

Parasites dominate food web links

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Communicated by G. David Tilman, University of Minnesota, St. Paul, MN, June 7, 2006 (received for review March 17, 2006)

Parasitism is the most common animal lifestyle, yet food webs rarely include parasites. The few earlier studies have indicated that including parasites leads to obvious increases in species richness, number of links, and food chain length. A less obvious result was that adding parasites slightly reduced connectance, a key metric considered to affect food web stability. However, reported reductions in connectance after the addition of parasites resulted from an inappropriate calculation. Two alternative corrective approaches applied to four published studies yield an opposite result: parasites increase connectance, sometimes dramatically. In addition, we find that parasites can greatly affect other food web statistics, such as nestedness (asymmetry of interactions), chain length, and linkage density. Furthermore, whereas most food webs find that top trophic levels are least vulnerable to natural enemies, the inclusion of parasites revealed that mid-trophic levels, not low trophic levels, suffered the highest vulnerability to natural enemies. These results show that food webs are very incomplete without parasites. Most notably, recognition of parasite links may have important consequences for ecosystem stability because they can increase connectance and nestedness.

connectance | parasitism | trophic | predation | trematode

Food webs trace the flow of energy through an ecosystem. In revealing how consumer–resource interactions lead to trophic cascades, apparent competition, and diversity–stability relationships, food webs provide a unifying theme for ecology (1). Ironically, the most common consumer strategy, parasitism (2), is usually left out of food webs because parasites are often more difficult to quantify by standard ecological methods (3). To fit the resulting parasite-free food webs, prominent theoretical concepts, such as the cascade (4) and niche (5) models, generally assume that consumers eat species smaller than themselves, suggesting that new theoretical models may be needed to accommodate parasites, which eat species larger than themselves. Before taking this step, however, it is expedient to consider how, if at all, parasites affect food webs.

Insect parasitoids are the only type of parasite commonly included in food webs. This is because parasitoids are large relative to host size, are easy to sample, and can affect insect population dynamics. However, insights gained from adding parasitoids to food webs may not extend to other infectious agents that have very different life histories (6). In comparison with highly host-specific parasitoids, individual life stages of typical parasites (an adult tapeworm in a dog's gut) can have a broad host range (7). Furthermore, many typical parasites have complex multiple-host life cycles that are embedded in food webs (3). Calls for considering typical parasites in food webs (3, 8–10) have gained few responses. The initial efforts have shown little effect of including parasites in food webs beyond obvious increases in species richness, number of links, trophic levels, and food chain length (11–14).

Connectance is an easily calculated metric that describes food web structure; a variety of theoretical studies have illustrated its role in determining ecosystem stability (15). These classic studies suggested that if interaction strength is roughly constant, then stability could only be achieved by decreases in connectivity as species diversity increased. Subsequent studies have shown that

this expected inverse relationship between connectance and stability might be offset by decreases in interaction strength with increased diversity or increases in the cohesiveness of food webs as measured by nestedness (16). For these reasons, connectance appears to be a particularly useful measure for evaluating the effect of parasites on food web structure.

Connectance (percentage of possible links realized) is a ratio with observed links (L_o) in the numerator and possible links in the denominator. For a web of F free-living species, the possible links comprise a matrix of size F^2 . Adding a list of P parasite species to a food web increases the number of observed and possible links. In past studies, two classes of links (parasite–parasite and predator–parasite) were unknowingly included in the connectance denominator [which is now a matrix of $(F + P)^2$] but were excluded from consideration in the numerator [which therefore had a maximum of $F(F + P)$ links]. As a result, the calculated ratio underestimated the percentage of the possible links that were realized, contributing to the conclusion of past studies that parasites slightly decrease connectance (11, 14, 17).

