

Article

## Effects of parasitism on robustness of food webs

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### Abstract

Food webs are always self-organizing systems. Parasitism is ubiquitous and important in the food webs. In present study we analyzed the CSM food web with parasites and the predator-prey sub-web without parasites based on some topological indices in order to understand the effects of parasitism on robustness of food webs. The results showed that parasites dominated the food web links. The full CSM food web had more basal species and preys, and the predator-prey sub-web without parasites had more top species and predators. Existence of parasitism did not affect the similarity degree of free-living species, but would reduce the robustness of food web and increase intervality and clustering coefficient of food web.

**Key words** parasites; CSM; food web; similarity; robustness; intervality; clustering coefficient.

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### 1 Introduction

Studies on ecological networks provide a powerful framework for ecology; it solves complexity of interactions between species and species, and species and the environment, and quantifies the direct and indirect effects of interacting species (McCann, 2000; Montoya et al., 2006; Pascual and Dunne, 2006; Brose and Dunne, 2007; Cardinale et al., 2009; Zhang 2011, 2012a, 2012b, 2012c; Jiang and Zhang, 2015). As a type of ecological networks, food webs are always self-organizing systems. Food webs describe ecological communities through nutritional relationships among species (Cohen et al., 1990; Martinez, 1992; Pimm et al., 1991; Williams and Martinez, 2000). Research of food webs includes the effects of relationships among species, habitat heterogeneity, environmental changes and nutritional dynamics on the structures of communities (Dunne et al., 2002a; Stouffer et al., 2007), the construction of models fitting the structural properties of food webs (Williams and Martinez, 2000; Petchey et al., 2008), and prediction of ecosystem changes from species deletions or extinctions. The applications of food web theory help to enhance pest control, prevent alien species, and so on (Winemiller and Polis, 1996). Therefore, food webs and ecosystem stability have drawn more and more

attentions worldwide (Dunne et al., 2005; May, 2006; Allesina and Pascual, 2008). However, the published food webs were different in terms of quality and details, and most analyzed the interactions among free living species, ignoring parasites. Parasitism is the most common existence, although parasites may be difficult to detect (Price, 1980).

Food webs are the topics of basic ecological research, such as the stability, diversity and complexity of ecosystems, so study on the impacts of parasites on the structure, dynamics and function of food webs is crucial (Pascual and Dunne, 2006). Parasites are important components of biodiversity, and often penetrate in the food web with their complex life cycle. More and more people have realized that the role of parasites in the ecosystem is important, and conducted a number of studies (Huxham et al., 1995; Marcogliese, 2003; Lafferty et al., 2006a, 2006b, 2009; Hernandez and Sukhdeo, 2008; Amundsen et al., 2009; Dunne et al., 2013). Parasites can get a lot of biomass in ecosystems, and have similar abundance and productivity with some free-living species, which may extend the applicable universality of metabolic ecology theory (Kuris et al., 2008; Hechinger et al., 2011). Because parasites have complex life cycles, they may require different multiple hosts in different stages of their lives, and contact hosts in different status in different ways. Therefore, parasites can modulate host richness (Anderson and May, 1978), and this regulation may reconstruct the entire community, and then change the ecosystem function (Sato et al., 2012).

Overall, parasites seem to have increased the complexity of the food web, potentially improved the biodiversity and productivity, and thus changed the stability of ecosystems (Dobson et al., 2006; Wood, 2007; Allesina and Pascual, 2008). There were a lot of researches showed that the addition of parasites can change the structure of food webs (Huxham et al., 1995; Lafferty et al., 2006a; Kuang and Zhang, 2011; Amundsen et al., 2012; Jiang and Zhang, 2015), but further test of the applicability of these findings and exploration of the impact of parasites on topological structures of different food webs is still a problem that needs to be settled. Topological properties of food webs, such as the number of species,  $S$ , and the number of links,  $L$ , can assess species richness. Other properties, such as connectance,  $C$  (equals to  $L / S^2$ ) and link density,  $D$  (equals to  $L / S$ ), can quantify the complexity of networks, and they are also important determinants of stability (Dunne, 2006; Allesina and Pascual, 2008; Zhang, 2011, 2012a, 2012b).

