



Network position of hosts in food webs and their parasite diversity

Hsuan-Wien Chen, Wei-Chung Liu, Andrew J. Davis, Ferenc Jordán, Ming-Jing Hwang and Kwan-Tsao Shao

H.-W. Chen and K.-T. Shao, Biodiversity Research Centre, Academia Sinica, Taipei, Taiwan. HWC also at: Dept of Life Science, National Taiwan Normal Univ., Taipei, Taiwan. – W.-C. Liu (wliu56@gate.sinica.edu.tw), Inst. of Statistical Science, Academia Sinica, Taipei, Taiwan. WCL and M.-J. Hwang, Inst. of Biomedical Sciences, Academia Sinica, Taipei, Taiwan. – A. J. Davis, Max Planck Inst. for Chemical Ecology, Jena, Germany. – F. Jordán, Collegium Budapest, Inst. for Advanced Study, Budapest, Hungary and Animal Ecology Research Group, HAS, Hungarian Natural History Museum, Budapest, Hungary.

Parasites are ubiquitous in ecological communities but it is only recently that they have been routinely included in food web studies. Using recently published data and the tool of network analysis, we elucidate features associated with the pattern of parasitism in ecological communities. First we show here that parasitism is non-random in food webs. Second we demonstrate that parasite diversity, the number of parasite species harboured by a host species, is related to the network position of a host species. Specifically, a host species with high parasite diversity tends to have a wide diet range, occupy a network position close to many prey species, or occupy a network position that can better accumulate resources from species at lower trophic levels. Lastly our results also suggest that a host species with higher vulnerability to predators, being at a network position close to many predatory species, or being involved in many different food chains, tends to be important in parasite transmission.

Parasites are organisms that live in other organisms, hosts, from which they obtain nutrients (Marcogliese and Cone 1997, Bush et al. 2002). More than half of the world's species behave as a parasite at some point of their life cycle and most organisms are parasitized (Poulin and Morand 2004). Parasites constitute a substantial proportion of the entire biomass of an ecosystem (Kuris et al. 2008) and have very strong community effects (Mouritsen and Poulin 2002, Dobson et al. 2005, Hatcher et al. 2006). However, despite their importance, the relationships of parasites to food webs have been neglected due, in part, to practical problems.

The small size of parasites compared to their hosts (Bush et al. 2002) has traditionally led to several practical and theoretical problems in ecology (Pimm 1982). The small size makes them difficult to detect and invasive techniques are often required to study parasites inside their hosts. Small parasites consuming their much larger hosts (Leaper and Huxham 2002) is also distinct from the majority of trophic interactions where species at high trophic levels are on average larger (predator–prey) or similar (parasitoid–host) in size to those at lower trophic levels (Memmott et al. 2000, Brose et al. 2006). This difference also makes problematic the use of body size as one of the criteria to establish trophic hierarchies (although body size is not the only criteria used) in food web models such as the cascade model (Cohen et al. 1990, 1993), the niche model (Williams and Martinez 2000) and the nested hierarchy

model (Cattin et al. 2004). Moreover, many parasites possess several distinct life stages and each stage may occur in different hosts or environments making it difficult to compile a comprehensive host list for the parasite life cycle. Different stages may thus also have different trophic positions in the food web raising the question of whether a parasite species is a single trophic component or several tropho-species in a food web (Huxham et al. 1995, 1996).

Given these difficulties, it is not surprising that many ecological studies have practically ignored parasites (Marcogliese and Cone 1997), and new general models are needed to explain the observed patterns of parasitism in food webs (Lafferty et al. 2006a, Poulin 2007).

Recent field studies have, however, provided an increasing amount of food web data involving parasites (Huxham et al. 1995, Thompson et al. 2005, Lafferty et al. 2006b). In addition, the neglect of parasites in traditional food web studies is being remedied by studies of what happens when parasites are included in food webs to fundamental web properties (Huxham et al. 1995, 1996, Thompson et al. 2005, Lafferty et al. 2006a). A food web is essentially a network of nodes; in this paper, rather than treating parasite species as individual nodes in food webs, we simply regard parasite diversity as a nodal attribute of a host species. We address a simple question of what determines the parasite diversity of host species in food webs. Our investigation of food webs goes a step further than the observation that parasitism tends to be concentrated at higher trophic levels

(Lafferty et al. 2006a). We first investigate whether parasitism is randomly distributed across all non-parasite species in a food web and second, use the tool of network analysis to investigate the issue of parasite diversity in food webs.

As networks, food webs can be analysed using network analysis, tools that have proven invaluable in several different fields of biological research from ecology to molecular biology (Jeong et al. 2001, Jordán et al. 2005, Liu et al. 2007). Each node occupies a position in a network, and one particular aspect of network analysis is how to characterise a network position. There exist different network indices that can characterise a network position from different perspectives (Jordán and Scheuring 2004, Jordán et al. 2006). By considering species as nodes, the importance of a species is its ability to affect others in the web by virtue of its network position; therefore, different network indices reflect different aspects of its importance in the web. For instance, a species with many direct interactors is important as it can affect many different species; and a species might be important if it is at a network position that serves as a bridge linking species at lower trophic levels to those at higher ones (e.g. a wasp-waist species in marine ecosystems). Network position can be expected to influence the number of parasite species a host species harbours because a host species can acquire parasites via predator–prey interactions and parasites seem to increase trophic transmission (Lafferty 1999). Furthermore, many parasite species have complex life cycles where different developmental stages require different host species. A host species in a parasite's life cycle in which the parasite species reaches sexual maturity is called a definitive host whereas those involved in earlier stages are called intermediate hosts (Bush et al. 2002). We therefore also investigate whether there are differences in network positions between definitive and intermediate hosts.

