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Article

Effect of parasitism on food webs: Topological analysis and goodness test of cascade model

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Abstract

In this study, we used Pajek to analyze the effect of parasitism on food webs collected from Carpinteria Salt Marsh (CSM). Results showed that median and mean of generality and vulnerability for predator-prey and parasite-host sub-webs were greater than the reported previously. Inclusion of parasites significantly increased the mean generality and vulnerability of the full food web. Effectiveness of cascade model was tested using CSM and arthropod food webs. The results demonstrated that fitting goodness on the predator-prey sub-web without parasites was lower than that on the full CSM food web. Also, cascade model performed worse in fitting arthropod food webs.

Keywords food webs; parasites; Pajek; network analysis; cascade model.

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1 Introduction

A food web is a network map, which not only describes between-species trophic relationship in a community, but also presents energy and matter flows in the web (Pimm et al., 1991). In the food webs, species are connected by lines and arrows, called links, and a species in the food web is generally treated as a node or vertex. Food webs are the focus for research of stability, diversity and complexity of ecosystems (Montoya and Pimm, 2006; Pascual and Dunne, 2006). A basic objective of food web studies is to understand how food webs affect the functioning of ecosystems, thus further predict the environmental problems such as climate changes and species invasion (Ings et al., 2009).

Although the food webs look very complicated, but studies show that all food webs, including terrestrial, freshwater and marine food webs share some common patterns and features. These patterns and features include (Pimm et al., 1991): (1) cycles are rare in the web; (2) the mean proportion, the proportion top species (T): intermediate species (I): basal species (B), is substantially an invariant value, and later Cohen and

Newman (1985) proposed a specific value of the proportion; (3) the proportion, between intermediate species links: intermediate to top species links : basal to intermediate species links : basal to top species links, is in average an invariant; (4) linkage density is almost an invariant in the food webs with fewer species, but linkage density may grow as the increase of species; (6) omnivores are rare in certain food webs; (7) compartments are rarely found in habitats; (7) for top predators, the food chain length is generally 2 or 3, and the length 1 or the values greater than 3 are uncommon. However, some conclusions are very controversial. An important controversy is the relationship between food web complexity and community stability (Montoya and Pimm, 2006). In recent years, with the advance of the food web studies, we have been obtaining more and more full and fine quantitative data (Ings et al., 2009). These data make the findings of food webs more rigorous and credible.

Nevertheless, most of the above findings were achieved by analyzing the interactions between free-living species. They often ignored the parasitism. Parasites are ignored mainly due to their small sizes, and lack of cross-disciplinary collaboration, identification and quantification of parasites in food webs, and parasitology skills (Lafferty et al., 2008). On the other hand, parasites are an important part of biodiversity. Their biomass is so large in some ecosystems. They have almost the same richness and productivity as their free-living hosts with the similar sizes and trophic levels. Furthermore, studies have demonstrated that in terms of the trophic relationship, parasites have the body size ratio to their hosts opposite to the most free-living consumer-resource body size ratio, which helps them to adjust the abundance of their host species. Parasites often have complex life cycles, and sometimes need to live in different host species with various body sizes. They may have the trophic specialization modes different from the free-living predators. They may be associated with their hosts in different topological positions. Their interactions with hosts can reorganize ecological communities and change the functioning of ecosystems. All these factors may lead to their difference in adapting food webs and affecting food web structures with free-living organisms. More and more evidence have demonstrated that parasites may uniquely alter the food chain length, connectance and robustness of food webs, and thus change the topology of food webs or even the stability, interaction strength and energy flow of food webs (Dunne et al. 2013).

Given the importance of parasites in food webs, how to include parasites in food web studies is becoming a very important topic in recent years (Huxham et al., 1996; Marcogliese and Cone, 1997; Memmott et al, 2000; Lafferty et al., 2006; Warren et al., 2010; Kuang and Zhang, 2011; Dunne et al., 2013). In present study, we used food web data from Carpinteria Salt Marsh (CSM) to find some new conclusions, and compared the results with previous studies, in order to further illustrate the effects of parasites on the food webs. In addition, the effectiveness of cascade model was tested using the CSM food web and arthropod food webs.