Carpinteria Salt Marsh food web (Lafferty et al., 2006b) is a topological network with high resolution. It describes the feeding relationships between predators and preys. The CSM food web is by far the relatively complete food web containing parasites. The predator-prey sub-web seems to be a complete CSM food web without parasites. Lafferty et al. (2006a, 2006b, 2008, 2009) found that connectance increased significantly after adding parasites, which made the network more complex. Interspecificity is a Boolean term, which refers to the niche overlap of predators in food webs, that is, if they can be described in one dimension, then the food web is interval (Cohen, 1978). Cohen et al. (1990) pointed out that the published food webs with higher interspecificity were due to smaller food webs. Warren (1994) showed that lower interspecificity in the higher food web might be caused by the incomplete data. Studies had shown that the size of the network had a significant impact on interspecificity of food web, and then the network turned into a complete triangulated structure (Pimm, 1982; Cohen and Palka, 1990; Cohen et al., 1990; Pimm et al., 1991). Triangulated structure is a complete sub-web composed of three vertices. All interval food webs have triangulated structures (Pimm, 1991). Therefore, the study on triangulated structures can better illustrate the basic features than interspecificity (Sugihara, 1984).

In this paper we excluded the limit of food web size by measuring the triangulated structure. In addition, we also analyzed CSM food web with hierarchical clustering method, which aimed to pick out those species with similar relationship model according to the similarity of species, thus peering into the coherence of a food web. The structural difference of food webs would be revealed in the analysis of these topological characteristics, which could determine the direct reaction of ecosystem faced disturbance to the environment.

Robustness is a system property to reflect stability of structure and function of food webs as uncertainty factor from external and internal disturbs them (Dunne et al., 2002b). Here we described the topological properties of the complete CSM food web and its predator-prey sub-web, aimed to compare the robustness of the food web with/without parasites by using the latest analytical methods.

## 2 Material and Methods

### 2.1 Material

#### 2.1.1 Data sources

Data were collected from the food web, Carpinteria Salt Marsh, California, reported by Lafferty et al. (2006a, 2006b, 2008). CSM food web includes four sub-webs, predator-prey sub-web, predator-parasite sub-web, parasite-host sub-web, and parasite-parasite sub-web. The CSM network contains eight kinds of basic species, 75 kinds of free-living species and 45 kinds of parasites (Kuang and Zhang, 2011; Jiang and Zhang, 2015). So the matrix of the complete CSM network is  $128 \times 128$ , and predator - prey sub-web is  $83 \times 83$  (<http://www.nceas.ucsb.edu/interactionweb/html/carpinteria.html>).

#### 2.1.2 Data conversion

Species were labeled with ID codes. In the Pajek environment, choose the directory and execute the command as follows: Open data → Data editors → Matrix editor, in the UCINET software, and save them as the files in “.##h” format. Finally, choose the directory and execute the command: File → Open → Ucinet dataset → network, in Netdraw software; choose and open the “.##h” file, and then save it to the file in “.net” format by the command: File → Save data as → Pajek → Net file. The resultant four “.net” files formed the basis for topological analysis (Kuang and Zhang, 2011; Jiang and Zhang, 2015).

### 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.

The Pajek step of triangulated structures: (1) Net → Transform → Arcs-Edges → All; (2) Build a net file of simple undirected complete triangulated group; (3) Nets → Fragment (First in Second) → find; (4) View results in the report page.

The Pajek step of Hierarchical clustering: (1) Cluster → Create Complete Cluster; (2) Operations → Dissimilarity → Network based → dl → All; (3) View results in the report page and save the tree in EPS format.

#### 2.2.2 R software

R is a complete set of data processing, computing and mapping software system. It not only provides a lot of statistical procedures, by which users can specify databases and parameters they need, but also provides some integrated statistical tools, by which users can create a flexible application of statistical calculation methods in line with their needs. In this paper, we used R software version 2.13 and the libraries Igraph package.

The R language codes of CDD analysis are as follows:

```
x < -v2
summary(x)
library(igraph)
split.screen(c(1,2))
```

```
screen(1)
```

```
plot(tabulate(x), log = "xy", ylab = "Frequency (log scale)", xlab = "Degree (log scale)", main = "Log-log plot of degree distribution", cex.main = 0.9, cex.lab = 0.9, cex.axis = 0.9)
```

```
screen(2)
```

```
y <- (length(x) - rank(x, ties.method = "first"))/length(x)
```

```
plot(x, y, log = "xy", ylab = "Fraction with min. degree k (log scale)", xlab = "Degree (k) (log scale)", main = "Cumulative log-log plot of degree distribution", cex.main = 0.9, cex.lab = 0.9, cex.axis = 0.9)
```

```
close.screen(all = TRUE)
```

```
power.law.fit(x, xmin = 50)
```

### 2.2.3 Some topological indexes of food webs

For the CSM food web and its predator-prey sub-web analyzed, we calculated four standard topological parameters: the number of species  $S$ , the number of links  $L$ , link density  $L/S$  and connectance  $C$  (Table 1). We also analyzed the cumulative degree distribution ( $CDD$ ), namely the frequency distribution of the link number of each species in food web, which also known as degree distribution of network (Estrada, 2007; Albert and Barabási, 2002). We summarized five properties of species in different trophic levels: top species  $T$ , intermediate species  $I$ , basal species  $B$ , predator category ( $Pred$ ) and prey category ( $Prey$ ), and counted their proportion, respectively. Table 1 summarized 12 topological indices and their definition.