The paper is organised as follows. We first describe the data used in our study. This is followed by a description of methods, including (1) randomisation tests; (2) network indices quantifying different aspects of importance of a network position; and (3) quantifying the propensity of being an intermediate host. We then present the results and discuss their implication in terms of the mechanism that might lead to the observed patterns of parasitism.

Methods

Data

We used three datasets: 'Car', the Carpinteria salt marsh community near Santa Barbara, USA (Lafferty et al. 2006b); 'Com', the intertidal mudflat community of Company Bay in Otago Harbour, New Zealand (Thompson et al. 2005); and 'Yth', the Ythan Estuary in Scotland, UK (Huxham et al. 1995). Since we are only interested in parasite diversity of non-parasite species and their network positions in food webs, we only considered predator–prey links (i.e. the conventional food webs) and numbers of parasite species per host species (i.e. parasitism) for all three datasets. Included in the Car dataset but not in the other two are micropredators (leech and two mosquitoes) and

microparasites (virus and malaria); we therefore initially omitted them from the analysis but subsequently analysed how retaining them (Car⁺) might affect the results. Bacteria can function both as food sources and decomposers, and we treated them as food sources in our analysis here. The Com and Yth food web data include a small number of loops (i.e. species A consumes species B, and species B consumes species A). Two of the network indices used rely on the partitioning of species into distinct trophic levels and this is impossible if there are loops. When we calculated these two network indices we therefore removed predator–prey links that create loops but used all the data otherwise. Details of the three food webs can be found in the original sources (Huxham et al. 1995, Thompson et al. 2005, Lafferty et al. 2006b).

The Car and Com datasets give clear definitions of intermediate and definitive hosts (Thompson et al. 2005, Lafferty et al. 2006b), but the original Yth data does not (Huxham et al. 1995, 1996). We therefore derived this information from Yamaguti (1975) and labelled all host species as either intermediate or definitive hosts for the Yth dataset. However, the Yth data is missing, in a few cases, the hosts required for a particular parasite to complete its life cycle. Thus, some host species occupy the final position in all identifiable transmission pathways but do not harbour sexually mature parasites. We refer to these hosts as 'final hosts' and reserve 'definitive host' for species containing the sexually mature stage of the parasite species.

Descriptive statistics

For each web, we determined the number of non-parasite species (Hos), the number of parasite species (Par), the number of predator–prey links (L_T) and the number of parasite–host interactions (L_P). For each non-parasite species (i), we determined the number of parasite species it harbours (i.e. parasite diversity, P_i) and for each parasite species (i), the number of different host species it uses (i.e. host specificity, H_i).

Randomisation of parasitism

For each original web, we generated 10 000 simulations. In each simulation only parasitism were randomised but the predator–prey links remained intact. For a parasite species i , this was achieved by randomly choosing H_i different host species from the total Hos non-parasite species in the web. The process was repeated for all the web's parasite species. An expected distribution of P_i was then obtained from those simulations and we used a modified χ^2 -test (to avoid low expected values and for continuity) to compare the observed and expected distributions of P_i .

For each web, we also determined the trophic position (Levine 1980) of each non-parasite species. We then determined for each web the mean trophic position of hosts species with parasites. Using the same procedure as before we again generated 10 000 simulations for each of which we then calculated the mean trophic position of hosts. The data mean should be well within the 95% confidence intervals of the model mean distribution if parasitism is indeed random.

Network indices for measuring the importance of a network position

We selected and used twelve network indices that, together, cover different aspects of importance of a network position (Jordán et al. 2006). Broadly speaking, these indices fall into two groups: centrality measures (Wassermann and Faust 1994, Jordán et al. 2006) and keystone measures (Jordán et al. 1999).

Centrality measures

Degree (D_i) is the number of nodes directly linked to a given node i . For a non-parasite species it is simply the number of its prey and predator species. The degree of a non-parasite species i can be decomposed into in-degree ($D_{in,i}$) and out-degree ($D_{out,i}$) to account for the direction of the links. In-degree is the number of species preyed upon and out degree is the number of predator species a species has. A species with high degree, in-degree or out-degree centralities is important because it directly interacts with many others.

Closeness centrality (C_i) measures how close node i is to all others in the network:

$$C_i = \sum_{j=1, i \neq j}^N d_{ij}, \quad (1)$$

where d_{ij} is the length of the shortest path (distance) between nodes i and j , and N is the number of nodes in the network (i.e. $N = \text{Hos}$). Closeness centrality is small if a node is very close to other nodes in the same network. Thus, the importance of such a node is that it can rapidly affect others and be affected quickly by others. Including the direction of links allows quantification of in-closeness ($C_{in,i}$) and out-closeness ($C_{out,i}$) for a given node i . These are different because, when links have direction, a pair of nodes may be linked in one direction but not in the other. In-closeness is calculated using Eq. 1 but replacing d_{ij} by $d_{i \rightarrow j}$ which is the length of the shortest path from node i to node j . Out-closeness is calculated similarly but d_{ij} is replaced by $d_{j \rightarrow i}$, the length of the shortest path from node j to node i . The quantities $d_{i \rightarrow j}$ and $d_{j \rightarrow i}$ are always greater than or equal to d_{ij} , and not necessarily equal to each other. In-closeness centrality measures how quickly food and energy can reach node i through predator-prey interactions. Similarly, out-closeness centrality measures how fast such resources from node i can reach all other nodes.