Two solutions to this problem are possible. First, one might assume that parasite–parasite and predator–parasite links are illogical and should be excluded from consideration in food webs. This issue applies to other sorts of webs, and a suitable solution has been to exclude illogical links when calculating connectance (18). This approach is particularly appropriate when working with clearly asymmetrical matrices, such as are found in plant–pollinator webs (19). Parasite–parasite and predator–parasite links can be excluded in both the numerator and the denominator of the connectance ratio such that connectance, $C = L_o/[F(F + P)]$, where L_o includes observations of parasite–host and predator–prey links. Alternatively, one could assume that parasite–parasite and predator–parasite links are logical and possible to quantify. Parasite–parasite links occur when parasites parasitize or prey on other parasites. For example, larval trematodes in snail hosts commonly engage in intraguild predation (20). Predator–parasite links, on the other hand, include cases when a predator eats an infected prey and digests the parasites inside. Predator–parasite links also include predation on free-living stages of parasite species. Parasite–parasite and predator–parasite links can be included in both the numerator and the denominator of the connectance ratio such that $C = L_o/[(F + P)^2]$, where L_o includes observations of parasite–parasite, predator–parasite, parasite–host, and predator–prey links.

We used data from four published food webs to determine how connectance and a variety of other food web metrics changed after the addition of parasites. The first version of each web included only free-living species. This “control” acted as a point of comparison for the effects of adding parasites to food webs. We then added parasites in three different ways: (i) parasite–parasite and predator–parasite links included as possible links but excluded as observed links (to mirror past studies),

Conflict of interest statement: No conflicts declared.

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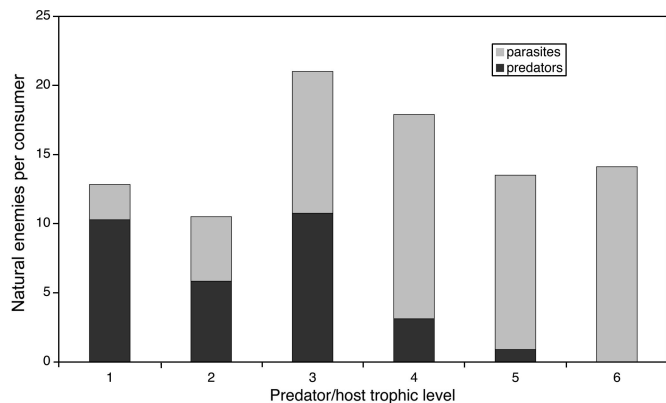


Fig. 1. Vulnerability to natural enemies peaks at intermediate trophic levels in the Carpinteria Salt Marsh. Trophic level represents the maximum chain length of a species. Bars represent the average number of natural enemy species that attack consumers in different trophic levels. Vulnerability to predators (dark shading) decreases with trophic level (top predators have no predators themselves). Vulnerability to parasites (light shading), in contrast, increases with trophic level.

(ii) parasite–parasite and predator–parasite links entirely excluded, and (iii), for one of the food webs, parasite–parasite and predator–parasite links entirely included.

Results

Parasites dominated food web links; on average, a food web contained more parasite–host links than predator–prey links. After completely including parasite–parasite and predator–parasite links, parasites were involved in 78% of the links in the Carpinteria Salt Marsh food web. For example, because of the diversity of parasites in prey, there were many more predator–parasite links (1,021) than there were predator–prey links (505). As expected, parasites increased food chain length.

New patterns emerged as a consequence of adding parasites to food webs. For instance, whereas vulnerability to predators decreased with the maximum trophic level of a species (as one would expect from the cascade model because upper trophic levels necessarily have fewer predators than do lower trophic levels), vulnerability of hosts to parasites increased with trophic level. In sum, mid-trophic levels were the most vulnerable to natural enemies (Fig. 1).

Parasites increased food web connectance (Fig. 2). After completely excluding parasite–parasite and predator–parasite links, parasites caused connectance to increase by an average of 11%. Completely including parasite–parasite and predator–parasite links increased connectance by 93% and relative nestedness by 439% (Table 1). In comparison, including parasite–parasite and predator–parasite links as possible but not observable links (as in past studies) incorrectly suggested that parasites decreased connectance by an average of 27%. When appropriately calculated, connectance corresponded to the weighted average of connectance in the Carpinteria Salt Marsh subwebs (Fig. 3). The 47 × 47 species parasite–parasite subweb had a directed connectance (7.8%) similar to the predator–prey subweb (6.7%). Directed connectance was more than double in the 47 × 87 species parasite–host subweb (15.0%) and nearly four times higher in the 87 × 47 species predator–parasite subweb (25.0%), indicating that parasite–host and predator–parasite links drove the increase in connectance in the complete web.