2 Materials and Methods

2.1 Data source

2.1.1 CSM food web

CSM data were collated from food webs of Carpinteria Salt Marsh, California, recorded by Lafferty et al. (2008) (Source: http: //www.nceas.ucsb.edu/interactionweb/html/carpinteria.html).

The CSM food web contains free-living species and parasites. Predator-prey links (sub-webs) include published, observed and inferred diet relationships. Parasites include macroparasites (primarily parasitic roundworm), parasitic castrators, parasitoids, pathogens and trophically transmitted parasites. However, some predators are underrated. For example, the samples of bird parasites, pathogens and skin ectoparasites are relatively fewer. Microbial pathogens are basically not detected. Plant pathogens are excluded from food webs. In addition, the data does not contain invertebrates with very small sizes (<~1 mm), free-living protozoa, bacteria, fungi and their hosts. In the complex life cycle of a parasite, the absence of any stage may lead to extinction of the parasite, so each parasite species is treated as a trophic taxon (Lafferty et al., 2006; Warren et al., 2010).

The CSM food web composes of four sub-food webs, predator-prey web, parasite-host web, predator-parasite web, and parasite-parasite web. Among them, the predators can be divided into six trophic levels. Predators feed on parasites indirectly or directly by consuming preys, or directly feed on free-living parasites. Parasites may feed on each other. An example is that trematode larvae mutually feed on in the body of a mollusk.

2.1.2 Arthropod food webs

Data of paddy arthropod food webs were collected from Liu et al. (2002a, b), Liu (2009), and Gu et al. (2006), as indicated in the following

Name	Matrix (S×S)	District	Period	Data sources
FW1	26×26	Unknown	The overall pattern	Liu et al. (2002a, b)
FW2	57×57	Hunan	The overall pattern	Liu (2009)
FW3a	23×23	Wengyuan, Guangdong	The overall pattern of early season rice	Gu et al.(2006)
FW3b	24×24	Wengyuan, Guangdong	The overall pattern of late season rice	Gu et al.(2006)

Paddy arthropod food webs are composed of natural enemies, pests, neutral insects and plants. The food webs in present study primarily describe the relationship between the natural enemies and rice pests. The arthropod food web FW1 contains 24 species of arthropods, including 19 species of predators and 5 species of preys which contain 4 rice insect pest species and 1 neutral insect species. There are 55 arthropod species in FW2, including 36 predator species, and 19 prey species which contain 13 rice insect pest species and 6 neutral insect species. FW3a has 21 arthropod species, including 16 species of predators, and 5 prey species which contain 4 rice insect pest species and 1 neutral insect species. FW3b contains 22 arthropod species, including 17 predator species and 5 prey species in which there are 4 rice insect pest species and 1 neutral insect species.

2.2 Methods

2.2.1 Pajek software

Pajek is a software platform for the network analysis of the large and complex networks with up to millions of nodes. It is a fast visualized tool for program operation. Pajek contains various methods/algorithms on analysis of topological properties.

2.2.2 Generality and vulnerability of a food web

Generality refers to the number of prey species fed by a given predator species (Dunne et al., 2013). Mean generality of a food web is defined as the value of the sum of all predators' generality divided by total number of predator species.

Vulnerability refers to the number of predator species feeding on a given prey species (Dunne et al., 2013). Mean vulnerability of a food web is defined as the value of the sum of all preys' vulnerability divided by total number of prey species.

In Pajek, generality and vulnerability of the food web are calculated by the command/directory, Net/Partitons/Degree/Input, and Net/Partitions/Degree/Output.