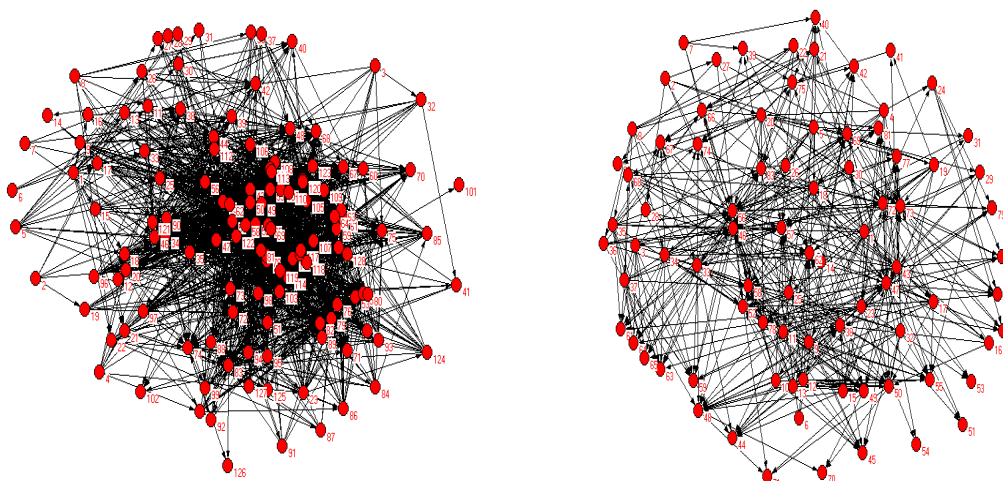
**Table 1** Definition of 12 structural properties of food webs.

Abbreviation	Indices	Definition	Sources
$S$	Number of species	Number of species (nodes) in the food web.	Dunne et al. (2013)
$L$	Number of links	Number of trophic feeding relationships in the food web.	Dunne et al. (2013)
$L/S$	Link density	Mean number of links per species.	Dunne et al. (2013)
$C$	Connectance	Proportion of possible trophic links that are realized. also referred to as 'directed connectance'. $C=L/S^2$ , where $S^2$ is the number of possible links, and $L$ is the observed number of links.	Dunne et al. (2013)
%- $T$	Proportion of top species	Top species are those that have preys but no predators in the food web.	Dunne et al. (2013)
%- $I$	Proportion of intermediate species	Intermediate species are those that have both preys and predators in the food web.	Dunne et al. (2013)
%- $B$	Proportion of basal species	Basal species are those that have predators but no preys in the food web.	Dunne et al. (2013)
%- $Pred$	Proportion of predator	Predator species are those that have at least one prey in the food web.	Cohen et al. (1990)
%- $Prey$	Proportion of prey	Prey species are those that have at least one predator in the food web.	Cohen et al. (1990)
$CDD$	Cumulative degree distribution	Cumulative distribution of the number of links that each species in the food web has.	Estrada (2007)
$Clus$	clustering coefficient	Average fraction of pairs of species one link away from a particular species also linked to each other.	Dunne et al. (2013)
$TS$	Triangulated structure	Triangulated structure is a complete sub-web composed of three vertices.	Huxham et al. (1996)