A sensitivity analysis of the Carpinteria Salt Marsh food web revealed that none of several alternative scenarios, alone or in combination, altered the qualitative nature of the connectance results. Adding parasites always reduced connectance when

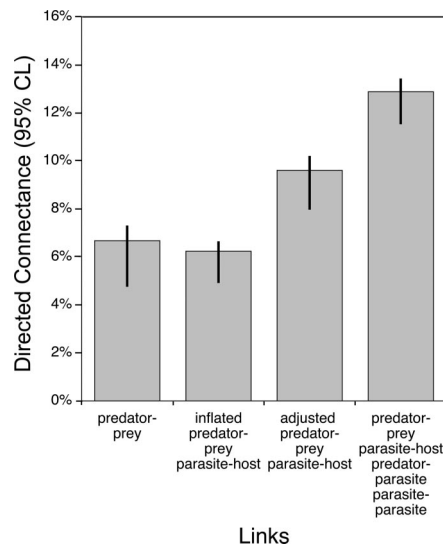


Fig. 2. Comparison of directed connectance with and without parasite links in Carpinteria Salt Marsh. The first bar includes only predator–prey links. The middle bar adds observed parasite–host links but, as in the few previous webs that have incorporated typical parasites, does so inappropriately (see Introduction). The third and fourth bars provide two new methods for determining how parasites affect connectance. The third bar excludes parasite–parasite and predator–parasite links. The fourth bar includes predator–parasite and parasite–parasite links. Comparison of the third and fourth bars with the first bar indicates that parasites increase connectance in food webs. Error bars represent 95% confidence limits.

calculated as in past studies. Parasites always increased connectance when it was calculated by the alternative methods we describe here. The single factor that most diminished the influ-

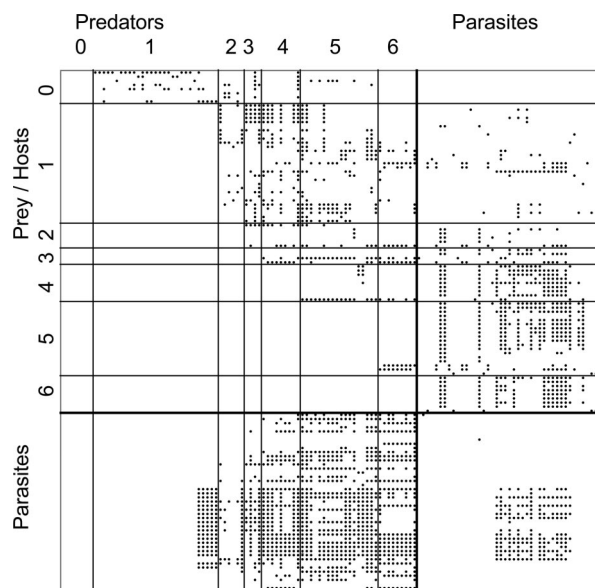


Fig. 3. A food web for Carpinteria Salt Marsh divided into four subweb matrices (12). Each consumer species is represented as a column. Rows contain the same list of species, but as prey or hosts. A dot indicates a link in the web. The upper left quadrant is the six-trophic-level predator–prey subweb (or classic food web). The upper right quadrant is the parasite–host subweb. The lower left quadrant is the predator–parasite subweb. Here predators eat parasites in prey, and predators eat free-living stages of parasites. The lower right quadrant is the parasite–parasite subweb, e.g., intraguild predation among larval trematodes in molluscan first-intermediate hosts.