Betweenness centrality (B_i) measures how frequently node i lies on all shortest paths between all other pairs of nodes in the network:

$$B_i = \sum_{j > k} g_{jk}(i) / g_{jk} \quad (2)$$

where $i \neq j$ and k ; g_{jk} is the number of equally shortest paths between nodes j and k , and $g_{jk}(i)$ is the number of these shortest paths that include node i . A node with high betweenness centrality is important in that it mediates many indirect interactions between pairs of nodes. To include the direction of interaction, directed betweenness centrality ($B_{dir,i}$) is calculated using Eq. 2 but replacing g_{jk} by $g_{j \rightarrow k}$ and $g_{jk}(i)$ by $g_{j \rightarrow k}(i)$. The quantity $g_{j \rightarrow k}$ is the number of directed equally shortest paths from node j to k , and $g_{j \rightarrow k}(i)$ is the number of these shortest directed paths that include

node i . Thus the importance of a node with high directed betweenness centrality is that it mediates many of the shortest food chains. All these centrality based-indices were calculated using UCINET (Borgatti et al. 2002).

Keystone measures

The second type of network indices includes the keystone indices that quantify the bottom-up and top-down effects within a food web (Jordán et al. 1999). Defining these two network indices require non-parasite species to be partitioned into clear trophic levels without loops.

From the bottom-up direction, the keystone index of a species i ($K_{bu,i}$) is defined as:

$$K_{bu,i} = \sum_{c=1}^n \frac{1}{d_c} (1 + K_{bc}), \quad (3)$$

where n is the number of predatory species eating species i (i.e. $n = D_{out,i}$), d_c is the number of prey species of its c th predator and K_{bc} is the bottom-up keystone index of the c th predator. The bottom-up keystone index of a given species measures its importance in terms of the diet range of its predators and of other species at higher trophic levels. It measures how well the efforts of predatory species are focused on a particular prey species. Symmetrically, from the top-down direction, the keystone index of a species i ($K_{td,i}$) is defined as:

$$K_{td,i} = \sum_{e=1}^m \frac{1}{f_e} (1 + K_{te}) \quad (4)$$

where m is the number of prey eaten by species i (i.e. $m = D_{in,i}$), f_e is the number of predators of its e th prey and K_{te} is the top-down keystone index of the e th prey. The top-down keystone index measures the importance of a given species by taking into account its diet range, that of its prey, and those of species at lower trophic levels. It thus measures how well resources are channelled into the focal species.

Measure of trophic position

We also quantified the trophic position of every non-parasite species in each of the three webs. Trophic position is defined as the averaged path length over which a species obtains energy from basal species (Levine 1980). This energy budget-based measure differs from the conventional trophic level in allowing loops in food webs. It measures the trophic function of a focal species by considering all paths leading to this species.

We determined trophic position by first creating a square matrix \mathbf{R} for each web where the i,j th element represents the fraction of energy of species i that is from species j . We then rearranged \mathbf{R} to create a new matrix, \mathbf{S} , in which all species to be considered basal come first. Basal species have a trophic position of zero by definition. Embedded in \mathbf{S} is a sub-matrix \mathbf{W} , which describes the energy flow between non-basal species. From \mathbf{W} we then calculated the trophic position of non-basal species as:

$$y = (\mathbf{I} - \mathbf{W})^{-1} \quad (5)$$

where \mathbf{I} is the identity matrix and \mathbf{y} is a vector containing the trophic position of non-basal species. We determined

the trophic position of non-parasite species for all three webs from the bottom-up ($T_{bu,i}$) and top-down ($T_{td,i}$) directions.

The propensity of being an intermediate host

Parasites often have a definitive host in which they reproduce sexually and intermediate hosts in which they grow or reproduce asexually. A non-parasite species may thus be a definitive host for one parasite species and an intermediate host for another. We quantified the propensity of being an intermediate host (Q_i) for a non-parasite species i as:

$$Q_i = \frac{h_i}{H_i} \quad (6)$$

where H_i is the number of parasite species in host species i while h_i is the number of parasite species passed onto at least one predator of the focal species i via predator-prey interaction. Some parasites are not transmitted by trophic interactions but, like the free living cercariae of some trematodes, use non-predator-prey interactions (Bush et al. 2002). We therefore identified and excluded such parasites when determining h_i . If a non-parasite species is the intermediate host for all of its parasite species, $Q_i = 1$. If it is the final host for all of its parasite species, then $Q_i = 0$. The index is undefined for non-parasite species in the web that are not a host for at least one parasite species.

Statistical tests

We tested the correlation between parasite diversity (P) and each network index calculated for the non-parasite species (D , D_{in} , D_{out} , C , C_{in} , C_{out} , B , B_{dir} , K_{bu} , K_{td} , T_{bu} and T_{td}). We used the Spearman rank correlation coefficient because the distributions of these indices are not suitable for the Pearson correlation tests. We also determined the Spearman rank correlation coefficient between the propensity of being an intermediate host (Q) and each of those twelve network indices. To avoid the family-wise error rate during the multiple pairwise comparisons, we apply Bonferroni corrections to adjust the p values at different levels of significance. The adjusted p -value equals the original p value multiplied by twelve since there are twelve network indices.