### 3 Results

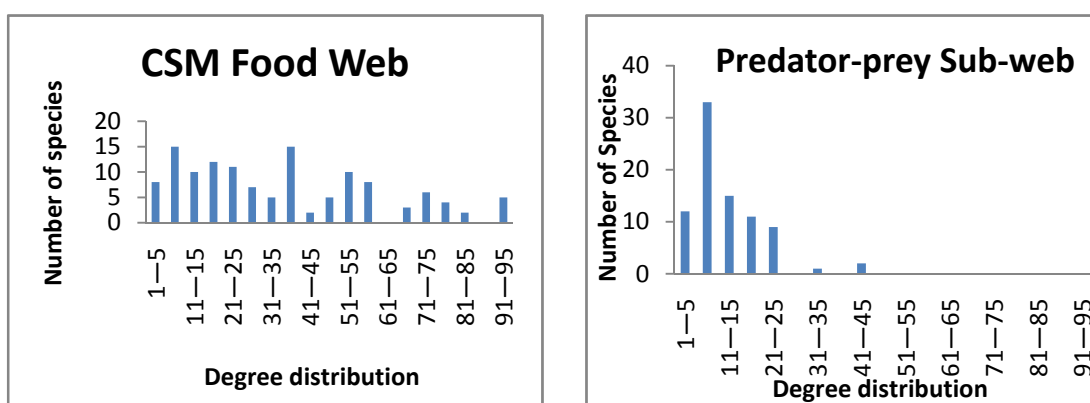
#### 3.1 Species categories analysis

The number of species and links differs considerably between CSM food web and predator-prey sub-web (see fig. 1). The complete CSM food web has 128 nodes and 2290 links, and predator-prey sub-web only has 83 nodes and 496 links. Despite parasites occupied 35.16% of the total species, about 78.34% of the total links are associated with parasites, which means that parasites dominate the food web links. The link density and connectance of CSM food web are 17.891 and 0.14, respectively; and predator-prey sub-web are 5.976 and 0.072, respectively. The number of species in CSM food web increases after adding parasites, and increases the number of links, link density and connectance significantly.



**Fig. 1** The relationships of species in the full food web (Left) and predator-prey sub-web (Right). Each node represents a species, and a link between two species represents a relationship between them.

As shown in Fig. 2, the degree of species in CSM food web with parasites is bigger than predator-prey sub-web. The average degree of CSM food web is 36.78, while for predator-prey sub-web is 12.28. Species with the maximum link number in predator-prey sub-web is *Pachygrapsus crassipes* (there are 45 links); while in CSM food web it is *Mesostephanus appendiculatoides* (up to 95 links). Although *Pachygrapsus crassipes* does not have the biggest number in CSM food web, its link number also increases from 45 to 78.



**Fig. 2** The degree distribution of the full food web (Left) and predator-prey sub-web (Right).

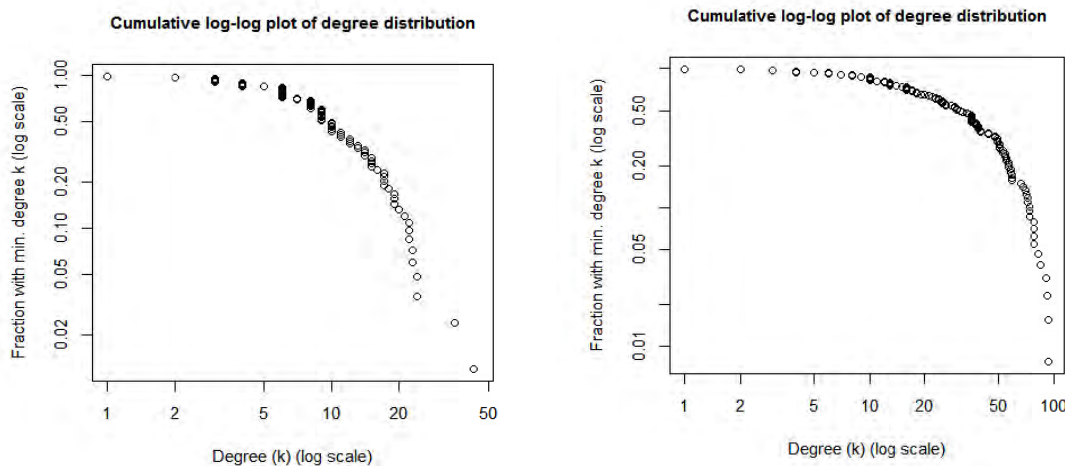
The topological properties of CSM food web and predator-prey sub-web are indicated in Table 2. The ratio of predators to preys in CSM food web is 0.96, and the proportion in predator-prey sub-web is 1.5. In other words, CSM food web has more preys, and predator-prey sub-web has more predators. Furthermore, the ratio of  $T : B$  is 0.375 (i.e., 3/8) while predator-prey sub-web is 4.125 (i.e., 33/8). The number of top species considerably reduces after adding parasites, indicating the CSM food web may become more complicated. The reason may be that top species in predator-prey sub-web become intermediate species after they are parasitized, and parasites are fed by other species, which causes a significant reduction in the top species. In summary, the number of preys in CSM food web is bigger than predators (the ratios  $T : B$  and  $Pred : Prey$  are both  $< 1$ , at 0.375 and 0.96, respectively), while predator-prey sub-web has more predators than preys ( $T : B = 4.125$ ,  $Pred : Prey = 1.5$ ; Table 2).