Table 1. Food web statistics for four food webs calculated under four different scenarios

Statistic	Food web	Matrix denominator	Parasites			
			None	Added	Added	Added
			$F \sim F$	$F \approx F, P \approx F$	$F \approx F, P \approx F$	$F \approx F, P \approx F, P \approx P$
			F^2	$(F + P)^2$	$F(F + P)$	$(F + P)^2$
<i>S</i>	Carpinteria		87	134	134	134
	Company		67	76	76	—
	Loch Leven		22	52	52	—
	Ythan		94	135–168	135–168	—
<i>L_o</i>	Carpinteria		505	1,120	1,120	2,313
	Company		500	610–613	610	—
	Loch Leven		32	75–86	75–86	—
	Ythan		415	590	590	—
<i>d</i>	Carpinteria		5.8	8.4	8.4	17.3
	Company		7.5	8.0	8.0	—
	Loch Leven		1.5	1.5–1.7	1.5–1.7	—
	Ythan		4.4	3.5–4.4	3.5–4.4	—
<i>L_p</i>	Carpinteria		7,569	17,956	11,658	17,956
	Company		4,489	5,776	5,092	—
	Loch Leven		484	2,704	1,144	—
	Ythan		8,836	18,225–28,224	12,690–15,792	—
<i>C, %</i>	Carpinteria		6.7	6.2	9.6	12.9
	Company		11.1	10.6	12.0	—
	Loch Leven		6.6	2.7–3.2	6.6–7.5	—
	Ythan		4.7–5.0	2.1–3.5	3.7–4.7	—
<i>MMaxL</i>	Carpinteria		6	7	7	15
	Company		3	4	4	—
	Loch Leven		4	5	5	—
	Ythan		9	10	10	—
<i>AMaxL</i>	Carpinteria		1.9	4.2	4.2	8.0
	Company		1.7	—	—	—
	Loch Leven		2.6	3.6	3.6	—
	Ythan		5.0	5.4–5.5	5.4–5.5	—
<i>MAvgL</i>	Carpinteria		3.1	3.5	3.5	5.1
<i>AAvgL</i>	Carpinteria		1.8	2.2	2.2	3.1
<i>n*</i>	Carpinteria		0.54	0.55	0.55	2.91

Food web statistics [species (*S*), observed links (*L_o*), possible links (*L_p*), link density (*d*), the maximum of the maximum chain lengths (*MMaxL*), the average of the maximum chain lengths (*AMaxL*), maximum of the average chain lengths (*MAvgL*), average of the average chain lengths (*AAvgL*), directed connectance (*C*), and relative nestedness (*n**)] for four food webs [Carpinteria Salt Marsh (12), Company Bay Mudflat (14), Loch Leven (11), and Ythan Estuary (11)] calculated under four different scenarios. $F \approx F$ represents free-living species that eat other free-living species (or predation), $P \approx F$ represents parasitic consumers of free-living species (parasitism), $F \approx P$ represents free-living consumers that coincidentally or intentionally consume parasites, and $P \approx P$ represents parasites that feed on other parasites (either when parasites interact within the same host or when one species parasitizes a parasite). Column three represents a typical predator–prey web. Column four (excluded/included) adds parasite–host links to the predator–prey web but unknowingly includes parasite–parasite and predator–parasite links as possible without considering them as observable (as in past studies). Column five excludes parasite–parasite and predator–parasites links. Column six includes parasite–parasite and predator–parasite links from the Carpinteria Salt Marsh food web. Ranges in the cells are from published reports (11, 12, 14) except that ranges for the Company Bay mudflat food web compare the effect of adding three links where anemones feed on free-living parasite larvae (trematode cercariae).

ence of parasites was considering mosquitoes to be free-living predators instead of parasites. In this case, including parasites still increased connectance from 7.8% (no parasites) to 9.4% (adjusted connectance) to 12.9% (after including predator–parasite and parasite–parasite links). The combination of scenarios that most diminished the influence of parasites on connectance was (i) to treat mosquitoes as free-living predators, (ii) to consider cercariae (parasite free-living “benthic” infective stages) as free-living prey species, and (iii) to not include predator–parasite links that could lead to transmission. In this case, including parasites still increased connectance from 6.5% (no parasites) to 7.7% (adjusted connectance) to 8.7% (after including predator–parasite and parasite–parasite links).