Results

In the Car web there are 83 non-parasite and 40 parasite species, with 496 predator-prey links and 515 parasite-host interactions. In Com, there are 67 non-parasite and 9 parasite species, with 428 predator-prey links and 71 parasite-host interactions. In Yth, there are 92 non-parasite and 42 parasite species, with 417 predator-prey links and 177 parasite-host interactions. Among the parasite-host interactions realised, 82% of them in Car transfer parasites to their definitive hosts while only 56% do so in Com and 55% in Yth.

Parasitism is not a random process

The random model of the number of non-parasite species having a given number of parasite species produces Poisson-like expected frequency distributions, whereas the observed frequency distributions are overly dispersed (Fig. 1). There are significant differences between the expected and observed frequency distributions for all three webs (Car: $\chi^2 = 204.59$, $DF = 7$, $\chi^2_{\alpha=0.001} = 24.32$, $p < < 0.001$; Com: $\chi^2 = 47.96$, $DF = 3$, $\chi^2_{\alpha=0.001} = 16.27$, $p < < 0.001$; Yth:

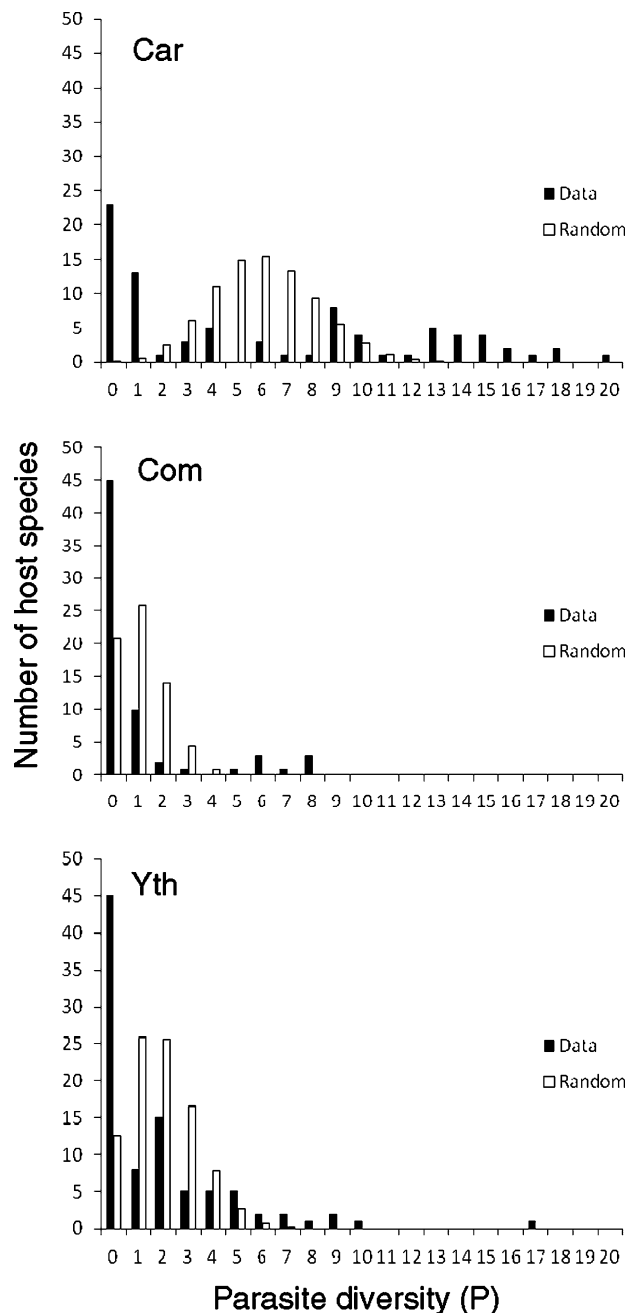


Figure 1. The distribution of the number of parasite species (parasite diversity) for the Carpinteria (Car), Company Bay (Com), and Ythan Estuary (Yth) ecosystems. The observed distributions (Data) are shown in filled bars and the expected distributions according to a random model (Random) are in open bars.

$\chi^2 = 132.81$, $DF = 5$, $\chi^2_{\alpha=0.001} = 20.52$, $p < < < 0.001$). Thus, in the three webs, the pattern of parasite–host interactions is not consistent with their being formed at random.

For the Car web, the average bottom–up trophic position of host species participating in parasite–host interactions is 2.10, for Com it is 2.47 and for Yth 1.98. The mean for the random Car web is 1.61 (95% CI = 1.55–1.67), for Com 1.60 (1.43–1.77) and for Yth 1.68 (1.57–1.80). Thus species that are hosts to parasites tend to be in higher trophic positions than expected in the random model. From the top–down direction, the average trophic position is 0.43 for the Car web, 0.77 for Com and 0.87 for Yth. The expected values derived from the random model are Car 0.91 (0.85–0.97), Com 1.54 (1.35–1.73) and Yth 1.28 (1.13–1.43). This suggests that there are more parasite species on hosts near the end of food chains than would be expected by chance. Parasitism is thus evidently not random and there is great heterogeneity in the number of parasite species a host species harbours.

