



The reduction of food web robustness by parasitism: Fact and artefact

Hsuan-Wien Chen^{a,b}, Kwang-Tsao Shao^b, Chester Wai-Jen Liu^c, Wen-Hsieh Lin^d, Wei-Chung Liu^{e,*}

^a Department of Life Science, National Taiwan Normal University, 88 Ting-Chow Road Sec. 4, Taipei 11677, Taiwan

^b Biodiversity Research Center, Academia Sinica, 128 Academia Road Sec. 2, Nankang, Taipei 11529, Taiwan

^c Department of International Business, Chang Jung Christian University, 396 Chang Jung Road Sec.1, Kway Jen, Tainan 71101, Taiwan

^d Department of Biological Sciences, Virginia Polytechnic Institute and State University, Blacksburg, VA 24060, USA

^e Institute of Statistical Science, Academia Sinica, 128 Academia Road Sec. 2, Nankang, Taipei 11529, Taiwan

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ABSTRACT

A robust food web is one which suffers few secondary extinctions after primary species losses. While recent research has shown that a food web with parasitism is less robust than one without, it still remains unclear whether the reduction in robustness is due to changes in network complexity or unique characteristics associated with parasitism. Here, using several published food webs, simulation experiments with different food web models and extinction scenarios were conducted to elucidate how such reduction can be achieved. Our results show that, regardless of changes in network complexity and preferential parasitism, the reduction in food web robustness is mainly due to the life cycle constraint of parasites. Our findings further demonstrate that parasites are prone to secondary extinctions and that their extinctions occur earlier than those involving free-living species. These findings suggest that the vulnerable nature of parasites to species loss makes them highly sensitive indicators of food web integrity.

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1. Introduction

All species of an ecosystem are embedded within an intricate web of trophic interactions (Pimm et al., 1991). Due to the structural complexity arising from the direct and indirect trophic linkages among species, it is not always a simple problem to predict how changes in the abundances of some species may affect the entire food web (Yodzis, 2000). One pressing issue in food web research is to investigate the response of a web to species losses (Duffy, 2002; Dunne et al., 2002a; Ebenman et al., 2004; Eklof and Ebenman, 2006) as some human activities, such as over-fishing, habitat destruction and alien species invasion, may cause the extinction of native species and indirectly trigger the collapse of an ecosystem (Grosholz et al., 2000; Dobson et al., 2006; Baum and Worm, 2009).

One strategy for understanding the response of a food web to species losses is to study its robustness (Dunne et al., 2002a, 2004). Such a methodology has its roots in network science where the integrity of a network under random errors and targeted attacks was first investigated by Albert et al. (2000). Network robustness in the traditional sense mainly focuses on how structural properties of a network change when nodes are progressively removed from it (Albert et al., 2000); a network starts to disintegrate into isolated parts when the proportion of removed nodes passes a

certain threshold (Callaway et al., 2000). In ecology, the issue of food web robustness takes a different approach. With the exception of producers, all species in a food web rely on at least one other species for survival; thus the loss of a species, in particular a prey species, will reduce the diet range of its predator species. When all prey species consumed by a predator species become extinct, this then drives the predator's own extinction, which in turn might cause the extinction of other species at higher trophic levels (Dunne et al., 2002a). Thus the study of food web robustness concerns here the cascading secondary extinctions of species caused by primary species losses. Quantitatively speaking, the robustness of a food web can be defined as the number of primary extinctions required in order to result in a total loss of species beyond a predetermined threshold (Dunne and Williams, 2009). To date, most studies of food web robustness have focused on the relationship between robustness and network properties such as the degree of distribution (i.e. the distribution of a number of trophic links associated with a species), food web size and connectance (i.e. connectance is normally equal to link density, L/S^2 , where L is the total number of realised trophic links and S is the number of species in a food web, and S^2 gives the total number of possible trophic links) (Dunne et al., 2002a; Melian and Bascompte, 2002; Estrada, 2007; Gilbert, 2009). More recently, through a systematic study on a variety of food web models, it has been demonstrated that a food web is less likely to collapse if it has higher species richness and connectance (Dunne and Williams, 2009).

One practical issue regarding food web robustness is whether there exist leading indicators that can signal the integrity or the

* Corresponding author. Tel.: +886 2 27835611x214; fax: +886 2 27831523.

E-mail address: wliu56@gate.sinica.edu.tw (W.-C. Liu).

state of health of an ecosystem (Carpenter et al., 2008; Petchey et al., 2008). Potential candidates for such indicators include parasites. Parasites are ubiquitous in nature (Poulin, 1999) and several species have complex life cycles in which different developmental stages require different host species. Parasites are often transmitted from one host species to another through trophic interactions between their hosts (Lafferty, 1999), and the absence of parasite species with complex life cycles sends a strong signal indicating the possible breakage of food chains (Marcogliese, 2002; Hernandez et al., 2007; Valtonen et al., 2010). Therefore, it has been suggested that the presence of certain parasite species can be regarded as an indicator of ecosystem integrity (Bhuthimethee et al., 2005; Marcogliese, 2005; Palm and Ruckert, 2009). More recently, by adopting the approach of Dunne et al., 2002; Lafferty and Kuris (2009) demonstrated that a Californian salt marsh ecosystem is less robust to species losses with the inclusion of parasite species than without. The authors suspect this is probably due to the nature of the parasites' complex life cycles making them more prone to secondary extinction than non-parasitic species.

