To address this point, we propose using some models in Table 1 that generate a variety of food webs as complex as natural ones.

One important feature of the models is whether they generate only acyclic food webs or not. As reviewed in Section 4, all definitions of FCL are applicable to acyclic food webs. In contrast, FCL defined in Sections 4.2, 4.3, and 4.4 cannot be applied in cyclic food webs, while the rest definitions can be applicable in cyclic food webs only if basal species or top predators exist. For this reason, it would be reasonable to use models that generate only acyclic food webs in the studies of FCL. Such models are the (generalized) cascade model, the one proposed by Kondoh and Ninomiya (2009), the preferential prey model, and the dynamical models (except for the WebWorld model) under certain conditions (Table 1). In contrast, the (generalized) niche model, the nested hierarchy model, the minimal potential niche model, and Webworld can generate cyclic food webs. Unless we use FCL that allows cycles (Section 4.1), these models are not appropriate in the studies of FCL.

Another important feature of the models is how a food web is generated: whether statically or dynamically.

445 The static models have small computational costs because an adjacency matrix is generated by some simple rules:  
446 we can generate many food webs in a short time. However, these models do not provide dynamical properties of  
447 generated food webs. This makes it difficult to analyze how disturbances affect FCL. One way to overcome this  
448 problem would be to simulate ecological dynamics (e.g., using the generalized Lotka-Volterra model or others in  
449 the dynamical models) given a food web generated by the statical models. The dynamic models, on the other  
450 hand, take a longer time to generate a food web because each food web is generated through meta-community  
451 or evolutionary dynamics. However, the dynamic models provide dynamical properties of FCL: the effect of  
452 disturbances on FCL can be implemented in a straightforward way. Another advantage of the dynamical models  
453 is that they addressed research questions that have not been widely investigated. One can ask, for example, how  
454 a network topology of local communities (Sullivan et al., 2015; Pomeranz et al., 2022) affects the distribution of  
455 FCL across space, or in which case FCL evolves the longest. These questions could also be empirically addressed  
456 using microcosms.

457 Once we choose the model to generate food webs, we need to consider how resource availability, disturbances,  
458 and ecosystem sizes affect food webs. Effects of resource availability can be implemented either as the number  
459 of basal species (see Kondoh and Ninomiya (2009) and Johnson et al. (2014)) or as maximum colonization rates  
460 of basal species. The disturbances can be seen as the random removal of species from a food web (Bellingeri  
461 et al., 2013) or extinction rates in patch dynamics (Gravel et al., 2011; Saravia et al., 2022). The ecosystem  
462 size would affect the number of patches in a system (with spatial structures), or the number of species in a food  
463 web (Cohen and Newman, 1991) (without spatial structures). We would see how FCL in a food web changes  
464 over these three parameters, rather than each of which is a dominant determinant.

465 We also reviewed the variation in the definitions of FCL. The difference in the definition determines whether  
466 we can calculate FCL in a cyclic food web or not (see above), and whether we need a whole food web or not.  
467 Indeed, only the empirical FCL (Section 4.5) allows us to calculate FCL in an imperfect food web. This could  
468 affect the quantitative comparison of FCL in theory and in empirical data. Within the rest definitions of FCL,  
469 we do not recommend FCL based on the mean path length (Section 4.3). As there is no algorithm to efficiently  
470 calculate this FCL, the computational cost in a complex food web can be huge. Of course, the advantage of this  
471 definition is that we can include information on all basal species and top predators, while the rest definitions  
472 use only the maximum shortest or longest path or the maximum top predator's trophic level. In Section 4.1, we  
473 show that the maximum shortest path approach has a problem: FCL can be determined by a non-top predator.  
474 To avoid this problem, we may define FCL as the maximum shortest path from a basal species to a top predator.  
475 However, another problem arises: an omnivore can strongly decrease FCL. For example, FCL in Fig. 3B is one  
476 when we define FCL by the maximum shortest path between the basal species (species 1) and either of two top  
477 predators (species 2 and 4). This indicates that the predation of species 3 by species 4 is not considered in this  
478 definition. A similar problem of omnivores occurs when FCL is defined by the longest path (Section 4.2): FCL  
479 can be overestimated by omnivores. FCL in Fig. 3A, for example, is three even when species 4 predaes species  
480 1 or 2 more frequently than species 3. These problems related to omnivores can be solved when FCL is given by  
481 the definition in Section 4.4. With this definition, we can balance the effect of omnivore using the weight  $w_{ij}$ .

482 However, we need to keep in mind that the distribution of  $w_{ij}$  affects FCL. We may need to consider whether  
483 resource availability, disturbances, and ecosystem sizes affect the distribution of  $w_{ij}$  or not. For example, an  
484 omnivore species may change its predation intensity on basal species depending on the resource availability  
485 because it would affect the abundances of the basal species.

## 486 **6 Conclusion**

487 Toward a comprehensive understanding of the determinants of FCL, we need to go beyond the simple systems  
488 and the simple hypotheses. We believe that this review provides a potential way to this research direction.  
489 First, graph theory is a useful tool to clarify characteristics that food webs in the analysis of FCL should satisfy,  
490 and how we can measure FCL. Second, we should use models that generate acyclic food webs as complex as  
491 empirical ones. Such models include the (generalized) cascade model and the preferential prey model. Using  
492 these models, we need to address how resource availability, disturbances, and ecosystem sizes interdependently  
493 affect FCL, rather than which is a dominant constraint on FCL.

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## **Conflict of interest**

We declare no conflict of interest.

## **Author contributions**

S.S. and A.T. conceived the ideas, S.S. wrote the first draft, and S.S. and A.T. revised the manuscript.

## **Data availability**

This manuscript has no data.

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