**Table 2** The topological properties of the full food web and predator-prey sub-web.

Topological indices	CSM food web	predator-prey sub-web
$S$	128	83
$L$	2290	496
$L/S$	17.891	5.976
$C = L/S^2$	0.140	0.072
%- $T$	2.34(3)	39.76(33)
%- $I$	91.41(117)	50.60(42)
%- $B$	6.25(8)	9.64(8)
$T/B$	0.375	4.125
%- $Prey$	0.977(125)	0.602(50)
%- $Pred$	0.938(120)	0.904(75)
$Pred/Prey$	0.96	1.5

### 3.2 Robustness analysis

As shown in Fig. 3, the difference of cumulative degree distributions between CSM food web and predator-prey sub-web is not distinct. The CSM food web shows a power-law distribution while predator-prey sub-web shows two different behaviors, namely an initial power law distribution followed by an exponential decay tail. A food web with power law distribution is the most vulnerable to external attack, demonstrating the CSM food web is more vulnerable to external attack, namely the robustness of the complete CSM food web is lower than that of predator-prey sub-web.

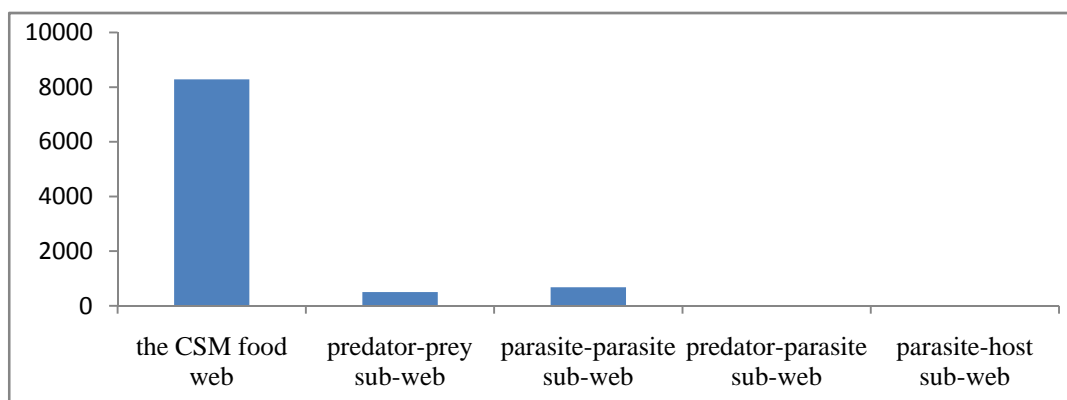


**Fig. 3** Cumulative degree distribution (CDD) of the CSM food web (Left) and predator-prey sub-web (Right). Degree ( $k$ ) denotes the nodes of a food web that have at least  $k$  links (both predator and prey links).

Lafferty and Kuris (2009) proposed that robustness of food webs refers to the proportion of primary extinctions that leads to a particular proportion of total extinctions. In general, free-living species rarely suffer secondary extinction; by contrast, it is common for parasites to suffer secondary extinction because of their complex life cycle. The predator-prey sub-web is very robust to random species extinctions, its maximum value of robustness is 50%, the median value is 49%, and the minimum is 44%. However, the maximum value of the CSM food web with parasites is 49%, the median value is 43%, and the minimum is 30%, which further illustrates the addition of parasites will reduce the robustness of the food web.

### 3.3 Triangulated structure analysis

We calculated the number of triangulated structure of CSM food web and its four sub-webs using Pajek software. The results are as follows: there are 8287 triangulated structure fragments in the CSM food web, and 504 triangulated structure fragments in the predator-prey sub-web, and 680 triangulated structure fragments in the parasite-parasite sub-web, but there is none in the parasite-host sub-web and predator-parasite sub-web, as seen as Fig. 4. However, connectance of CSM food web, parasite-parasite sub-web and predator-prey sub-web are 0.1398, 0.0849 and 0.072, respectively. Adding parasites, the number of triangulated structures of CSM food web is more than predator-prey sub-web.



**Fig. 4** The number of the triangulated structure of the full CSM food web and four sub-webs.

Warren (1994) suggested that the reduced intervality of published large-scale food webs may reflect the decrease of connectance of these networks. High connectance can increase the intervality possibility of food webs, which is consistent with the conclusion in this paper. In addition, due to the addition of parasites, the number of triangulated structure of CSM food web is 16 times of predator-prey sub-web, and the number of triangulated structure of parasite-parasite sub-web is also higher than predator-prey sub-web. So we can make a conclusion that parasites increase the number of triangulated structure of food webs. The reason may be: (1) intrinsic characters of parasites. Parasites are smaller, and they usually parasitize on hosts whose body size is bigger than themselves; (2) parasites have complex life cycles, which involves "different feeding stages" (Yodzis, 1984) or "omnivorous life history" (Pimm and Rice, 1987), and (3) The increase of triangulated structure may reflect the change of connectance. Although the above three factors may affect the number and type of niche overlap, these results indicate that parasites have a strong impact on the triangulated structure of food webs.