Although the reliance of parasites on specific host species at different stages of their life cycle can be a risk factor contributing to their sensitivity to secondary extinction, the addition of parasites into a food web may change the structure of the web and might potentially affect its robustness. For example, the inclusion of new species can change the degree of distribution and the connectance of a food web (Dunne et al., 2002b; Montoya and Sole, 2003; Jordan and Osvath, 2009), and it is well known that food web robustness is closely related to those two structural properties (Dunne et al., 2002a; Estrada, 2007; Dunne and Williams, 2009). Furthermore, it has been shown recently that parasitism does not occur at random locations within a food web (Chen et al., 2008); in particular, intermediate hosts utilised by the larval or juvenile stages of many parasite species tend to occupy important positions in a food web. Thus, we suspect that the reduction in robustness of a food web that includes parasites might also be due to host species occupying peculiar network positions within the web such that they are more prone to secondary extinction than other parasite-free species.

In this paper, we conduct a series of simulation experiments to demonstrate the influence of parasitism on food web robustness; by doing so, factors contributing to changes in food web robustness will be elucidated. Whether parasites are indeed good indicators of food web robustness will be determined by examining how sensitive they are to species losses in comparison with non-parasitic species. We perform our analysis on five published food webs in order to test the generality of our findings. First, we describe the data used in this study, followed by an account of methods used, including: (i) a definition of food web robustness; (ii) a detailed description of the simulation procedure for various extinction scenarios that teases apart factors that may or may not affect food web robustness; and (iii) how to assess the sensitivity of parasites

to secondary extinction. The results are followed by a discussion on whether the inclusion of parasites can reduce food web robustness and how this may be achieved. We then conclude with comments on parasites as indicators of ecosystem integrity.

2. Materials and methods

2.1. Food web data

Five published food webs that incorporate parasites were used in this study: "CAR", the Carpinteria salt marsh community near Santa Barbara, USA (Lafferty et al., 2006); "COM", the intertidal mudflat community of Company Bay in Otago Harbor, New Zealand (Thompson et al., 2005); "MUS", the forest stream community of Muskingum Brook in the New Jersey Pinelands, USA (Hernandez and Sukhdeo, 2008); "TAK", the pelagic community of the subarctic Lake Takvatn in Norway (Amundsen et al., 2009); and "YTH", the Ythan River estuary community in Scotland (Huxham and Raffaelli, 1995; Huxham et al., 1996). Each dataset contains predator–prey (i.e. who eats whom) and parasite–host interactions (i.e. who parasitises whom). The CAR, COM and TAK data also contain extra information on parasites as food sources for non-parasitic species and we define those as predator–parasite interactions. The size of the food webs and the number of different trophic links they include are summarised in Table 1.

2.2. Extinction simulation and food web robustness

An extinction simulation consists of a sequence of events, with T denoting the T^{th} event. Initially we set $T = 0$ and we start with an intact food web. The simulation then proceeds by repeating the following steps: (1) set $T = T + 1$; (2) during the T^{th} event, a species is selected randomly and then deleted from the food web, which we denote as the T^{th} primary extinction (note that in this study we assume producers have unlimited resource supply such that they will not go to extinction); (3) the remaining food web is then checked for species (bar producers) that are left with no prey species following the primary extinction, and those species are then deleted from the food web (here we assume a species becomes extinct when all of its food sources are absent); (4) step (3) is repeated until there are no further species losses; and (5) we denote those species deleted following the T^{th} primary extinction as the T^{th} secondary extinctions. Following Dunne and Williams (2009), the simulation then stops when the number of species remaining in the food web is less than half of the number of species in the original food web. If N and M represent the number of species in the original food web and the required number of primary extinctions, respectively, then the robustness of a food web, R_{50} , is defined as M/N .

An extinction sequence is also recorded for each simulation, and it contains information on: (i) in which T^{th} event extinction occurs;

Table 1

Summary of basic food web statistics for the datasets used in this study. These are: the numbers of non-parasite and parasite species followed by the numbers of predator–prey, parasite–host and predator–parasite interactions, and finally by the total number of trophic links in each food web. Included in parentheses is the connectance of the corresponding subweb (i.e. the predator–prey, parasite–host or predator–parasite sub-webs).

Food webs	No. Non-parasites	No. Parasites	Predator–prey	Parasite–host	Predator–parasite	Total links
CAR	83	45	496 (0.07)	630 (0.17)	992 (0.27)	2118 (0.13)
COM	67	9	494 (0.11)	71 (0.12)	42 (0.07)	607 (0.11)
TAK	37	12	193 (0.14)	75 (0.16)	159 (0.33)	282 (0.17)
MUS	48	14	216 (0.09)	66 (0.10)	N.A.	427 (0.07)
YTH	92	42	417 (0.05)	177 (0.05)	N.A.	594 (0.03)

N.A.: measures are not applicable. Also note that the overall numbers of trophic links and connectance were calculated from three sub-webs for CAR, COM and TAK webs and from only two sub-webs for MUS and YTH webs.

CAR, Carpinteria salt marsh; COM, Company Bay mudflat; TAK, Lake Takvatn; MUS, Muskingum Brook; YTH, Ythan River estuary.