Network indices and parasite diversity

Of the twelve network indices calculated, five are significantly correlated with parasite diversity (P) for all three webs (Table 1). These five indices are in-degree centrality (D_{in}), in-closeness centrality (C_{in}), top–down keystone index (K_{td}), bottom–up trophic position (T_{bu}), and top–down trophic position (T_{td}). Degree centrality (D) and betweenness centrality (B) show significant correlation with parasite diversity for Com and Yth webs. Out-degree centrality (D_{out}), out-closeness centrality (C_{out}) and bottom–up keystone index (K_{bu}) only significantly correlate with parasite diversity for the Car web. Closeness centrality (C) only shows significant correlation with parasite diversity for the Com web. Directed betweenness centrality (B_{dir}) is the only centrality measure that is not significantly correlated with parasite diversity for any of the three webs. Across all three webs, D_{in} , C_{in} and K_{td} show strong correlation with parasite diversity. Thus parasite diversity is associated with having a wide diet range (D_{in}), being at a network position close to many prey species (C_{in}), or occupying a network position that can accumulate resources from species at lower trophic levels (K_{td}).

Some network indices show similar correlations with parasite diversity (Table 1). This might be the result of some indices being intrinsically related as they quantify similar characteristics of a network position. Principal component analysis (PCA) was then performed on those indices in order to determine their interrelationships. In the PCA (Fig. 2), the first and the second principal axes together explain 77.89% of the variance in the Car data, 76.32% of that for Com and 75.66% for Yth. The centrality measures D, B and B_{dir} form a small cluster for all three webs (Fig. 2) indicating they measure similar characteristics of a network position. Other indices seem to be relatively far from this cluster but there are two loose clusters. One of these is D_{in} , K_{td} , T_{bu} and C_{out} and the other is D_{out} , K_{bu} , T_{td} and C_{in} , with C as an outlier. The three clusters and C represent four moderately different qualities of a network position.

Table 1. Spearman rank correlations between parasite diversity (P) and different network indices (as identified by the top row) for each of the webs studied (as identified by the left column). In each cell the top value is the Spearman rank correlation and the bottom value is the associated levels of significance after Bonferroni corrections (*: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$, ns: not significant). Entries in bold indicate significant correlations at the 0.05 level.

	D	D_{in}	D_{out}	C	C_{in}	C_{out}	B	B_{dir}	K_{bu}	K_{td}	T_{bu}	T_{td}
Car	0.185 ns	0.745***	-0.446**	-0.232 ns	-0.695***	0.616***	0.083 ns	-0.105 ns	-0.509***	0.645***	0.634***	-0.663***
Com	0.422**	0.527***	-0.022 ns	-0.348*	-0.590***	0.336 ns	0.403**	0.020 ns	-0.151 ns	0.529***	0.508***	-0.431**
Yth	0.413***	0.411***	-0.002 ns	-0.262 ns	-0.390**	0.142 ns	0.375**	0.182 ns	-0.013 ns	0.415***	0.323*	-0.432***
Car+	0.077 ns	0.777***	-0.576***	-0.126 ns	-0.769***	0.733***	-0.009 ns	-0.204 ns	-0.634***	0.718***	0.732***	-0.774***