Discussion

Food webs provide a paradigmatic view of ecosystems, but they have been largely lacking the most common consumer–resource interaction: parasitism. Even the relatively exhaustive Carpinteria Salt Marsh food web underestimates the number of infectious agents more than it does free-living species, suggesting that these new results still underestimate the role of parasites in food webs.

With the integration of parasites into food webs, “top predators” are conceivably not the highest trophic level because few species completely lack parasites (9). However, including parasites as analogues of predators may obscure how infectious agents affect different trophic levels of free-living species to parasites (17). Creating a separate parasite–host subweb (Fig. 3)

clarified the distribution of natural enemies among traditional free-living trophic levels. Free-living species occupying upper trophic levels (e.g., herons) served disproportionately as hosts. However, consumers at mid-trophic levels, like the killifish, had the highest combined vulnerability to natural enemies because they were subjected to diverse parasites and many predator species. This finding conflicts with the cascade model, which predicts that vulnerability will decline with trophic level. Future theoretical models could consider a role for parasites by allowing small consumers to feed on larger-bodied resources.

If parasite–parasite and predator–parasite links are not enumerated in a food web, an asymmetrical matrix (i.e., excluding parasite–parasite and predator–parasite links as possible) is necessary to properly determine the percentage of possible links that are realized. Asymmetrical matrices are also useful for calculating connectance in parasite–host subwebs (just as in plant–pollinator webs). For instance, our calculation of directed connectance in the parasite–host subweb of the Ythan Estuary using $L_p = PF$ (2.8–4.4%) was higher than that reported by the authors 0.9–0.7% (21). This difference is because the latter used a symmetrical matrix ($L_p = S^2$). The same discrepancy was found in the Carpinteria Salt Marsh food web. Directed connectance of the parasite–host subweb would have been 3.4% if we had used $L_p = S^2$, compared with the 15% we found using $L_p = PF$. Ignoring the asymmetry of this subweb would have given us the impression that parasite–host links were much less dense than predator–prey links when, in fact, the opposite was true. This difference in calculation explains why others have incorrectly concluded that parasite–host subwebs are relatively poor in links (11, 14).

Including parasites alters statistical measures of food webs, but do parasites alter the process and function of food webs? It is generally assumed that infectious agents, being small, are insignificant contributors to the flow of energy through food webs (3). It is true that some parasites have negligible effects on their hosts. However, other parasites can be abundant, and their biomass can be substantial. For instance, the larval acanthocephalan population in New Jersey Pine Barrens streams has the expected biomass of a top predator population (and with a likely higher turnover rate) (13). Likewise, in Carpinteria Salt Marsh the biomass of larval trematodes is comparable to the biomass of the top predators (our unpublished observations). Furthermore, many parasites have significant effects on host survival, reproduction, growth, and competitive ability. Parasites divert host energy toward investment in immune function, reduce mating success, and can increase susceptibility to predators or to stress. The effect on the host depends on the parasite's life history, of which there are several discrete types (6, 22). Some, like trematodes in snails, may have little discernable effect on longevity but, as parasitic castrators, permanently prevent reproduction of their host. Parasites can also strengthen predator–prey links by impairing the ability of infected prey to avoid predators [both as an incidental consequence of pathology and as an evolved strategy to achieve transmission (23)]. Many examples exist of parasites that manipulate food chain links to facilitate transmission (24, 25). For instance, in the Carpinteria Salt Marsh web the most abundant larval trematode, *Euhaplorchis californiensis*, makes killifish swim erratically, leading to a 10- to 30-fold increase in predation by birds that then serve as the final host for that parasite (26). These examples and a growing body of literature point to the importance of infectious disease in food webs.