2.2.3 Cascade model

The cascade model was firstly proposed by Cohen and Newman (1985). All species are arranged as a cascade structure so that the top species can feed on the lower species. The adjacent matrix $A_{s\times s}$, built from the food web, is thus a strict upper triangular matrix (a_{ij}=0, $i>j$), i.e., it is a strict trophic hierarchy or cascade (Zhang, 2012a). Therefore, the food web has not any cycle. The species with ID No.1 are only fed by other species and they do not feed on any other species, etc. The species with ID No.S may feed on any other species. Furthermore, this model assumes that there is a positive real value c ($c=2CS^2/(S-1)$, and C is the connectance, $C=L/S^2$), so that for $S\geq c$, all elements a_{ij}, $i\leq j$, follow the Bernoulli distribution with the parameter $p=c/S$. Thus some properties of the food web can be derived.

Suppose $p=c/S$, $q=1-p$, and $c\geq 0$, $S\geq c$. Topological structure of a food web can be derived by (Cohen and Newman, 1985)

$$E(T) = E(B) = (1-q^S)/p$$

$$E(I) = S[1-2(1-q^S)/c+q^{S-1}]$$

$$E(L) = pS(S-1)/2 = c(S-1)/2$$

$$E(L_{BI}) = E(L_{IT}) = (S-1)(1+q^{S-1}) - (1+q)(1-q^{S-1})/p$$

$$E(L_{BT}) = (1-q^{S-1})/p-(S-1)q^{S-1}$$

$$E(L_{II}) = pS(S-1)/2-(S-1)(2+q^{S-1})+(1-q^{S-1})(1+2q)/p$$

From the first three formulae, we can calculate the proportions of number of top species T, number of intermediate species I, and number of basal species B, divided by total number of species. And from the last three formulae, we may calculate the proportions of number of top species – basal species links BT, number of top species - intermediate species links IT, number of intermediate species - intermediate species links II, and number of intermediate species - basal species links BI, divided by total number of species.

3 Results

3.1 Generality and vulnerability

Generality and vulnerability were calculated for CSM food webs. Fig. 1 and 2 illustrate explicitly the between-species quantitative relationships. As indicated in Table 1, the median of generality of parasite-parasite sub-web is the smallest (=0) in the four sub-webs, seconded by predator-prey sub-web (=4). The median of generality of both parasite-host and predator-parasite sub-webs is the greatest (=10). The mean generality of parasite-host sub-web is the greatest (=14.0) in the four sub-webs, i.e., in mean a parasite species parasitizes 14 host species. As a consequence, considering parasites in a food web increases the mean generality.

Table 2 shows that the mean vulnerability of predator-parasite sub-web reaches 22.0, i.e., meanly each parasite is fed by 22 predators, directly or indirectly. This sub-web substantially increases the mean vulnerability of the full food web.

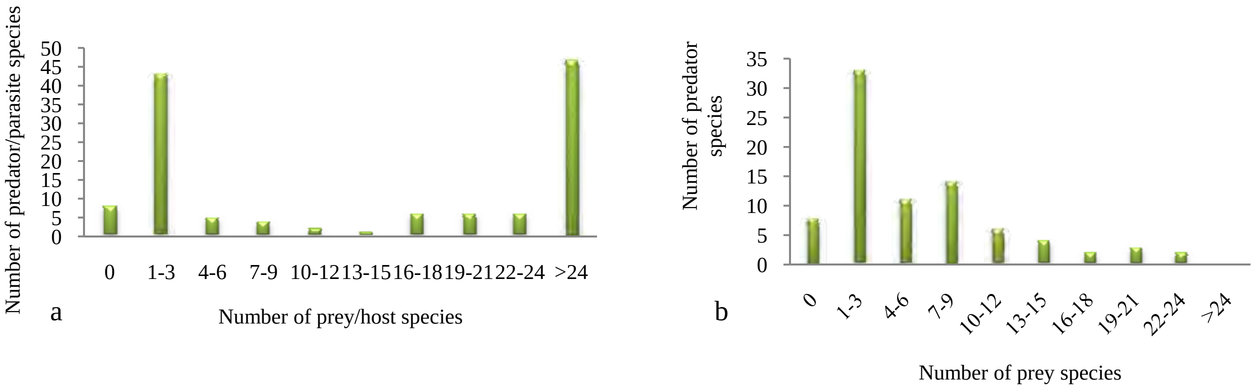

Fig. 1 Generality of the full food web (a) and predator-prey sub-web (b).

