Supporting Information

Alyssa R. Cirtwill *a and Daniel B. Stouffer †a

*aSchool of Biological Sciences, University of Canterbury, Christchurch, New Zealand

†Corresponding author: daniel.stouffer@canterbury.ac.nz
Materials & Methods

S1. Additional References and Description of Food Webs

Table S1: Locations and original sources for food-web datasets. The Ythan web used is version 3 from Huxham, Beaney & Raffaelli (1996). Following Huxham, Beaney & Raffaelli (1996), species 100 in this web was removed as it is an animal with no recorded resources in the food web. This also resulted in the removal of one link 100 $\rightarrow$ 85 where species 100 appeared as a resource.

| Site      | Source                           | Location                   |
|-----------|----------------------------------|----------------------------|
| Bahia     | Hechinger et al. (2011)          | Bahia Falsa, Baja California, Mexico |
| Carpinteria | Hechinger et al. (2011)      | Carpinteria Salt Marsh, California, USA |
| Estero    | Hechinger et al. (2011)          | Estero de Punta Banda, Baja California, Mexico |
| Fjord     | Zander et al. (2011)             | Flensburg Fjord, Baltic Sea, Germany/Denmark |
| Otago     | Mouritsen et al. (2011)          | Otago Harbour, New Zealand |
| Sylt      | Thielges et al. (2011)           | Sylt Tidal Basin, North Sea, Germany/Denmark |
| Ythan     | Huxham, Beaney & Raffaelli (1996) | Ythan Estuary, Scotland, UK |

Trophic groups of free-living species were defined based on the free-living webs.

Top predators (T) were defined as species with prey but no predators, basal resources (B) as species with predators but no prey, and intermediate consumers (I) were all remaining species (that is species with both predators and prey).

Cannibalistic species were considered to be intermediate consumers, as some individuals serve as prey to their conspecifics even if they are not prey to other species (Williams & Martinez, 2000). Parasites were defined by the authors of the original
food webs, and included species ranging from apicomplexan and ciliate protozoans to nematode, trematode, and cestode worms to parasitic copepods (Dunne et al., 2013; Huxham, Beaney & Raffaelli, 1996; Hechinger et al., 2011; Mouritsen et al., 2011; Thieltges et al., 2011; Zander et al., 2011). Any species with both parasitic and free-living life stages was considered a parasite.

Table S2: Representation of each type of species across the different food webs. Type “free-living” refers to webs with free-living species only while type “par & con” refers to “parasite” and “concomitant” webs which include parasites and free-living species. \( S \) refers to the total species richness in each web. \( \%_F, \%_T, \%_I, \%_B, \) and \( \%_P \) refer to the proportion of species that are free-living, top predators, intermediate consumers, basal resources, and parasites, respectively.

| Site   | Type       | \( S \) | \%_F | \%_T | \%_I | \%_B | \%_P |
|--------|------------|--------|------|------|------|------|------|
| Bahia  | free-living| 119    | 100  | 7    | 79   | 14   | 0    |
| Bahia  | par & con  | 171    | 70   | 5    | 55   | 10   | 30   |
| Carpinteria | free-living | 107  | 100  | 5  | 84 | 11 | 0    |
| Carpinteria | par & con  | 165    | 65   | 3   | 55   | 7    | 35   |
| Estero | free-living| 138    | 100  | 7   | 83   | 10   | 0    |
| Estero | par & con  | 214    | 64   | 4   | 54   | 6    | 36   |
| Flensburg | free-living | 77 | 100  | 12  | 80  | 8   | 0    |
| Flensburg | par & con  | 123    | 62   | 7   | 50   | 5    | 38   |
| Otago  | free-living| 123    | 100  | 26  | 71   | 3    | 0    |
| Otago  | par & con  | 142    | 87   | 23  | 61   | 3    | 13   |
| Sylt   | free-living| 126    | 100  | 21  | 74   | 5    | 0    |
| Sylt   | par & con  | 161    | 78   | 17  | 58   | 3    | 22   |
| Ythan  | free-living| 91     | 100  | 34  | 62   | 4    | 0    |
| Ythan  | par & con  | 133    | 68   | 23  | 42   | 3    | 32   |
Table S3: Frequency of different types of links across the different food webs. $L$ refers to the total number of links in each web while $F \rightarrow F$, $P \rightarrow F$, $P \rightarrow P$, $F \rightarrow P$, and $F \Rightarrow P$ to the number of links describing predation among free-living species, parasitism, predation between parasites, target predation of free-living species on parasites, and concomitant predation on parasites, respectively. Note that neither $F \rightarrow P$ nor $P \rightarrow P$ links were observed in the Ythan web.