### 3.4 Similarity analysis (hierarchical clustering)

The clustering coefficients of CSM food web and predator-prey sub-web are 0.185 and 0.094, respectively. The larger clustering coefficient is, the greater probability of parasitism is; namely the spread speed of disease

is faster. Using hierarchical clustering algorithm can compute dissimilarity of different nodes, and then build a tree based on the similarity, as shown in Figs 5, 6. Dissimilarity is calculated based on the network structure, the more adjacent nodes two nodes share, the more similar they are. In this paper, the dissimilarity value of two nodes refers to the number of adjacent nodes which are not shared by the two nodes. The indicator takes the incoming links and outgoing links into consideration, increasing the accuracy of the analysis results.

Fig. 6 shows the tree of CSM food web, which can clearly distinguish two very dissimilar cloud groups: one cloud group consists of 85 species, including all basal species, parasites, and a few free-living species; the other cloud group consists of 43 free-living species. Compared with the tree of predator-prey sub-web, we can find that parasites do not affect the similarity degree of free-living species, such as species No. 56 and No. 46, who are similar in the CSM food web and predator-prey sub-web.

#### 4 Conclusions and Discussion

Previous studies have shown that parasites are an important part of food webs, and they have a greater effect on the structure and function of nutrition network. Addition of parasites leads to the multiplied links of food web that may cause changes of some topological properties, such as link density, connectance, and degree of nodes and so on. And the increase of these properties mean that the food web becomes more complex (Allesina and Pascual, 2008; Lafferty et al., 2008). Parasites are direct or indirect correlated with other species, and increase species richness of food webs. In this paper, we verified that parasites play a very important role in the food web. Specific results are as follows:

- (1) Most of links are contacted with parasites; parasites dominate the food web links. So adding parasites into the food web is important and necessary.
- (2) Change of the ratios  $T : B$  and  $Pred : prey$ . The predator-prey sub-web has more top species and predators, and CSM food web has more basal species and preys.
- (3) Reduction of the robustness of food web. From the results of cumulative degree distribution analysis and secondary extinctions caused by the removal of species, the robustness of CSM food web with parasites was lower than predator-prey sub-web without parasites.
- (4) Increase of the intervality of food webs. Triangulated structure analysis shows that parasites increase the number of triangulated structure fragments.
- (5) Increase of the clustering coefficient. There is a significant difference in the similarity of parasites and free-living species. Addition of parasites does not affect the similarity degree of free-living species.

Our results showed that link density and connectance were different in CSM food web and predator-prey sub-web. The link density and connectance of CSM food web were greater than predator-prey sub-web, especially the link density of CSM food web was about three times ( $17.891/5.976$ ) of predator-prey sub-web. MacArthur (1955) proposed that the complexity of a food web was a key feature of the stability of food webs. He also defined the food web complexity for the diversity of energy flow paths, and typically measured by link density and connectance. So it can be considered that stability of food webs enhances as link density and connectance increase. All changes of these properties are related to species diversity and complexity of food web, for example, consumer diversity is affected by the ratio of predators and preys (Bruno and O'Connor, 2005), and the increase of prey diversity reduces the number of plants and herbivores (Shurin et al., 2002; Thébault et al., 2007), and the increase of predator diversity strengthens nutritional cascade effects (Bruno and O'Connor, 2005). Because predator-prey sub-web has more top species and predators, so it might be sensitive to the missing of top species, and the secondary extinction in this food web would spread faster. In contrast, the CSM food web is more sensitive to the removal of basal species.