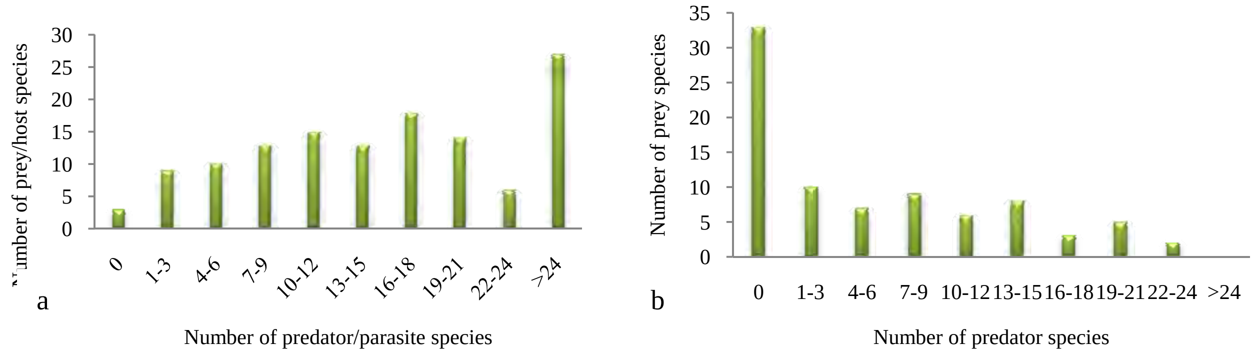

Fig. 2 Vulnerability of the full food web (a) and predator-prey sub-web (b).

Compared Table 1 with Table 2, we find that the mean generality and vulnerability of the full food web, predator-prey sub-web, and parasite-parasite sub-web are the same. Moreover, an equation is obtained from these results: the mean generality * 45 = the mean vulnerability * 83. For predator-parasite sub-web, the mean generality * 83 = the mean vulnerability * 45.

As a comparison, Memmott et al. (2000) demonstrated that the median of generality and vulnerability for predator-prey sub-web was 2 and 5.5, respectively, and for parasitoid-host sub-web was 1 and 3, respectively. Schoener (1989) studied 98 predator-prey sub-webs in seven full food webs, and found that the mean generality and vulnerability of food webs were approximately 2, different from our results (6.0). These differences are largely attributed to the difference in types and sizes of food webs.

Table 1 Median and mean of generality of the full food web and four sub-webs.

	Full	Predator-prey	Parasite-host	Parasite-parasite	Predator-parasite
Median	16	4	10	0	10
Mean	17.9	6.0	14.0	3.8	12.0

Table 2 Median and mean of vulnerability of full food web and four sub-webs.

	Full	Predator-prey	Parasite-host	Parasite-parasite	Predator-parasite
Median	16	2	6	0	23
Mean	17.9	6.0	7.6	3.8	22.0

3.2 Cascade model

3.2.1 Fitting CSM food web

Table 3 shows the results of fitting cascade model to the full CSM food web and predator-prey sub-web.

Table 3 Fitting topological properties of the full food web and predator-prey sub-web.