(ii) whether a particular extinction involves a non-parasitic species or a parasitic species; and (iii) whether a particular extinction is a primary or secondary extinction. This information is then used to investigate whether parasites are more prone to secondary extinction than non-parasitic species. This can be done in two ways. First, the numbers of parasitic species involved in primary extinctions, Y_p , and secondary extinctions, X_p , are determined; similarly, the equivalent numbers are obtained for non-parasitic species and denoted as Y_{NP} and X_{NP} respectively. If Z_p is the number of parasitic species in a food web, then $Z_p - Y_p$ represents the number of parasitic species that could potentially be lost as secondary extinctions; thus the quantity $X_{p\%} = X_p / (Z_p - Y_p)$ denotes the proportion of parasitic species involved in secondary extinctions out of the available pool of parasitic species. Z_{NP} and $X_{NP\%}$ are similarly defined for non-parasitic species. If parasites are more sensitive to secondary extinction than non-parasitic species, then $X_{p\%}$ should be significantly larger than $X_{NP\%}$. Second, we argue that if parasitic species are more sensitive to species losses, then generally speaking their extinctions should occur earlier than those of non-parasitic species. In terms of T , secondary extinctions involving parasitic species should have smaller T values than those involving non-parasitic species. Since the values of T are not normally distributed, the median T can serve as a measure of central tendency of where in the event sequence secondary extinctions involving parasitic species occur, and we denote this as T_p . We then standardise T_p by dividing it with the maximum T , $T_{p,Max}$, to obtain $T_{p\%}$ (i.e. $T_{p\%} = T_p / T_{p,Max}$). Likewise, the equivalent statistics can be defined for non-parasitic species (i.e. T_{NP} and $T_{NP\%}$). If parasites are more sensitive to species losses than non-parasitic species, then $T_{p\%}$ should be significantly smaller than $T_{NP\%}$.

2.3. Extinction experiments

For each of the five food webs, a series of extinction experiments was conducted in order to investigate whether and how parasites affect food web robustness. Different extinction experiments consider different modifications of a food web, and for simplicity we refer to those as food web models; they are described in more detail in the next section. Each extinction experiment consisted of 1,000 extinction simulations; thus there are 1,000 values of R_{50} , $X_{p\%}$, $X_{NP\%}$, $T_{p\%}$ and $T_{NP\%}$, which in turn form their respective distributions.

2.4. Food web models

In order to elucidate the effect of parasitism on food web robustness, we performed extinction experiments using different food web models that account for changes in food web size, degree of distribution, connectance and preferential parasitism.

These models were:

- i. Predation only (H): this model only considers the interactions between non-parasitic species, namely the conventional predator–prey interactions.
- ii. Parasitism with (HP_{LC}) or without (HP) the life cycle constraints of parasites: here, both models include predator–prey and parasite–host interactions. In model HP_{LC} , a parasite species becomes extinct when all host species for any one of its developmental stages have gone extinct; whereas in model HP, this constraint is relaxed by assuming that a parasite species goes to extinction if and only if all of its host species have become extinct regardless of developmental stages. While the HP model seems not to be realistic at first glance, it may correspond to cases where parasites facultatively truncate their life cycles when one or more of their hosts are absent (Poulin and Cribb, 2002; Lagrue and Poulin, 2009).
- iii. Additional random predation (HH_R): one difference between food webs with and without parasitism is the increase in the numbers of nodes and links when parasites are included, resulting in changes in network complexity (e.g. degree distribution). In order to ascertain whether the change in food web robustness after adding parasites is indeed caused by factors that are different from those resulting from the simple addition of more predators, we must consider the following food web model (i.e. HH_R). First, the number of parasite species, A , is determined from model HP; model HH_R is then constructed by adding A new species to model H, with each of those newly added species having its number of prey species sampled from the in-degree distribution of model H (in-degree here refers to the number of prey species consumed by a predator species). For each of those new A species, all predator–prey links are connected to random positions in the food web model H. Moreover, each simulation was carried out by using a separately generated model HH_R .
- iv. Random parasitism with ($HP_{R,LC}$) or without (HP_R) the life cycle constraints of parasites: in order to investigate whether the change in food web robustness is due to the sensitivity of the host species' network positions to species losses, we must consider a model setting with random parasitism. Both models $HP_{R,LC}$ and HP_R are essentially the same as HP_{LC} and HP, respectively; the only difference here is that models $HP_{R,LC}$ and HP_R consider random parasitism by randomising the host species in all parasite–host interactions. Again, for those models involving randomisation, namely $HP_{R,LC}$ and HP_R , each simulation was carried out by using a newly generated food web.
- v. Parasites as food resources with ($HP_{F,LC}$) or without (HP_F) the life cycle constraints of parasites: of the five food webs used in this paper, three (CAR, COM and TAK) contain information

Table 2

Summary of the sub-webs used and other aspects considered in the food web models applied in the current study.

Models	Predator–prey interactions	Parasite–host interactions	Predator–parasite interactions	Parasite life cycle constraints	Random parasitism	Additional random predation
H	✓					
HP_{LC}	✓	✓		✓		
HP	✓	✓				
HH_R	✓					✓
$HP_{R,LC}$	✓	✓		✓	✓	
HP_R	✓	✓			✓	
$HP_{F,LC}$	✓	✓	✓	✓		
HP_F	✓	✓	✓			

H, predation only; HP, parasitism without life cycle constraints; HP_{LC} , parasitism with life cycle constraints; HH_R , additional random predation; HP_R , random parasitism; $HP_{R,LC}$, random parasitism with life cycle constraints; HP_F , parasites as food sources without life cycle constraints; $HP_{F,LC}$, parasites as food sources without life cycle constraints.