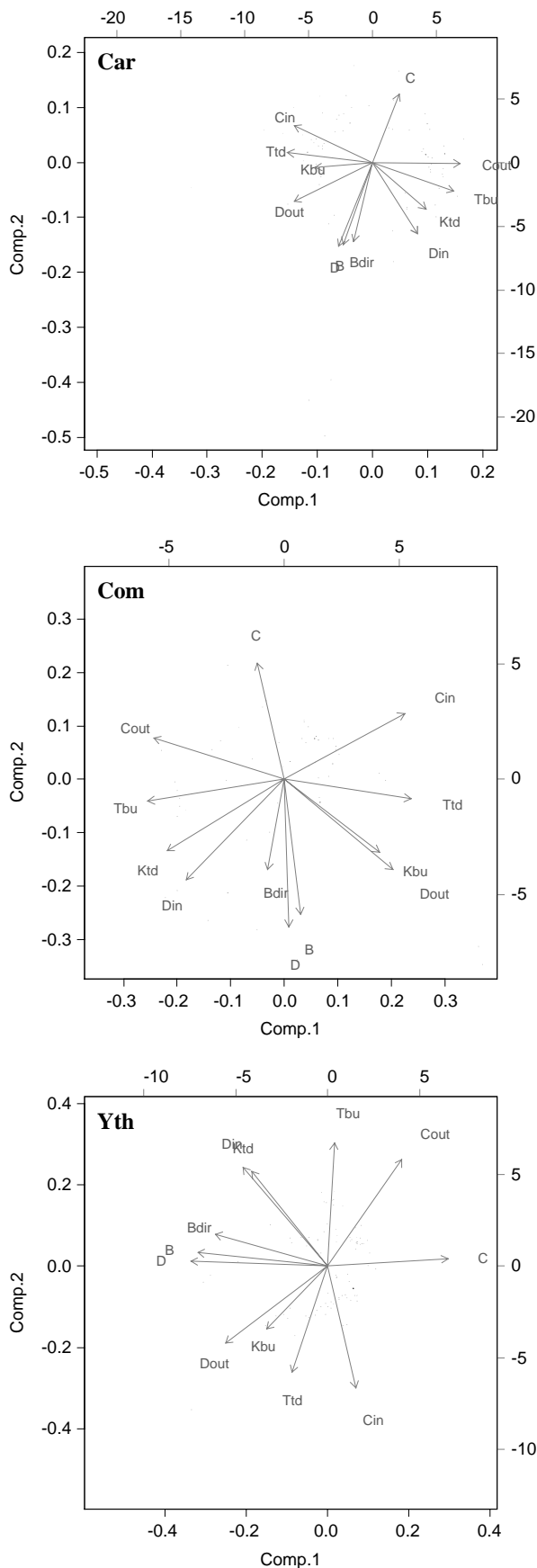


Figure 2

Network indices and the propensity of being an intermediate host

In all three webs, six of the twelve network indices, D , D_{out} , C_{out} , B_{dir} , K_{bu} and T_{td} , are significantly correlated with Q (Table 2). Two indices, C and B , show significant correlations with Q for two of the three webs. Car is the only web in which D_{in} , C_{in} , K_{td} , and T_{bu} all show significant correlation with Q . Across all three webs, D_{out} , C_{out} , K_{bu} and B_{dir} persistently show strong correlation with Q . Thus, in general, being an intermediate host for several species is linked with higher vulnerability to predators (D_{out}), being at network positions close to predatory species (C_{out} and K_{bu}) or being involved in many different food chains (B_{dir}).

The effect of retaining parasite links previously omitted from the Carpinteria data

In the Car^+ web there are 83 non-parasite and 45 parasite species, with 496 predator-prey links and 630 parasite-host interactions. The average bottom-up trophic position of host species participating in parasite-host interactions is 2.13 while the mean for the random Car^+ web is 1.61 (95% CI = 1.55–1.65), and their top-down counterparts are 0.39 and 0.91 (0.86–0.96) respectively. Therefore the results for the Car^+ data still suggest that parasitism is not a random process. The replacement of the five parasite species does not alter the correlation between parasite diversity and network indices too drastically (Table 1). The same applies to the correlation between the propensity of being an intermediate hosts and network indices despite that the correlation with D_{in} is now non-significant while that with C is now significant (Table 2).

Discussion

It is clear from our results that parasite diversity, the number of parasite species using each host species, is very different from random and consistently over dispersed in all three food webs. Only a few host species harbour many parasite species and many have few or no parasite species. It is thus probable that there are common factors influencing the parasite diversity of host species in our three webs and, therefore, potentially in all food webs. There are non-random patterns in parasitism of individuals and of communities (Poulin 1998, 2007). The significant covariation in parasite richness of different parasite taxa across vertebrate hosts suggests that common underlying mechanisms may operate (Poulin and Morand 2004). Non-randomness is congruent with previous findings in the comparative study of parasite diversity at the macroecological scale (Poulin 1995)

Figure 2. PCA plots of the twelve network indices measuring different characteristics of a network position for the Carpinteria (Car), Company Bay (Com), and Ythan Estuary (Yth) ecosystems. There are four visible clusters. The first consists of degree, betweenness and directed betweenness centralities that form a tightly packed cluster. Closeness centrality stands out from other network indices while the remaining ones form two loosely packed clusters.

Table 2. Spearman rank correlation between the propensity of being an intermediate host (Q) and different network indices (as identified by the top row) for each of the webs studied (as identified by the left column). In each cell the top value is the Spearman rank correlation and the bottom value is the associated levels of significance after Bonferroni corrections (*: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$, ns: not significant) Entries in bold indicate significant correlations at the 0.05 level.

	D	D _{in}	D _{out}	C	C _{in}	C _{out}	B	B _{dir}	K _{bu}	K _{td}	T _{bu}	T _{td}
Car	0.463 **	-0.436**	0.862 ***	-0.358 ns	0.635 ***	-0.843***	0.399 *	0.683 ***	0.866 ***	-0.459**	-0.707***	0.785 ***
Com	0.636 *	0.024 ns	0.783 ***	-0.680**	0.364 ns	-0.732**	0.458 ns	0.823 ***	0.814 ***	-0.444 ns	-0.506 ns	0.683 **
Yth	0.607 ***	-0.020 ns	0.719 ***	-0.567***	0.169 ns	0.657 ***	0.657 ***	0.784 ***	0.716 ***	-0.144 ns	-0.320 ns	0.665 ***
Car ⁺	0.500 ***	-0.335 ns	0.919 ***	-0.361*	0.635 ***	-0.894***	0.489 ***	0.826 ***	0.920 ***	-0.405*	-0.707***	0.854 ***

and in host–parasite interaction networks (Vázquez et al. 2005). Parasitism therefore fits the general rule that interaction ties in ecology, for instance predator–prey links and plant–pollinator interactions, tend to be non-random (Dunne et al. 2002, Montoya and Solé 2002, Bascompte et al. 2003, Vázquez and Aizen 2003, Vázquez et al. 2005, Poulin 2007).

There have been repeated studies of factors contributing to non-randomness in parasitism. These have included life history traits (i.e. body size, geographic range and diet) and epidemiological parameters (i.e. host density, host longevity and parasite transmission rate) (Poulin and Morand 2004). Our study examines parasite diversity from a different perspective by looking at the network position of host species in the food web. A large part of the non-randomness in parasite diversity is, as we have demonstrated, strongly related to the network position of host species. The importance of a species is its ability to affect others in the web by virtue of its network position. We used different network indices to emphasize different aspects of a network position. High parasite diversity is associated with species having a wide diet range, occupying a network position close to many prey species, and species to which many resources are efficiently channeled. Thus the better a species can acquire or accumulate resources from species at lower trophic levels, the more parasite species it is likely to have. Factors such as ‘what you eat’ and the ‘feeding habit of your prey’ importantly affect the likelihood of a host species acquiring many parasite species (Marcogliese 2002).