Predators often coincidentally ingested parasites when feeding, and such links had a large effect on connectance. Are such links of sufficient consequence to the population of predators and parasites that they are worth including in a food web? For instance, when a rabbit accidentally eats an ant on a blade of grass, it is hard to imagine it matters much for either the rabbit

or ant population. With few exceptions (parasitoids and parasitic castrators), the parasites in infected prey make up a relatively small energetic contribution to a predator. However, the consequences for the parasite of its host being eaten are clearly dire. Although death by rabbit is a rare event for an ant, predation may often be a major source of parasite mortality because predators ultimately consume most hosts, and this can be very important for parasite dynamics (27). In some cases, the effect of predation is even greater on the parasite than on the prey. For instance, when a predator eats a snail castrated by a trematode, the only viable genotype removed from the system is that of the trematode. Predation on parasites is clearly important enough that it shapes parasite life histories. For instance, parasites must be under strong selection pressure to parasitize the predators of their hosts (28–30) because one-third (338) of the predator–parasite links can lead to parasite transmission in the Carpinteria Salt Marsh food web. Although the interaction strengths of predator–parasite links may be asymmetrical, they seem sufficiently meaningful to parasites to be considered in food webs.

If parasites are an important component of food webs, does their loss impact the stability of ecosystems, such as San Francisco Bay, where exotic species [lacking parasites (31)] have accumulated in number and diversity? The effects of parasites on connectance and nestedness suggest a potentially major role for parasites as determinants of food web stability. For instance, robustness of food webs to the threat of extinction increases with connectance (32). Similarly, the removal of highly connected species reduces stability in a food web (33). In particular, if the additional links are very asymmetrical (such as predator–parasite links), then their geometrical mean interaction strength may be minimal/negligible; this may help enhance stability (34). The increased nestedness provided by predator–parasite links should increase the cohesion of the food web by linking specialist species to a dense core of generalists; the asymmetries that result make the system more robust to perturbations because they provide pathways for the persistence of specialists (16). A significant proportion of the increased connectance in the Carpinteria Salt Marsh web was due to trematodes with complex life cycles that sequentially infect hosts on two or more trophic levels. These parasites create long loops of plausibly weak interactions that may increase overall web stability (35). That such links greatly alter food web statistics may call into question general relationships (e.g., stability and connectance) formulated exclusively through the study of conventional free-living links. Recent models (36) indicate that pathogens (modeled as microparasites) can alter the process and function of food webs as follows. In randomly constructed food webs, host-specific parasites can bring hosts to low abundance, although not to extinction. This impact can have numerous indirect effects that, depending on the food web, can decrease or increase stability.

Because the specificity of parasites for hosts is generally higher than the specificity of predators for prey, parasite diversity may be particularly dependent on host diversity. For this reason, parasites may be excellent indicators of food web structure (3, 10, 37–39). A strong relationship exists between the diversity of bird species that serve as final hosts and trematode diversity (as measured in snails) among sites within the Carpinteria Salt Marsh food web (40). Here the common snail *Cerithidea californica* serves as the sole first intermediate host for at least 19 trematode species. Without it, they and their corresponding 977 links would disappear from the web. In short, parasites may be able to affect the stability of food webs and, in turn, may be particularly sensitive to changes in food web topology themselves.

In conclusion, parasites strongly affect food web structure. Indeed, they disproportionately dominate food web links. Most food webs have ignored parasites because parasites are hidden and are perceived to have negligible biomass, yet some parasites

have population dynamic impacts that are hugely disproportionate to their small size. Exclusion of parasites has created potential biases in earlier attempts to meld food web theory with empirical data: most measures of food web stability are derived from underlying population dynamic models whereas most sets of empirical data are distorted toward free-living species visible without a microscope. Unfortunately, the few previous studies that included parasites could not detect the substantial effect of parasitism on food web topology because connectance was improperly calculated. We hope that our efforts provide new tools for further exploration of the role of parasites in food webs and for the nature of trophic dynamics in general. Future work should be extended to see whether the results we obtained from lentic and estuarine ecosystems apply to terrestrial systems as well.