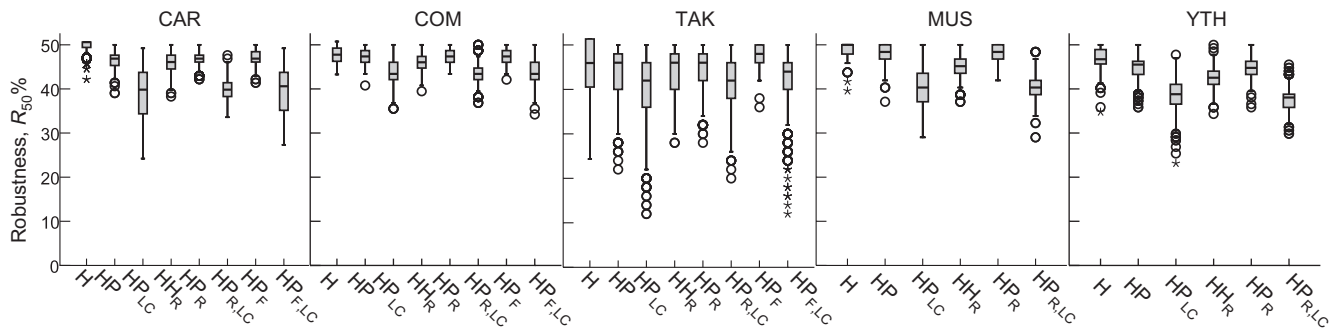


Fig. 1. Plots of food web robustness (R_{50}), showing medians, quartiles, outliers (\circ) and extreme values ($*$), based on the results of 1,000 simulations. Each sub-figure is the result considering specific food web models (i.e. H, HP, HP_{LC} , HH_R , HP_R , $HP_{R,LC}$, HP_F or $HP_{F,LC}$) for each of five food webs (CAR, COM, TAK, MUS, and YTH). Also noted that models HP_F or $HP_{F,LC}$ are available only for CAR, COM and TAK. H, predation only; HP , parasitism without life cycle constraints; HP_{LC} , parasitism with life cycle constraints; HH_R , additional random predation; HP_R , random parasitism; $HP_{R,LC}$, random parasitism with life cycle constraints; HP_F , parasites as food sources without life cycle constraints; $HP_{F,LC}$, parasites as food sources without life cycle constraints; CAR, Carpinteria salt marsh; COM, Company Bay mudflat; TAK, Lake Takvatn; MUS, Muskingum Brook; YTH, Ythan River estuary.

on predator–parasite interactions (i.e. parasites serving as food resources for some non-parasitic species). Here, models $HP_{F,LC}$ and HP_F are essentially the same as models HP_{LC} and HP , respectively, except that the new models also consider predator–parasite links. While the transmission and energetic significances of predators preying on parasites have been demonstrated in aquatic food webs (Hopper et al., 2008; Kuris et al., 2008; Johnson et al., 2010), these two new models provide an opportunity to further assess the impact of predation-on-parasites on food web robustness.

Table 2 summarises the similarities and differences among the above-mentioned food web models. Note that each parasite species is considered as a distinct node in a food web, and we do not consider a parasitic species with different developmental stages as different tropho-species.

3. Results

3.1. Food web robustness

By comparing the median robustness value (or median R_{50} for short) of model H with those of the other models, we can observe that increasing food web size, by including parasites or additional predators, often reduces food web robustness (Fig. 1). On average, adding more top predators in a random manner reduces median R_{50} by 3% from 48% (H) to 45% (HH_R), whereas adding parasites with no life cycle constraints only reduces median R_{50} by 1% from 48% (H) to 47% for models without parasite lifecycle constraints (i.e. HP , HP_R , and HP_F). The largest reductions in food web robustness are observed in models with parasite life cycle constraints: on average, median R_{50} declines by 7% from 48% (H) to 41% (i.e. HP_{LC} , $HP_{R,LC}$ and $HP_{F,LC}$).

To rule out the effect of unequal food web sizes and changing network complexity (e.g. degree of distribution) on food web robustness, we compared median R_{50} of model HH_R with that of models involving parasitism (i.e. HP_{LC} , $HP_{R,LC}$, $HP_{F,LC}$, HP , HP_R and HP_F). On average, median R_{50} drops only by 4%, from 45% (HH_R) to 41% for models considering parasite lifecycle constraints (i.e. HP_{LC} , $HP_{R,LC}$ and $HP_{F,LC}$), but it increases by 2%, from 45% (HH_R) to 47% for models without parasite lifecycle constraints (i.e. HP , HP_R and HP_F).

There is no significant difference in robustness between models with random and non-random parasitism. The averaged medians, R_{50} , are both 47% for models HP and HP_R and the same measures for $HP_{R,LC}$ and HP_{LC} are also the same (i.e. both are 41%). As for

including parasites as food sources for non-parasitic predators, median R_{50} makes no difference between HP and HP_F (i.e. both are 47%) but slightly increases by 1% from HP_{LC} (42%) to $HP_{F,LC}$ (43%) after averaging the results from the CAR, COM and TAK datasets.

Our study also shows the negative correlation between species number in a food web and its network connectance (Fig. 2; $n = 36$, $r = -0.622$, $P < 0.001$). Therefore, increasing food web size may result in lower connectance and thus leads to lower network robustness (Dunne et al., 2002, 2004 but see Rudolf and Lafferty, 2011). Furthermore, our results suggest two separate logarithmic relationships between network robustness and connectance (Fig. 3). One regression line is made up by data points from food web models with parasite life cycle constraints (the dashed line in Fig. 3; $R_{50} = 0.034 \times \ln(\text{Connectance}) + 0.497$, $r^2 = 0.692$, $P < 0.001$), whereas the other line is for data points from models with the parasite life cycle constraints relaxed (the solid line in Fig. 3; $R_{50} = 0.016 \times \ln(\text{Connectance}) + 0.508$, $r^2 = 0.183$, $P < 0.05$).