**Pajek - General 0.63 0.63 -0.25 0.00 [0.00,1.76]**

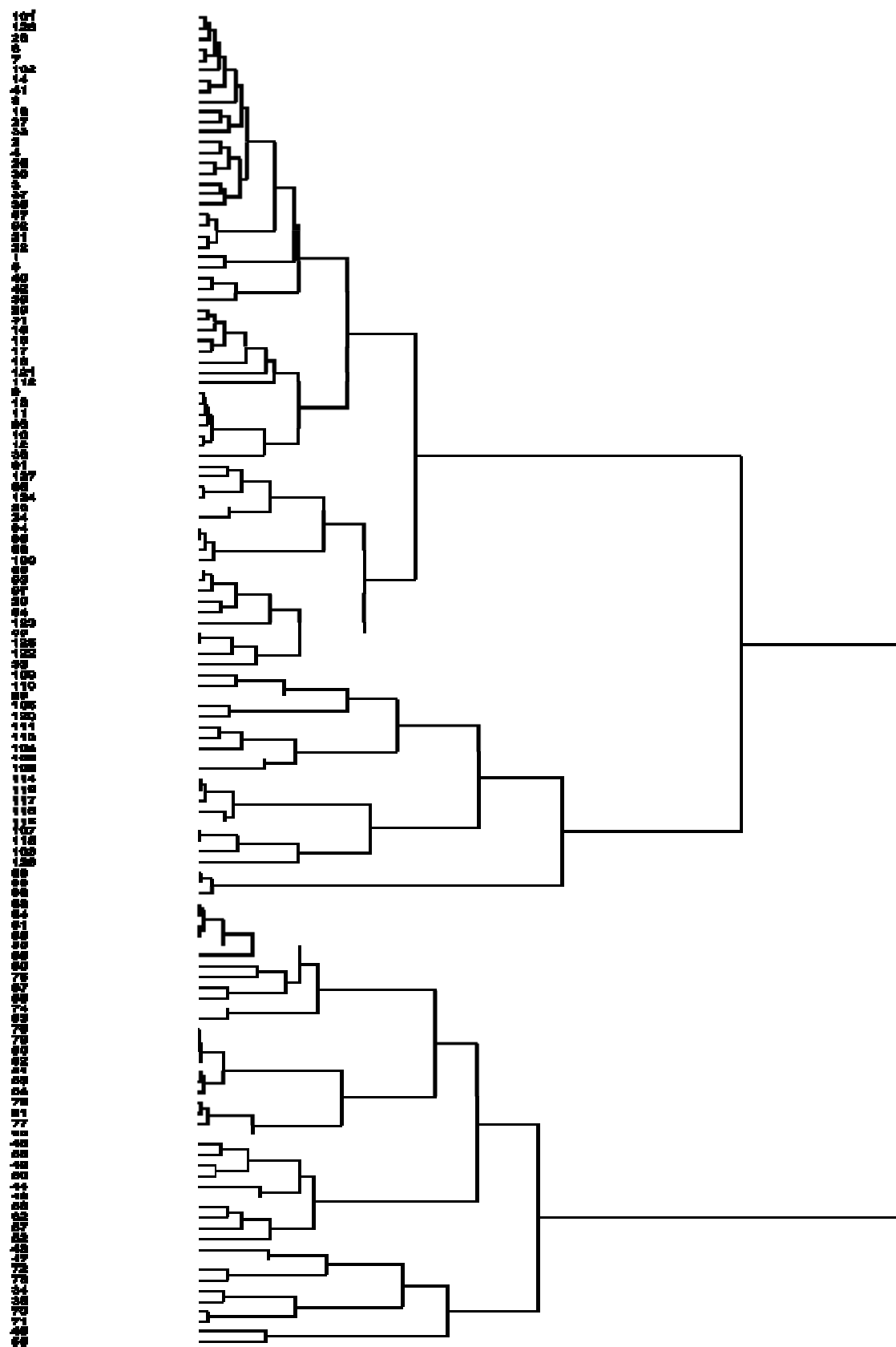


Fig. 5 The hierarchical clustering of the predator-prey food web.