	Predator-prey sub-web			Full food web		
	Observed	Fitted	Relative error	Observed	Fitted	Relative error
T	0.398	0.083	0.249	0.023	0.028	0.001
I	0.506	0.835	0.213	0.914	0.944	0.001
B	0.096	0.083	0.002	0.063	0.028	0.019
BI	0.135	0.138	0.000	0.033	0.052	0.011
BT	0.018	0.014	0.001	0.000	0.002	0.000
II	0.300	0.710	0.558	0.949	0.894	0.003
IT	0.546	0.138	0.305	0.018	0.052	0.001
Total			1.328			0.036

Note: T, I and B denotes the proportion of top species, intermediate species and basal species divided by total species, respectively; BI, BT, II, and IT represents the proportion of basal-intermediate links, basal-top links, intermediate-intermediate links and intermediate-top links divided by total links in the food web. Relative error = (observed-predicted)^2/observed.

The values of T (top species/total species, 0.398), I (intermediate species/total species, 0.506) and B (basal species/total species, 0.096) in Table 6 are different from the invariants 0.29, 0.53 and 0.19, reported by Cohen and Newman (1985). The values of BI, BT, II and IT in our study (0.135, 0.018, 0.300 and 0.546, respectively) are also different from the invariants 0.27, 0.08, 0.30 and 0.35 of Cohen and Newman (1985). In addition, linkage density in Table 5 (=5.98) is greatly larger than the invariant (=1.86) of Cohen and Newman (1985).

As pointed out by Marcogilese and Cone (1997), the cascade model is not applicable to predict the properties of the food webs with parasites. Inclusion of parasites into a food web, the strict upper triangular matrix may not hold because sizes of parasites are far less than their host, and cycles may thus occur. However, our results showed that the cascade model, with a greater relative error, failed to predict the properties of predator-prey sub-web without parasites. A reason is probably that the two assumptions, upper triangular matrix and Bernoulli distribution of elements with the parameter $p=c/S$, always do not hold in true food webs. The total of relative errors of predator-prey sub-web is significantly greater than that of the full food web (0.036). It means that the cascade model is more appropriate in predicting the full food web with parasites.

3.2.2 Fitting arthropod food webs

As indicated in Table 4, proportions of different trophic levels of species of arthropod food webs are different from Briand and Cohen (1984). Fitting deviation of FW2 is larger than that of other three arthropod food webs. Also, proportions of different link types of arthropod food webs are different from Briand and Cohen (1984).

Calculated number of intermediate species - intermediate species links using cascade model are larger than the total links, which is actually impossible. The calculated number of total links for four arthropod food webs (FW1=81, FW2=175, FW3a=69, and FW3b=97) are basically coincident with the observed ones (78, 172, 66 and 93). Chi-square test ($\chi^2_{0.05,3}$=7.815) indicates that fitting goodness is worse for all arthropod food webs.

Table 4 Fitting topological properties of arthropod food webs.

		FW1			FW2			FW3a			FW3b		
		Obs.	Fit.	Rel. error	Obs.	Fit.	Rel. error	Obs.	Fit.	Rel. error	Obs.	Fit.	Rel. error
Species	T	13	4	20.25	31	9	53.78	11	4	12.25	12	3	27
	I	11	18	2.72	24	39	5.77	10	15	1.67	10	18	3.56
	B	2	4	1	2	9	5.45	2	4	1	2	3	0.33
	χ^2			23.97			65			14.92			30.89
Links	BI	5	23	14.09	19	55	23.57	5	20	11.25	5	21	12.19
	BT	0	1	1	0	1	1	0	1	1	0	2	2
	II	21	**195**(*34*)	*4.97*	32	**1314**(*65*)	*16.75*	11	**142**(*28*)	*10.32*	14	**135**(*53*)	*28.7*
	IT	52	23	36.57	121	55	79.2	50	20	45	74	21	133.76
	χ^2			56.63			120.52			67.57			176.65

Note: T, I and B denotes the proportion of top species, intermediate species and basal species, divided by total species, respectively; BI, BT, II, and IT represents the proportion of basal-intermediate links, basal-top links, intermediate-intermediate links and intermediate-top links, divided by total links in the food web. Relative error = (observed-predicted)^2/observed. Bold values were calculated by the sixth formula in the text. Italic values were calculated by subtracting the other three types of links from total links.