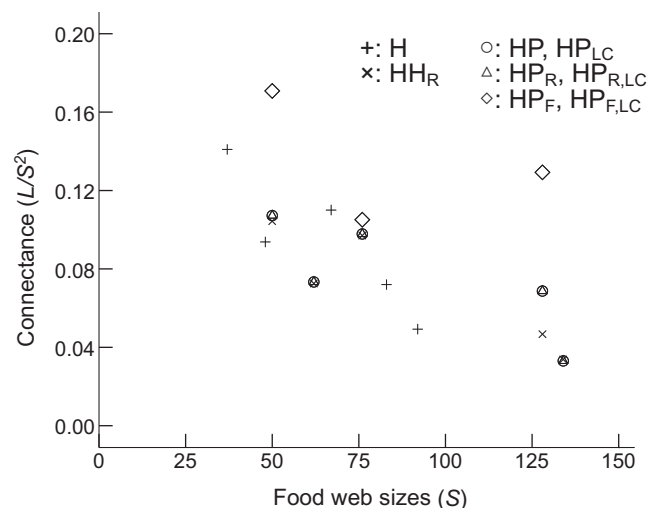


Fig. 2. The relationship between the number of species in a food web (S) and connectance (L/S^2). Different symbols represent different food web models: H (+), HH_R (\times), HP and HP_{LC} (\circ), HP_R and $HP_{R,LC}$ (\triangle), and from HP_F and $HP_{F,LC}$ (\diamond). Note that placing parasite life cycle constraints does not change the connectance. H, predation only; HP , parasitism without life cycle constraints; HP_{LC} , parasitism with life cycle constraints; HH_R , additional random predation; HP_R , random parasitism; $HP_{R,LC}$, random parasitism with life cycle constraints; HP_F , parasites as food sources without life cycle constraints; $HP_{F,LC}$, parasites as food sources without life cycle constraints.

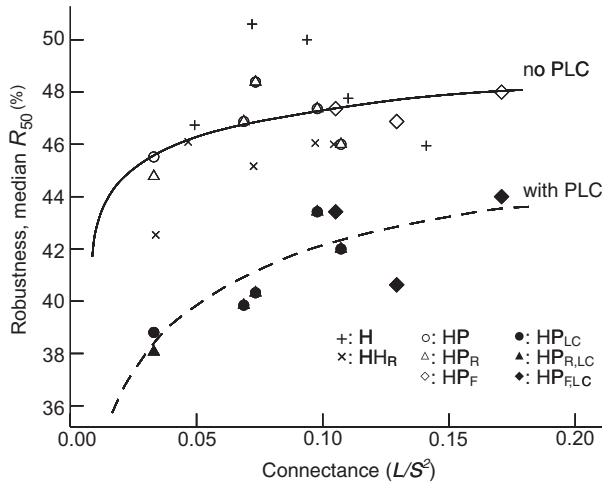


Fig. 3. The relationship between network robustness (R_{50}) and connectance (L/S^2). Different symbols represent different food web models: H (+), HH_r (x), HP (o), HP_{LC} (●), HP_R (△), $HP_{R,LC}$ (▲), HP_F (◇) and $HP_{F,LC}$ (◆). The dashed regression line is computed by using data points from models without parasite life cycle constraints (no PLC) while the solid line is for models with parasite life cycle constraints (with PLC). H, predation only; HP, parasitism without life cycle constraints; HP_{LC} , parasitism with life cycle constraints; HH_r , additional random predation; HP_R , random parasitism; $HP_{R,LC}$, random parasitism with life cycle constraints; HP_F , parasites as food sources without life cycle constraints; $HP_{F,LC}$, parasites as food sources with life cycle constraints.

3.2. The proportion of non-parasitic and parasitic species involved in secondary extinction

On average, 4% of non-parasitic species out of the available pool suffered secondary extinction, while this number was much higher, i.e. 30%, for parasitic species (Fig. 4). When parasite life cycle constraints were relaxed, $X_{P\%}$ was 11% after averaging the results from models HP, HP_R and HP_F ; however, when these constraints were in place, $X_{P\%}$ achieved a value of 52% after averaging over models HP_{LC} , $HP_{R,LC}$, $HP_{F,LC}$. For non-parasitic species, a noticeable difference existed in the TAK web whether or not parasites were treated as food sources for non-parasitic species: $X_{NP\%}$ for models without parasites as food sources were lower than those for models with this additional complexity, and on average those figures differed by 9%, from 9% in models HP and HP_{LC} to 0% in models HP_F and $HP_{F,LC}$.

3.3. The observed sequence of secondary extinctions involving non-parasitic and parasitic species

Fig. 5 summarises the standardised median T for secondary extinctions involving non-parasitic and parasitic species. The averaged median values of $T_{NP\%}$ and $T_{P\%}$ over all models are 86% and 67%, respectively, (note that a smaller percentage implies extinctions occurring at earlier stages in the extinction sequence). Food web models with parasite life cycle constraints (i.e. models HP_{LC} ,