Materials and Methods

We used data from the four most detailed food webs [Carpenteria Salt Marsh (12), Company Bay Mudflat (14), Loch Leven (11), and Ythan Estuary (11)] that contain parasites (Table 1). All were relatively comprehensive, although some natural enemies were underestimated. For instance, subpatent microbial pathogens and plant pathogens were excluded, and avian pathogens and ectoparasites were likely under-sampled. Because persistent extinction of any one stage in a complex life cycle would mean that all stages go extinct, each parasite species was kept a separate trophic taxon. The Carpenteria Salt Marsh web had the most complete inclusion of parasites, and this permitted additional analyses not possible for the other food webs. For instance, this web included predator–parasite and parasite–parasite links. Detailed data for the Carpenteria Salt Marsh web are in Lafferty *et al.* (12) and available at the National Center for Ecological Analysis and Synthesis Interaction Web Database (www.nceas.ucsb.edu/interactionweb/html/datasets.html), which is free and accessible to the public.

We calculated a variety of food web metrics. Species richness, S , and number of links, L , were reported from the published webs. Linkage density, d , was simply the average number of links per species. Maximum chain length, $\text{Max}L$, is the longest number of links between a consumer and a basal taxon. Long maximum chain lengths can seem at odds with predictions about limits to trophic levels because calculating the maximum for each species does not consider all of the ways that energy flows to a consumer. For this reason we also calculated the chain length for a species as the average of the possible chains to basal taxa. We report the mean and maximum of each chain length statistic in each food web.

For each food web, we report directed connectance, a measure that is robust among high-quality food webs and includes can-

nibalistic interactions as possible links (32). We also calculated directed connectance for each subweb of the Carpenteria Salt Marsh food web (Fig. 3) to help better understand how links were distributed. Because two subwebs (predator–parasite and parasite–host) were asymmetrical, we calculated connectance in the manner done for plant–pollinator webs (19). In other words, for a subweb composed of two separate species lists (such as P parasites and F free-living species), the number of cells in the matrix is clearly FP , not S^2 , and $C = L_o/FP$.

Adding the predator–parasite subweb to the Carpenteria Salt Marsh food web required the following rules for chain length to account for parasites with complex life cycles. The effect of feeding on an infected prey was to increase a consumer's chain length by one. For example, because the snail host for trematodes had a trophic level of one, trematodes in those snails, and the cercariae leaving those snails, had a trophic level of two. So, feeding on trematode cercariae or on an infected herbivorous snail occurred on the third trophic level (even though many trematodes, by virtue of using top predators as final hosts, achieved the highest trophic level as adults).

Two measures were calculated for the Carpenteria Salt Marsh food web that could not be calculated from the other webs. The first was the distribution of vulnerability of free-living species to predators and parasites by trophic level. The second was relative nestedness (16), which we derived using NESTEDNESS CALCULATOR software (41). Relative nestedness allows across-network comparison because it accounts for variation in species richness and the number of links. It is defined as $n^* = (n - R)/R$, where n is the value of nestedness in the actual matrix and R is the average nestedness of randomized versions of that matrix.

Some of the decisions to include or not include links or species in various categories could alter the results. We inspected the sensitivity of connectance in the Carpenteria Salt Marsh food web to the following rules that would seem, *a priori*, to diminish the influence of parasites: (i) nonmetazoans excluded from the food web, (ii) mosquitoes considered free-living instead of parasitic, (iii) cercarial feeding not considered a predator–parasite link, (iv) cercariae considered free-living trophic species, and (v) deletion of those predator–parasite links that could lead to transmission. We also investigated the combination of the above five scenarios that most diminished the effect of parasitism on connectance.

Ryan Hechinger, Jenny Shaw, Kathleen Whitney, and the rest of our research team provided considerable assistance. We thank Jennifer Dunne and Jordi Bascompte for insightful comments on networks and our research team for numerous contributions. The National Institutes of Health/National Science Foundation Ecology of Infectious Disease Program Grant DEB-0224565 provided support.

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