| Site   | Type       | $L$ | $F \rightarrow F$ | $F \rightarrow P$ | $P \rightarrow P$ | $F \rightarrow P$ | $P \rightarrow P$ |
|--------|------------|-----|-------------------|-------------------|-------------------|-------------------|-------------------|
| Bahia  | free-living| 1075| 1075              | 0                 | 0                 | 0                 | 0                 |
| Bahia  | parasite   | 2232| 1075              | 807               | 165               | 185               | 0                 |
| Bahia  | concomitant| 3765| 1075              | 807               | 165               | 185               | 1533              |
| Carpinteria | free-living | 963 | 963              | 0                 | 0                 | 0                 | 0                 |
| Carpinteria | parasite | 2180| 963              | 755               | 166               | 296               | 0                 |
| Carpinteria | concomitant | 3762| 963              | 755               | 166               | 296               | 1582              |
| Estero  | free-living| 1647| 1647              | 0                 | 0                 | 0                 | 0                 |
| Estero  | parasite   | 3324| 1647              | 835               | 169               | 673               | 0                 |
| Estero  | concomitant| 5805| 1647              | 835               | 169               | 673               | 2481              |
| Fjord   | free-living| 577 | 577              | 0                 | 0                 | 0                 | 0                 |
| Fjord   | parasite   | 966 | 577              | 271               | 40                | 78                | 0                 |
| Fjord   | concomitant| 1428| 577              | 271               | 40                | 78                | 462               |
| Otago   | free-living| 1200| 1200             | 0                 | 0                 | 0                 | 0                 |
| Otago   | parasite   | 1481| 1200             | 173               | 19                | 89                | 0                 |
| Otago   | concomitant| 1852| 1200             | 173               | 19                | 89                | 371               |
| Sylt    | free-living| 1047| 1047             | 0                 | 0                 | 0                 | 0                 |
| Sylt    | parasite   | 1944| 1047             | 552               | 69                | 276               | 0                 |
| Sylt    | concomitant| 3033| 1047             | 552               | 69                | 276               | 1089              |
| Ythan   | free-living| 416 | 416              | 0                 | 0                 | 0                 | 0                 |
| Ythan   | parasite   | 593 | 416              | 177               | 0                 | 0                 | 0                 |
| Ythan   | concomitant| 1268| 416              | 177               | 0                 | 0                 | 675               |
S2. Quantifying Species’ and Links’ Roles

Interactions between species are a direct consequence of the motif structure of a food web. Motifs are the set of 13 three-species subwebs describing all possible interaction patterns of three species (Milo et al., 2002; Stouffer et al., 2007, Fig. S1). Each motif contains one or more unique positions, indicating a unique way in which a species’ interactions are organised in that motif (e.g., the top predator, intermediate consumer, and resource in a three-species food chain) (Stouffer et al., 2012). In the 13 three-species motifs, there are 30 such positions (Kashtan et al., 2004; Stouffer et al., 2012). Similarly, there are 24 unique link types connecting species (Fig. S2). By counting the frequency $c_{ij}^w$ with which each species $i$ in community $s$ in web type $w$ (i.e., free-living, parasite, or concomitant) occurs in each position $j$, we obtained a vector $\vec{f}_{si}^w$ describing the overall role of that species within its food web,

$$\vec{f}_{si}^w = \{c_{i1}, c_{i2}, ..., c_{i29}, c_{i30}\}_s^w.$$  \hspace{1cm} (1)

The same process was used to determine the roles of links between species,
Figure S2: Three-species motifs with unique links numbered.

\[ \vec{f}_{sl} = \{ c_{l1}, c_{l2}, \ldots, c_{l23}, c_{l24} \}_s^w. \]  

(2)

that describes the role \( \vec{f}_{sl} \) for each link \( l \) in community \( s \) in web type \( w \).