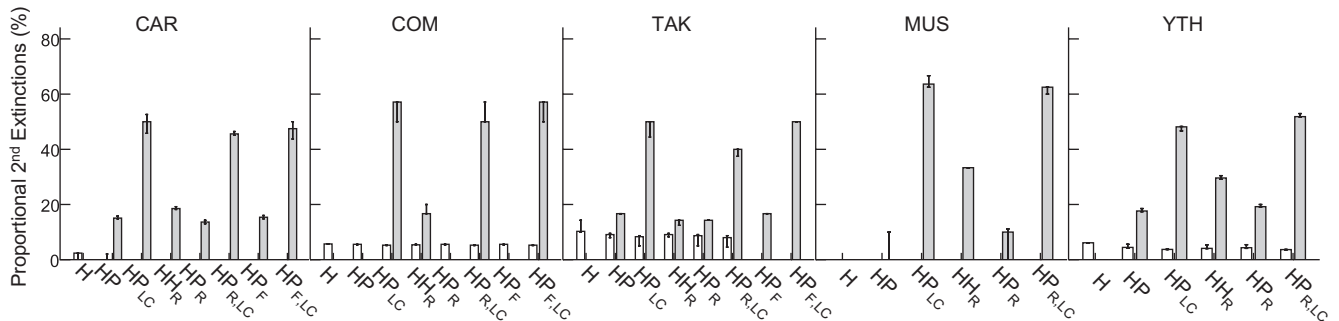


Fig. 4. The medians and 95% confidence intervals for the proportions of secondary extinctions of non-parasitic species ($X_{NP\%}$) and parasitic species ($X_{P\%}$) based on 1000 simulations. Each sub-figure is the result of considering specific food web models (i.e. H, HP, HP_{LC} , HH_r , HP_R , $HP_{R,LC}$, HP_F or $HP_{F,LC}$) for each of five food webs (CAR, COM, TAK, MUS, and YTH). Also note that models HP_F or $HP_{F,LC}$ are available only for CAR, COM and TAK. H, predation only; HP, parasitism without life cycle constraints; HP_{LC} , parasitism with life cycle constraints; HH_r , additional random predation; HP_R , random parasitism; $HP_{R,LC}$, random parasitism with life cycle constraints; HP_F , parasites as food sources without life cycle constraints; $HP_{F,LC}$, parasites as food sources with life cycle constraints; CAR, Carpinteria salt marsh; COM, Company Bay mudflat; TAK, Lake Takvatn; MUS, Muskingum Brook; YTH, Ythan River estuary.

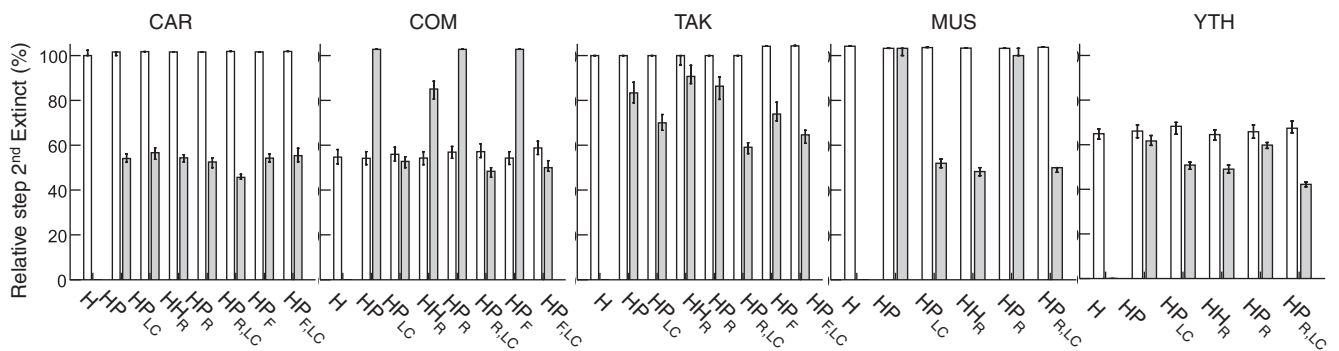


Fig. 5. The medians and 95% confidence intervals for the times at which secondary extinctions involving non-parasitic species ($T_{NP\%}$) and parasitic species ($T_{P\%}$) occurred in the extinction sequences based on 1000 simulations. Each sub-figure is the result of considering specific food web models (i.e. H, HP, HP_{LC} , HH_r , HP_R , $HP_{R,LC}$, HP_F or $HP_{F,LC}$) for each of five food webs (CAR, COM, TAK, MUS and YTH). Also note that models HP_F or $HP_{F,LC}$ are available only for CAR, COM and TAK. H, predation only; HP, parasitism without life cycle constraints; HP_{LC} , parasitism with life cycle constraints; HH_r , additional random predation; HP_R , random parasitism; $HP_{R,LC}$, random parasitism with life cycle constraints; HP_F , parasites as food sources without life cycle constraints; $HP_{F,LC}$, parasites as food sources with life cycle constraints; CAR, Carpinteria salt marsh; COM, Company Bay mudflat; TAK, Lake Takvatn; MUS, Muskingum Brook; YTH, Ythan River estuary.

HP_{R,LC}, HP_{F,LC}) have an averaged median $T_{P\%}$ of 54%; once such constraints were relaxed, this value increased to 79% (i.e. models HP, HP_R and HP_F), a value not very different from its counterpart for non-parasitic species (i.e. the averaged median $T_{NP\%} = 86\%$). However, there were cases which did not follow this general trend: for the COM dataset, non-parasitic species often became extinct before parasitic species in food web models without the parasite life cycle constraints (Fig. 5). We suspect this deviation observed in the COM web may be due to the relatively low parasite–host ratio and the large number of host species utilised by each parasitic species in this particular system.