4 Major Conclusions

Major conclusions are drawn from the present study as follows

(1) Median and mean of generality and vulnerability for predator-prey and parasite-host sub-webs are greater than the reported previously. Inclusion of parasites significantly increases the mean generality and vulnerability of the full food web.

(2) Fitting goodness of cascade model on predator-prey sub-web without parasites is lower than that on the full CSM food web. Also, cascade model performs worse in fitting arthropod food webs.

5 Discussion

In the food web studies, the precise definition of species is important. Here we used the conventional definition, i.e., taxonomical species. It was suggested that trophic species should be adopted in order to avoid methodological biases (Williams and Martinez, 2000). Because parasites always have complex life cycles and multiple host species (Marcogliese and Cone, 1997), we may choose to treat a parasite species as several “species” based on its life stages. Furthermore, an individual can sometimes be treated as a “species” (Ings et al., 2009).

In addition to the present methods, we may analyze the intervality and grouping of the full food web. For example, Huxham et al. (1996) calculated the non-triangulated quads of a food web and found that parasites reduced the intervality of the food web. In the grouping method, there are several subgroups in a food web. Many strong interactions exist within a subgroup but there are a few weak interactions between subgroups. Theoretically the grouping enhances the stability of the food web (Pimm and Lawton, 1980; Krause et al., 2003). In the future studies, we suggest combining mutualistic webs (Ings et al., 2009). In addition, all links were treated to be equivalent in present study. Ideally, the interaction strength of food web links can be considered in the future studies (Rydelek et al., 1992; Berlow et al., 2004; Zhang, 2007; Banasek et al., 2009; Zhang, 2011).

According to Dunne et al. (2013), parasites could uniquely change the topological structure of in terms of motifs, breadth and contiguity of feeding niches. These factors should be further considered in the future.

In present study we only used the cascade model to fit the topological structure of food webs. Niche model and inverse niche model have been used to CSM food webs in previous studies (Dunne et al., 2013; Warren et al., 2010). The niche model fitting of 14 properties of the food webs containing parasites was not so accurate compared to the food web without parasites, which are coincident with that of Warren et al. (2010). Reduction of fitting goodness can be attributed to the two reasons. First, fitting goodness decreases with the increase of number of total species (e.g., addition of parasites), regardless of whether there are parasites in the food webs. Second, parasites have broad trophic niches and more niche gaps, and moreover, a parasite has a smaller secondary trophic niche. Parasites thus do not follow the assumption of the niche model that species should possess continuous or nearly continuous trophic niche. Therefore the niche model is not suitable to the food webs with parasites. The inverse niche model, proposed by Warren et al. (2010), was proved to be the best among five models in fitting topological properties of food webs. However, there are still not standard methods to evaluation these models. Evaluation of models is suggested using some methods like the likelihood method (Allesina et al., 2008).

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References

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

Banasek-Richter C, Bersier LF, Cattin MF, et al. 2009. Complexity in quantitative food webs. Ecology, 90(6): 1470-1477

Berlow EL, Neutel AM, Cohen JE, et al. 2004. Interaction strengths in food webs: issues and opportunities. Journal of Animal Ecology, 73(3): 585-598

Briand F, Cohen JE. 1984. Community food webs have scale-invariant structure. Nature, 307(5948): 264-267

Cohen JE, Newman CM. 1985. A stochastic-theory of community food web. 1. Models and aggregated data. Proceedings of the Royal Society of London B Biological Science, 224: 421-448

Dunne JA, Lafferty KD, Dobson AP, et al. 2013. Parasites affect food web structure primarily through increased diversity and complexity. Plos Biology, 11(6): e1001579

Gu DX, Xia Q, Zhang GR, et al. 2006. The paddy spider community structure and trophic relationships. In: Structure and Fucntions of Spider Communities in Paddy Fields of China (Wang HQ, ed). 136-141, Hunan Normal University Press, Changsha, China