S3. Role Dispersion & Diversity

As described in the main text, we quantified the distribution of species’ and links’ roles by their role dispersion and role diversity (Fig. 2, main text). In order to quantify role diversity, we first needed to identify subsets of species (or links) that have statistically-similar motif-based roles; that is, clusters of species (or links) that appear in the same motif positions more often than one would expect by chance. To perform a clustering of this nature, we followed a recently-proposed method that is an extension of community detection algorithms for complex networks to the case of detecting groups of nodes in bipartite networks with weighted edges (Sales-Pardo et al., 2007; Stouffer et al., 2012). Here, the bipartite network consists of each species (or link) in our dataset on one side and the different motif positions on the other. Each edge in this network is weighted by the frequency \( c_{sij}^w \) with which the species or link \( i \) in community \( s \) in web type \( w \) occupies position \( j \). The
clustering algorithm consists of maximising an objective function $M$ (referred to as “modularity”) that is high when nodes in the same cluster tend to occupy the same positions with similar frequencies and low otherwise (Stouffer et al., 2012).

We used a stochastic and heuristic optimisation method known as simulated annealing (Kirkpatrick, Gelatt & Vecchi, 1983) to cluster nodes (species or links) while maximising modularity (Sales-Pardo et al., 2007; Girvan & Newman, 2002). Since this procedure is not always guaranteed to find a global optimum, and since we are most interested in the expected variety of clusters per group as a proxy for role diversity, we performed this modularity maximisation 100 separate times for roles of species and links in each community. As with dispersion, we included the roles of free-living species from the “free-living” web as well as the roles of parasites from both the “parasite” and “concomitant” webs. We then calculated the weighted average number of clusters containing each type of species (or link) across the 100 modularity-maximised clusterings following

$$\hat{N}_j = \sum_i p_i N_{ij} \quad , \quad p_i = e^{M_i} / \sum_k e^{M_k} ,$$

where $M_i$ is the modularity of a given clustering $i$, $\sum_k e^{M_k}$ is the sum of modularities over all $k$ clusterings, and $p_i$ is the relative probability of obtaining a clustering $i$ weighted by its modularity; $N_{ij}$ is the number of clusters containing...
species type \( j \) in clustering \( i \), and \( \hat{N}_j \) is the weighted average of the number of clusters containing species (or link) type \( j \) (Sales-Pardo et al., 2007). We assume that each cluster represents a unique structural role, therefore this average number of clusters provides an estimate of the role diversity for each type of species and links.

**Results**

**S4. Median Roles**

When comparing across different types of species, we found that trophic group was a significant predictor of median roles, as hypothesised \((F_{4,1432} = 218.15, p=0.001; \) Fig. 3A, main text). The P roles were between those of I and T free-living species, and they slightly overlapped with each. The P\(_c\) roles, in contrast, were distinct from all other role types. They were separated from T, I, and P roles along the first correspondence analysis axis (which accounted for 64.9% of total variance in species roles) and separated from B roles along the second correspondence analysis axis (which explained 13.0% of total variance).

The first axis corresponds mainly to a split between positions in motifs containing only one-way interactions and positions in motifs with at least one two-way interaction (Fig. S3A). T, I, and P roles are associated with a greater frequency of one-way motifs, while P\(_c\) roles are associated with a greater frequency of two-way interactions.
motifs. The second axis was largely defined by the frequencies of positions 3 and 9 (Fig. S2). Position 3 represents the base of a three-species food chain, while position 9 represents a species which is preyed upon by two other species (apparent competitors). These positions are more frequent in B roles and less frequent in other types of roles.