The three webs do not have exactly the same parasite diversity–network position relationships. In particular, only in the Car web is there a significant relationship between parasite diversity and host species with few predators. At this stage, with only three webs, it is not possible to say whether Car is unusual. Such a decision awaits the examination of many more webs. The discrepancy might be due simply to the uniqueness of the Carpinteria salt marsh system. Alternatively, the difference may relate to Car having a much larger proportion (82%) of parasite–host interactions connecting parasites to their definitive hosts than do the other two webs. Parasites at the final stage of their life cycle might prefer a stable host environment in which to fully complete their development; and host species that are free from predation might just be good targets for those parasites. Theoretical models illustrate that selective predation on prey with many macroparasites can rapidly drive extinct the parasite species (Packer et al. 2003, Hatcher et al. 2006), and macroparasites are usually highly aggregated on certain individuals of a host population (Poulin 1998, 2007). Extending this idea to the ecosystem raises the expectation that parasites may persist if they exploit host species that suffer low predation, and this may be the case in Car.

One reason why high parasite diversity is associated with important or prominent network positions may be that a non-parasite species at a more peripheral position may be prone to extinction. This is because such a species relies on only a few species for its survival (Allesina et al. 2006). Therefore, over time, parasites of such a host species will experience more fluctuations in host availability and be at a greater risk of extinction. Host species occupying prominent network positions, in contrast, have many interacting

partners and the associated parasite species are therefore buffered against fluctuations in host availability. If an interacting partner goes extinct the parasite can use others to continue its life-cycle and survive. The correlation with important network positions might be counteracted, however, by competition between parasite species (Bates and Kennedy 1990). The correlations between parasite diversity and network indices do not, of course, exclude other factors that might influence the pattern of parasitism. These factors include the abundance of host species (Vázquez et al. 2005, 2007) and phylogenetic constraints (Mouillot et al. 2008).

Species serving as intermediate hosts tend to lie in different food web positions to that for host species in general. Species occupying these positions tend to have many different predators, are the focus of many predatory effects from species at higher-trophic levels, or mediate many food chains. Such properties favour frequent and stable predator-prey interactions between host species that can ensure successful completion of parasite life cycles. Our finding that the network position of intermediate hosts is associated closely with material accumulation and transmission is therefore similar to the notion of PITT (parasite increased trophic transmission) (Lafferty 1999, Mouritsen and Poulin 2002).

The study of food webs with parasites is a new challenge in ecology. There are two dimensions of complexity. The first is the interaction between parasites and their definitive hosts (Vázquez et al. 2005, 2007). The second is that of how parasites are intertwined with food webs such that parasites can be transmitted from one host species to another via predator-prey links (Dobson et al. 2005, Lafferty et al. 2006b). The existing food web models (Cohen et al. 1990, Williams and Martinez 2000, Cattin et al. 2004) do not portray the interplay between parasitism and food webs, and we argue there is a need for a new food web model with parasites. Such a new model has to capture the characteristics of the underlying food web as well as the pattern of parasitism; and our results indicate that the network position of hosts is an important factor influencing the pattern of parasitism.

Our results make a substantial contribution to a general law for food web models by demonstrating two important features of parasitism in food webs. The first of these is that parasitism is not random within food webs. The second is that parasite diversity is positively related to the network position of the host species. Parasites preferentially exploit highly connected hosts species at higher trophic positions as well as those with wide diet range. There are also more parasite species using hosts mediating many food chains and those vulnerable to many predators. Considering parasitism from a network perspective as we have done reveals strong general patterns of parasitism in food webs.

Acknowledgements – The authors thank their home institutes for supporting the research leading to this paper. We also thank Mark Huxham, Dave Raffaelli, Kevin Lafferty, Ross Thompson and Robert Poulin for allowing us to use their web data. FJ is fully supported by Society in Science: The Branco Weiss Fellowship,

ETH Zürich, Switzerland. We also thank Ulrich Brose for comments and suggestions.