# Pajek - Ward [0.00,2.45]

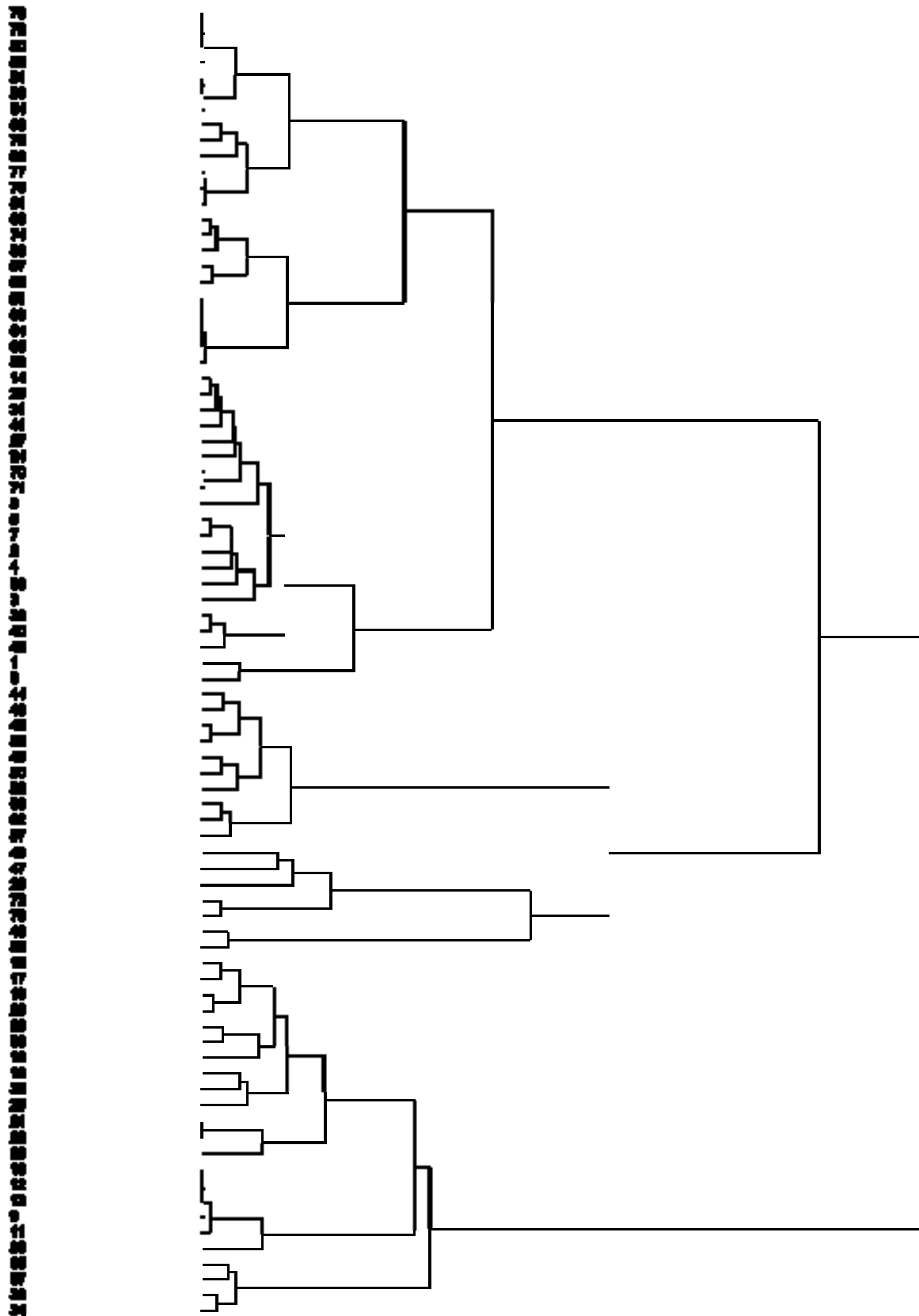


Fig. 6 The hierarchical clustering of the predator-prey food web.

Although the cumulative degree distribution of the CSM food web and its predator-prey sub-web showed a few difference, it should has a great impact on the robustness of food webs. Albert et al. (2000) proposed that networks performing power-law distribution CDD are more vulnerable to the removal of the node with the most links, which leads to a catastrophic collapse of the network. Networks with exponential decaying are also fragile to the missing of the most connected node, but better tolerated than networks performing power-law distribution (Albert et al., 2000; Estrada, 2007). However, networks with exponential decaying are more vulnerable to the removal of a random node, under the same conditions; the power-law networks have no threshold. Therefore, power-law distribution of CSM food web suggests that it may be more vulnerable to the removal of the most connected nodes, and exponential decaying of predator-prey sub-web indicates that it may has lower robustness against random perturbations than CSM food web. This implies that the removal of the most connected node in the CSM food web, *Mesostephanus appendiculatoides*, may lead to the collapse of the entire network. Topological analysis of the two food webs suggests that predator-prey sub-web has the higher robustness against external disturbances than CSM food web. The reason may be due to that parasites in the CSM food web have extremely complicated life cycles. Although most published food web data did not take parasites into consideration, parasites are considered to be important indicators to maintain the integrity of food webs, and also important factor to detect the robustness and stability of food webs.

Due to the complex life cycles of parasites, adding parasites may increase intervality of food webs. But Huxham et al. (1995) proposed that parasites reduced intervality of the food web, and the reason may be that we did not separate the different life stages of parasites in this paper. Furthermore, in the process of studying triangulated structures by using Pajek software, every species had participated repeatedly in the formation of triangulated structures, which led to different conclusions with previous ones. Finally, we attempted to analyze the similarity of species in the food webs, and the results showed that adding parasites did not affect the similarity degree of free-living species. Parasites are prevalent (Price, 1980). Parasites have not only direct impact on food webs, such as the number of species, the number of links, the chain length, trophic level changes, but also indirect effects. Duun et al. (2012) proposed that parasites had an indirect impact on alien species invasion. Given parasites have bigger impacts on food webs, and yet food web data with parasites are still lacking. In future studies, we should further enhance the understanding of parasites, and build more comprehensive and rich food web data, in order to provide reliable scientific data support for future research.

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