4. Discussion

Based on the results from a previous study (Lafferty and Kuris, 2009) and those presented here, it is clear that food webs with parasitism are less robust to species loss than those without. Comparing the results from models H, HH_R and HP_R suggests that simply adding more consumers, no matter whether they are parasites or top predators, can reduce food web robustness. Since only consumers would suffer secondary extinction under the current robustness simulation, an intuitive expectation is that the more consumers there were, the larger the pool vulnerable to secondary extinction and the less the robustness of food webs analysed. In addition, it has been shown that adding parasites to a food web can change its network complexity (Huxham and Raffaelli, 1995; Huxham et al., 1996; Thompson et al., 2005; Lafferty et al., 2006; Hernandez and Sukhdeo, 2008), which can consequently alter its robustness (Dunne et al., 2002a; Gilbert, 2009). One measure of network complexity is connectance, and it has been shown that food webs with high connectance tend to be structurally robust (Dunne et al., 2002a, 2004; Dunne and Williams, 2009; but see Rudolf and Lafferty, 2011). We found that this was indeed the case as models H tended to have higher connectance and food web robustness than models HH_R and HP_R (Fig. 3). In light of this, it is therefore important to understand and clarify whether the reduction in food web robustness after the inclusion of parasitism is due to factors associated with the characteristics of parasites, or simply an inevitable artefact of the addition of new nodes and links to an existing network. These arguments motivated us to develop several extinction experiments to elucidate the factors responsible for reduction in food web robustness. Based on the reasons above, we argue that the difference made by parasitism in food web robustness can only be revealed meaningfully by comparisons with results derived from food webs of similar sizes and complexity. Hence, in this study, we explored several unique aspects of parasitism and their effects on food web robustness, including: (i) the life cycle constraints of parasites, (ii) the preferential host use by parasites, and (iii) treating parasites as food sources for non-parasitic species.

Starting with the life cycle constraints of parasites, our results show that substantial reductions in food web robustness occur only when food web models consider such constraints (i.e. models HP_{LC}, HP_{R,LC}, and HP_{F,LC}, Fig 1). Even for food webs having similar network connectance, models considering parasite life cycle constraints are less robust than those without (Fig. 3). Parasites are also four times more vulnerable to random species loss in food web models with parasite life cycle constraints than in those without (Fig. 4). Furthermore, parasites appear much earlier in the extinction sequence in models with parasite life cycle constraints than in those without (Fig. 5). All of these findings suggest that life cycle constraints contribute substantially to the sensitivity of parasites to species loss and to reduced food web robustness. Moreover, we suggest that future studies on food web robustness should consider the effect of life cycle constraints for non-parasitic

species if they have well-defined developmental stages with noticeable ontogenetic diet shifts between different stages (Yodzis and Winemiller, 1999). We suspect this additional complexity will further reduce food web robustness to a level lower than those reported here or in previous studies. A recent paper by Rudolf and Lafferty (2011) elegantly demonstrated that the reduction in resources overlap in stage-structured food webs could also alter or reverse current perceptions of the relationship between complexity and stability in ecological networks.

Parasitism has been demonstrated to occur at non-random positions in food webs (Chen et al., 2008; Warren et al., 2010). However, it is surprising that food web robustness for models with non-random parasitism (models HP_R and HP_{R,LC}) did not differ significantly from those with random parasitism (models HP and HP_{LC}). A possible explanation is that parasites tend to aggregate only on or in a few host species at specific positions in the web (Chen et al., 2008), and through random primary loss these host species would seldom be removed from the food web. Therefore primary extinctions are unlikely to involve those highly infected host species, such that food web models with non-random parasitism produce robustness values similar to those of models with random parasitism. Moreover, it is known in network research that real biological networks are highly robust to random deletions (Albert et al., 2000; Melian and Bascompte, 2002), and our findings fit this general trend. There is one fact worth mentioning regarding the distributions of R_{50} values for the Carpinteria ecosystem (i.e. CAR). For CAR, although the means and medians of R_{50} are similar for both models HP_{LC} and HP_{R,LC}, their respective distributions of R_{50} values are very different in shape (Fig. 6). The distribution of R_{50} is bimodal and highly dispersed for model HP_{LC} compared with that for model HP_{R,LC}. The implication of this result is that a few hosts in the Carpinteria food web may serve as hubs harbouring many parasite species; deleting those host species causes the extinction of the majority of parasite species, resulting in low robustness values that constitute the left peak of the R_{50} distribution. Recently, Lafferty and Kuris (2009) identified a key snail intermediate host for 16 trematode parasites in the CAR food web that appears to fit the description of a hub in this food web.

It has been emphasised that a complete food web with parasitism should have four sub-webs, including predator–prey, parasite–host, predator–parasite and parasite–parasite trophic interactions (Lafferty et al., 2006; Poulin, 2010). It has also been demonstrated that parasite species, in particular the free-living cercarial stages of trematodes, can serve as important food sources for non-parasitic species in ecological communities (Mouritsen and Poulin, 2003; Hopper et al., 2008; Thieltges et al., 2008; Johnson et al., 2010). Among the food webs used in this study, three datasets contain information on parasites being used as food sources by non-parasitic consumers. Our results suggest that when treating parasites as resources for non-parasitic species (i.e. model HP_F and HP_{F,LC}), food web robustness tends to increase. This is because non-parasitic species have extra resources for survival, together with an increase in the overall network connectance, which results in a more robust food web. Particularly for the TAK ecosystem, parasites apparently serve as a major proportion of food sources for the non-parasitic predators since food web robustness increases drastically in models HP_F and HP_{F,LC}. However, as predators obviously cannot solely rely on feeding parasites for their survival, it is doubtful whether the current resource- and topology- based robustness analysis overstates the functional roles parasites played as essential food supplies for non-host consumers in ecosystems.