When comparing different types of links, we found that link type significantly predicted median roles ($F_{4,20908} = 1018.75, p < 0.001$; Fig. 3B, main text). There was a great deal of overlap between the median roles of $F \rightarrow P$ and $F \rightarrow F$ links while the median roles of $P \rightarrow P$ links were highly variable across communities. In general, the roles of $P \rightarrow F$ and $P \rightarrow P$ links showed more variation along the first principal-component axis (which accounted for 60.7% of total variance in link roles) while the roles of $F \rightarrow F$ links, $F \rightarrow P$ links, and $P \rightarrow F$ links showed more variation along the second principal-component axis (which accounted for 15.2% of total variance).

As with species roles, the first correspondence axis corresponds to a split between one-way interactions and two-way interactions (Fig. S3B). Two-way interaction positions were more frequent in the roles of concomitant predation links and less frequent in other groups. The second axis corresponds to mainly to link positions 10 and 12, which represent species with a common prey that consume each other and species which consume each other and have a common predator,
respectively (Fig. S3). These link positions are most common in links describing predation among parasites.
Figure S3: The major axes of variation for median roles demonstrated key differences in the roles of different types of species and links.  

(A) The first major axis of variation for species roles corresponded to a split between positions in motifs containing only one-way interactions and positions in motifs containing at least one two-way interaction. This axis separates the roles of parasites including concomitant predation from other types of roles (Fig. 3A). The second major axis was largely defined by positions representing the base of a three-species food chain (3) and a species with two predators which do not eat each other. These positions are most common in the roles of basal resources.  

(B) The first major axis of variation for link roles also corresponds to a split between positions in motifs that contain only one-way interactions and those in motifs containing at least one two-way interaction. Positions associated with two-way interactions were more frequent in the roles of concomitant predation links than in other role types (Fig. 3B). The second axis is largely determined by two positions representing mutual predation between species with a common prey or common predator. These positions are most common in the roles of links describing predation between parasites.
S5. Species roles

Dispersion

We determined the overall relationship between species-richness and role dispersion using the model

\[
\sigma_{gs} = \beta_1 B_g + \beta_2 I_g + g + \beta_3 T_g + \beta_4 P_g + \beta_5 P_{cg} + \beta_6 N_{gs} + \beta_6 P_g N_{gs} . \tag{4}
\]

where \( \sigma_{gs} \) is the dispersion of group \( g \) (B, I, T, P, or P\(_c\)) in community \( s \) (e.g., Ythan), \( B_g, I_g, T_g, P_g, \) and \( P_{cg} \) are dummy variables that equal 1 if \( g \) is the corresponding group type (i.e., \( B_g=1 \) if \( g \) represents the roles of basal resources), \( N_{gs} \) is the number of species \( N \) in group \( g \) at community \( s \), and \( P_g N_{gs} \) represents the number of species \( N \) in group \( g \) at community \( s \) if \( g \) represents the roles of parasites without concomitant predation links.

We then removed the non-significant overall effect of species richness (Table S4), leaving the model,

\[
\sigma_{gs} = \beta_1 B_g + \beta_2 I_g + \beta_3 T_g + \beta_4 P_g + \beta_5 P_{cg} + \beta_6 P_g N_{gs} , \tag{5}
\]

which was used to compare the dispersions of B, I, T, and P\(_c\) roles as well as the slope of P role dispersion over species richness.
Table S4: Standardised effects, $t$-values, and $p$-values for all terms included in models 1 and 2, as well as the $F$-statistic, degrees of freedom, and $p$-value of each model overall

| Parameter | Model 1 | | Model 2 | |
|-----------|---------|---------|---------|---------|
|           | Effect  | $t$-value | $p$-value | Effect  | $t$-value | $p$-value |
| $B$       | 0.251   | 11.903   | <0.001   | 0.261   | 12.703   | <0.001   |
| $I$       | 0.255   | 3.961    | <0.001   | 0.352   | 17.133   | <0.001   |
| $T$       | 0.213   | 9.050    | <0.001   | 0.233   | 11.344   | <0.001   |
| $P$       | 0.189   | 3.157    | 0.004    | 0.189   | 3.081    | 0.005    |
| $P_c$     | 0.268   | 6.825    | <0.001   | 0.320   | 15.611   | <0.001   |
| $N_{gs}$  | 0.001   | 1.563    | 0.129    | NA      |          |          |
| $P_{g^2}N_{gs}$ | 0.002 | 1.128 | 0.269 | 0.003 | 2.195 | 0.036 |
| $F$-statistic | 160.6 | | 178.1 | |
| Degrees of freedom | 7, 28 | | 6, 29 | |
| Overall $p$-value | <2.2e-16 | | <2.2e-16 | |