Huxham M, Beaney S, Raffaelli D. 1996. Do parasites reduce the chances of triangulation in a real food web? Oikos, 284-300

Ings TC, Montoya JM, Bascompte J, et al. 2009. Ecological networks - beyond food webs. Journal of Animal

Ecology, 78(1): 253-269

Krause AE, Frank KA, Mason DM, et al. 2003. Compartments revealed in food-web structure. Nature, 426(6964): 282-285

Kuang WP, Zhang WJ. 2011. Some effects of parasitism on food web structure: a topological analysis. Network Biology, 1(3-4): 171-185

Lafferty KD, Allesina S, Arim M, et al. 2008. Parasites in food webs: the ultimate missing links. Ecology Letters, 11(6): 533-546

Lafferty KD, Dobson AP, Kuris AM. 2006. Parasites dominate food web links. Proceedings of the National Academy of Sciences of the United States of America, 103(30): 11211-11216

Liu WH. 2009. The construction of paddy predatory arthropod food web. Journal of Xiangtan Normal University (Natural Science Edition), 31(1): 56-59

Liu YF, Gu DX, Zhang GR, et al. 2002a. Enemy-linked immunosorbent assay used to explore the predation of *Chironomus sp.* (*Diptera: Chironomide*) by predators in paddy fields. Acta Ecologica Sinica, 22(10): 1699 -1703

Liu YF, Gu DX, Zhang GR, et al. 2002b. The structure analysis of predatory food webs in paddy ecosystem. In: Entomology Innovation and Development Engineers. Beijing: China Science and Technology Press, China, 207-213

Marcogliese DJ, Cone DK. 1997. Food webs: a plea for parasites. Trends in Ecology and Evolution, 12: 320-325

Memmott J, Martinez ND, Cohen JE. 2000. Predators, parasitoids and pathogens: species richness, trophic generality and body sizes in a natural food web. Journal of Animal Ecology, 69(1): 1-15

Montoya JM, Pimm SL. 2006. Sole R. V.. Ecological networks and their fragility. Nature, 442(7100): 259-264

Navia AF, Cortes E, Mejia-Falla PA. 2010. Topological analysis of the ecological importance of elasmobranch fishes: A food web study on the Gulf of Tortugas, Colombia. Ecological Modelling, 221(24): 2918-2926

Pascual M, Dunne JA. 2006. From Small To Large Ecological Networks in A Dynamic World. 3-24, Oxford University Press, New York, USA

Pimm SL, Lawton JH. 1980. Are food webs divided into compartments? The Journal of Animal Ecology, 879-898

Pimm SL, Lawton JH, Cohen JE. 1991. Food web patterns and their consequences. Nature, 350: 669-674

Rydelek PA, Sacks IS, Pacheco JF, et al. 1992. Food-web analysis through field measurement of per capita interaction strength. Nature, 355: 73

Schoener TW. 1989. Food webs from the small to the large: The Robert H. MacArthur Award Lecture. Ecology, 70(6): 1559-1589

Warren CP, Pascual M, Lafferty KD, et al. 2010. The inverse niche model for food webs with parasites. Theoretical Ecology, 3(4): 285-294

Williams RJ, Martinez ND. 2000. Simple rules yield complex food webs. Nature, 404(6774): 180-183

Zhang WJ. 2007. Computer inference of network of ecological interactions from sampling data. Environmental Monitoring and Assessment, 124: 253-261

Zhang WJ. 2011. Constructing ecological interaction networks by correlation analysis: hints from community sampling. Network Biology, 1(2): 81-98

Zhang WJ. 2012a. Computational Ecology: Graphs, Networks and Agent-based Modeling. World Scientific, Singapore

Zhang WJ. 2012b. Several mathematical methods for identifying crucial nodes in networks. Network Biology, 2(4): 121-126