Through our extinction experiments using models with parasite life cycle constraints, we have demonstrated that parasites are more likely to be involved in secondary extinctions than non-parasitic species, and the extinction of the former occurs much earlier than that of the latter on average. Those two findings provide the

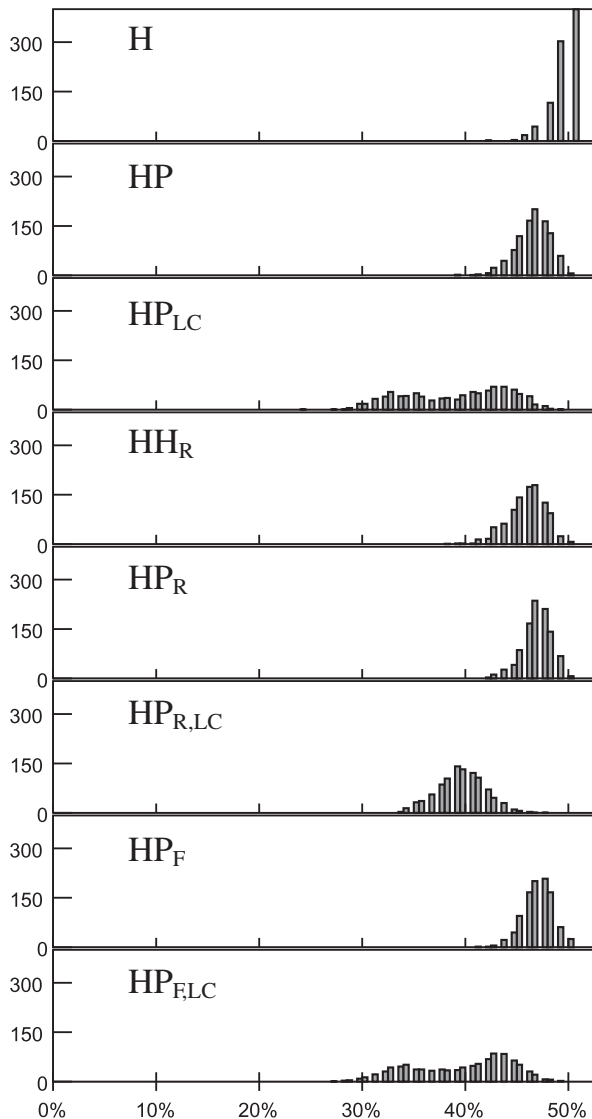


Fig. 6. Distribution of robustness (R_{50}) from 1,000 simulations of extinction experiments using eight modelling scenarios for the Carpinteria (CAR) food web. Although the means and medians of R_{50} are similar for both non-random (HP_{LC}) and random model ($HP_{R,LC}$) with parasite life cycle constraints in the CAR food web, the actual distribution of R_{50} values for model HP_{LC} is bi-modal in comparison with that for model $HP_{R,LC}$. This discrepancy between the real data (HP_{LC}) and the random infection model ($HP_{R,LC}$) indicates that a few hosts in the CAR food web may serve as hubs harbouring many parasite species, and deleting those host species causes the extinction of the majority of parasite species, resulting in low robustness values that constitute the left peak of the R_{50} distribution.

explicit evidence supporting the speculation that parasites are sensitive to species loss (Lafferty and Kuris, 2009). This finding also echoes the idea of using parasites as a means to monitor the integrity of an ecosystem (Huspeni and Lafferty, 2004; Marcogliese, 2005; Palm and Ruckert, 2009). In practice, since the majority of parasitic species have their final or definitive hosts occupying positions at the very end of food chains (Chen et al., 2008), one can simply examine those hosts and check for the presence of those parasitic species. If many parasitic species are absent in their final hosts, then it is possible that the life cycles of those parasites are interrupted due to the loss of intermediate hosts at various positions in the web (Marcogliese, 2002; Hechinger and Lafferty, 2005; Palm and Ruckert, 2009; Valtonen et al., 2010). Such observations can therefore provide early cues signalling the state of health or the integrity of an ecosystem (Carpenter et al., 2008; Lafferty, 2008; Palm and Ruckert, 2009).

The study of food webs with parasites is a new challenge in ecology and parasitology (Beckerman and Petchey, 2009; Byers, 2009; Poulin, 2010). The results of our study have shown conclusively that the inclusion of parasitism reduces the robustness of a food web. This reduction is not simply due to alterations in network complexity, but is mainly caused by the sensitive nature of parasites to secondary extinction due to their reliance on specific host species at different developmental stages of their life cycle. While one must go further and ask why some species are more vulnerable to primary species loss than others (Petchey et al., 2008; Allesina and Pascual, 2009), it is also crucial to emphasise the sensitive nature of parasites in food webs and test the applicability of using parasites as leading indicators for monitoring the state of health of ecosystems (Marcogliese, 2005). Our study is based on the analysis of static food webs where the effect of cascading extinction spreads in the bottom-up direction (Dunne and Williams, 2009; Lafferty and Kuris, 2009). In reality, interactions between species are dynamic and the effect of species loss can also spread through the entire food web in top-down and horizontal directions (Liu et al., 2010). Given that parasites are considered as a critical top-down controller in the dynamics of ecological communities (Hudson et al., 2006; Lafferty et al., 2008), our analyses could be further refined by considering those two additional aspects to better understand the effects of parasitism on food web robustness. Another possible extension of the present work would be to construct dynamic models and investigate how species losses can dynamically affect the robustness and stability of a food web (Ebenman et al., 2004; Eklof and Ebenman, 2006). Because the food webs considered here are complex in structure and their behaviour can be sophisticated, such an extension will only be possible and meaningful when detailed information on the parameter values of underlying ecological processes becomes available in future.

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