117 Diversity

We tested the effect of species richness on role diversity using the model,

$$\delta_{gs} = \beta_1 B_g + \beta_2 I_g + \beta_3 T_g + \beta_4 P_g + \beta_5 P_{cg} + \beta_6 N_{gs},$$

(6)

where $\delta_{gs}$ is the role diversity of trophic group $g$ in community $s$ and all other symbols are as in the dispersion models above. Only $P_c$ roles had a diversity significantly different from zero and there was no significant effect of species richness. This model was also used in the Tukey’s HSD test of mean diversities across groups, as the reduced model used to establish the mean diversity of $P_c$ roles,
\[ \delta_{gs} = \beta_0 + \beta_1 P_{cg} + \beta_2 N_{gs}, \] (7)

did not include intercepts for other role types (Table S5).

S6. Link roles

Dispersion

We examined the effect of link richness on the dispersion of link roles using the model,

\[ \sigma_{ls} = \beta_1 F \rightarrow F_l + \beta_2 F \rightarrow P_l + \beta_3 P \rightarrow F_l + \beta_4 P \rightarrow F + \beta_5 P \rightarrow P_l + \beta_6 N_{ls} + \beta_7 P \rightarrow P_l N_{ls}, \] (8)

Table S5: Standardised effects, z-values, and p-values for all terms included in models 3 and 4, as well as the AIC and degrees of freedom of each model overall

| Parameter | Model 3 | Model 4 |
|-----------|---------|---------|
|           | Effect  | t-value | p-value | Effect  | t-value | p-value |
| Intercept | NA      |          |         | 0.189   | 0.802   | 0.422   |
| B         | 0.291   | 0.901   | 0.368   | NA      |         |         |
| I         | 0.566   | 0.892   | 0.372   | NA      |         |         |
| T         | -0.128  | -0.320  | 0.749   | NA      |         |         |
| P         | 0.617   | 1.407   | 0.159   | NA      |         |         |
| P_c       | 1.558   | 4.081   | <0.001  | 1.151   | 5.632   | <0.001  |
| N         | 0.007   | 1.000   | 0.317   | 0.012   | 2.968   | 0.003   |
| AIC       | 122.56  |         |         | 108.83  |         |         |
| Degrees of freedom | 26     |         |         | 29      |         |         |
where \( \sigma_{ls} \) is the dispersion of the roles of link type \( l \) in community \( s \), \( F \to F_l \), \( F \to P_l \), \( P \xrightarrow{L} F_l \), \( P \xrightarrow{C} F_l \), and \( P \to P_l \) are dummy variables that are equal to 1 if link type \( l \) is the relevant type (i.e., \( F \to F_l = 1 \) for \( F \to F \) links) and 0 otherwise, \( N_{ls} \) is the number of links of type \( l \) in community \( s \), and \( P \to P_l N_{ls} \) is an additional effect of link richness specific to \( P \to P \) roles, only the model above which includes the interaction between link richness and \( P \to P \) roles showed any significant effect of link richness on link role dispersion. This model was used to conclude that link richness does not affect the dispersion of \( F \to F_l \), \( F \to P_l \), \( P \xrightarrow{L} F_l \), and \( P \xrightarrow{C} F_l \) roles.

We then used the reduced model,

\[
\sigma_{ls} = \beta_1 F \to F_l + \beta_2 F \to P_l + \beta_3 P \xrightarrow{L} F_l + \beta_4 P \xrightarrow{C} F_l + \beta_5 P \to P_l + \beta_7 P \to P_l N_{ls}, \tag{9}
\]

which includes an effect of link richness for \( P \to P \) roles only, to calculate the confidence intervals in Fig. 6 (main text). The best parameter estimates returned by the two models were very similar (Table S6).