References

- Allesina, S. et al. 2006. Secondary extinctions in ecological networks: bottlenecks unveiled. – *Ecol. Modell.* 194: 150–161.
- Bascompte, J. et al. 2003. The nested assembly of plant–animal mutualistic networks. – *Proc. Natl Acad. Sci. USA* 100: 9383–9387.
- Bates, R. M. and Kennedy, C. R. 1990. Interactions between the acanthocephalans *Pomphorhynchus laevis* and *Acanthocephalus anguillae* in rainbow trout: testing an exclusion hypothesis. – *Parasitology* 100: 435–444.
- Borgatti, S. P. et al. 2002. Ucinet for Windows: software for social network analysis. – Analytic Technologies, Harvard.
- Brose, U. et al. 2006. Consumer–resource body-size relationships in natural food webs. – *Ecology* 87: 2411–2417.
- Bush, A. O. et al. 2002. Parasitism: the diversity and ecology of animal parasites. – Cambridge Univ. Press.
- Cattin, M. F. et al. 2004. Phylogenetic constraints and adaptation explain food-web structure. – *Nature* 427: 835–839.
- Cohen, J. E. et al. 1990. Community food webs: data and theory. – Springer.
- Cohen, J. E. et al. 1993. Body sizes of animal predators and animal prey in food webs. – *J. Anim. Ecol.* 62: 67–78.
- Dobson, A. et al. 2005. Parasites and food webs. – In: Pascal, M. and Dunn, J. A. (eds), *Ecological networks: linking structure to dynamics in food webs*. Oxford Univ. Press, pp. 119–135.
- Dunne, J. A. et al. 2002. Food-web structure and network theory: the role of connectance and size. – *Proc. Natl Acad. Sci. USA* 99: 12917–12922.
- Hatcher, M. J. et al. 2006. How parasites affect interactions between competitors and predators. – *Ecol. Lett.* 9: 1253–1271.
- Huxham, M. et al. 1995. Parasites and food web patterns. – *J. Anim. Ecol.* 64: 168–176.
- Huxham, M. et al. 1996. Do parasites reduce the chances of triangulation in a real food web. – *Oikos* 76: 284–300.
- Jeong, H. et al. 2001. Lethality and centrality in protein networks. – *Nature* 411: 41–42.
- Jordán, F. and Scheuring, I. 2004. Network ecology: topological constraints on ecosystems dynamics. – *Phys. Life Rev.* 1: 139–172.
- Jordán, F. et al. 1999. A reliability theoretical quest for keystones. – *Oikos* 86: 453–462.
- Jordán, F. et al. 2005. Topological constraints on the dynamics of wasp-waist ecosystems. – *J. Mar. Syst.* 57: 250–263.
- Jordán, F. et al. 2006. Topological keystone species: measures of positional importance in food webs. – *Oikos* 112: 535–546.
- Kuris, A. M. et al. 2008. Ecosystem energetic implications of parasite and free-living biomass in three estuaries. – *Nature* 454: 515–518.
- Lafferty, K. D. 1999. The evolution of trophic transmission. – *Parasitol. Today* 15: 111–115.
- Lafferty, K. D. et al. 2006a. Parasites dominate food web links. – *Proc. Natl Acad. Sci. USA* 103: 11211–11216.
- Lafferty, K. D. et al. 2006b. Food webs and parasites in a salt marsh ecosystem. – In: Collinge, S. and Ray, C. (eds), *Disease ecology: community structure and pathogen dynamics*. Oxford Univ. Press, pp. 119–134.
- Leeper, R. and Huxham, M. 2002. Size constraints in a real food web: predator, parasite and prey body-size relationships. – *Oikos* 99: 443–456.

- Levine, S. 1980. Several measures of trophic structure applicable to complex food webs. – *J. Theor. Biol.* 83: 195–207.
- Liu, W. C. et al. 2007. A network perspective on the topological importance of enzymes and their phylogenetic conservation. – *BMC Bioinf.* 8: 121.
- Marcogliese, D. J. 2002. Food webs and the transmission of parasites to marine fish. – *Parasitology* 124: S83–S99.
- Marcogliese, D. J. and Cone, D. K. 1997. Food webs: a plea for parasites. – *Trends Evol. Ecol.* 12: 320–325.
- Memmott, J. et al. 2000. Predators, parasitoids and pathogens: species richness, trophic generality and body sizes in a natural food web. – *J. Anim. Ecol.* 69: 1–15.
- Montoya, J. M. and Solé, R. V. 2002. Small world patterns in food webs. – *J. Theor. Biol.* 214: 405–412.
- Mouillot, D. et al. 2008. Connectance and parasite diet breadth in flea-mammal webs. – *Ecography* 31: 16–20.
- Mouritsen, K. N. and Poulin, R. 2002. Parasitism, community structure and biodiversity in intertidal ecosystems. – *Parasitology* 124: S101–S117.
- Packer, C. et al. 2003. Keeping the herds healthy and alert: implications of predator control for infectious disease. – *Ecol. Lett.* 6: 797–802.
- Pimm, S. L. 1982. Food webs. – Chapman and Hall.
- Poulin, R. 1995. Phylogeny, ecology, and the richness of parasite communities in vertebrates. – *Ecol. Monogr.* 65: 283–302.
- Poulin, R. 1998. Evolutionary ecology of parasites: from individuals to communities. – Chapman and Hall.
- Poulin, R. 2007. Are there general laws in parasite ecology? – *Parasitology* 134: 763–776.
- Poulin, R. and Morand, S. 2004. Parasite biodiversity. – Smithsonian Books.
- Thompson, R. M. et al. 2005. Importance of parasites and their life cycle characteristics in determining the structure of a large marine food web. – *J. Anim. Ecol.* 74: 77–85.
- Vázquez, D. P. and Aizen, M. A. 2003. Null model analyses of specialization in plant–pollinator interactions. – *Ecology* 84: 2493–2501.
- Vázquez, D. P. et al. 2005. Species abundance and the distribution of specialization in host–parasite interaction networks. – *J. Anim. Ecol.* 74: 946–955.
- Vázquez, D. P. et al. 2007. Species abundance and asymmetric interaction strength in ecological networks. – *Oikos* 116: 1120–1127.
- Wassermann, S. and Faust, K. 1994. Social network analysis. – Cambridge Univ. Press.
- Williams, R. J. and Martinez, N. D. 2000. Simple rules yield complex food webs. – *Nature* 404: 180–183.
- Yamaguti, S. 1975. Synoptical review of life histories of digenetic trematodes of vertebrates. – Keigaku Publishing.