**Diversity**

Finally, we determined that there was no effect of link richness on link role diversity using the model
\[ N_{ls} = \beta_1 F \rightarrow F_l + \beta_2 F \rightarrow P_l + \beta_3 P \downarrow F_l + \beta_4 P \leftarrow F_l + \beta_5 P \rightarrow P_l + \beta_7 N_{ls}, \]  

where \( N_{ls} \) is the role diversity for link type \( l \) in community \( s \) and all other symbols are as above. We then used the model

\[ \delta_{ls} = \beta_1 F \rightarrow F_l + \beta_2 F \rightarrow P_l + \beta_3 P \downarrow F_l + \beta_4 P \leftarrow F_l + \beta_5 P \rightarrow P_l, \]

to generate confidence intervals in Fig. S4. Although the estimated diversities for each link type differed between models (Table S7), the standard errors on these estimates were large, such that different types of links did not have significantly

Table S6: Standardised effects, \( t \)-values, and \( p \)-values for all terms included in models 5 and 6, as well as the \( F \)-statistic, degrees of freedom, and \( p \)-value of each model overall

| Parameter | Model 5 |   |   | Model 6 |   |   |
|-----------|---------|---|---|---------|---|---|
|           | Effect  | \( t \)-value | \( p \)-value | Effect  | \( t \)-value | \( p \)-value |
| \( F \rightarrow F_l \) | 0.345 | 12.066 | <0.001 | 0.359 | 19.342 | <0.001 |
| \( F \rightarrow P_l \) | 0.295 | 13.524 | <0.001 | 0.302 | 16.282 | <0.001 |
| \( P \downarrow F_l \) | 0.264 | 12.504 | <0.001 | 0.267 | 13.338 | <0.001 |
| \( P \leftarrow F_l \) | 0.450 | 14.179 | <0.001 | 0.466 | 25.095 | <0.001 |
| \( P \rightarrow P_l \) | 0.262 | 6.709 | <0.001 | 0.262 | 6.783 | <0.001 |
| \( N_{ls} \) | <0.001 | 0.640 | 0.528 | NA |   |   |
| \( P \rightarrow P_l N_{ls} \) | 0.001 | 4.095 | <0.001 | 0.001 | 4.195 | <0.001 |
| \( F \)-statistic | 260.3 |   |   | 310.4 |   |   |
| Degrees of freedom | 7, 26 |   |   | 6, 27 |   |   |
| Overall \( p \)-value | <2.2e-16 |   |   | <2.2e-16 |   |   |
different role diversities.

Table S7: Standardised effects, $z$-values, and $p$-values for all terms included in models 7 and 8, as well as the AIC and degrees of freedom of each model overall.

| Parameter | Model 7 |        |        | Model 8 |        |    |
|-----------|---------|--------|--------|---------|--------|
|           | Effect  | $t$-value | $p$-value | Effect  | $t$-value | $p$-value |
| $F \rightarrow F_l$ | 12.147 | 2.676 | 0.013 | 8.616 | 2.886 | 0.007 |
| $F \rightarrow P_l$ | 9.022 | 3.465 | 0.015 | 7.201 | 2.412 | 0.023 |
| $P \uparrow F_l$ | 9.483 | 3.350 | 0.009 | 8.533 | 2.646 | 0.013 |
| $P \downarrow F_l$ | 14.730 | 2.929 | 0.007 | 10.553 | 3.535 | 0.001 |
| $P \rightarrow P_l$ | 7.507 | 2.316 | 0.028 | 7.133 | 2.212 | 0.035 |
| $N_{ls}$ | -0.004 | -1.032 | 0.311 | NA | NA | |
| AIC | 237.35 | | | 236.63 | | |
| Degrees of freedom | 27 | | | 28 | | |

Figure S4: Diversity of unique roles was not related to the number of links in a community for any link type. Diversity of unique roles did not differ across link types.
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