Wood, Matthew J ORCID logoORCID: https://orcid.org/0000-0003-0920-8396 (2007) Parasites entangled in food webs. Trends in Parasitology, 23 (1). pp. 8-10. doi:10.1016/j.pt.2006.11.003

Official URL: http://www.sciencedirect.com/science/article/pii/S1471492206002868
DOI: http://dx.doi.org/10.1016/j.pt.2006.11.003
EPrint URI: https://eprints.glos.ac.uk/id/eprint/557

RESEARCH FOCUS:

Parasites entangled in food webs

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Abstract:

Food webs are a fundamental concept in ecology, in which parasites have been virtually ignored. In a recent paper, Lafferty et al. address this imbalance, finding that the inclusion of parasites in food webs may be of greater importance to ecosystem stability than was previously thought. Furthermore, the bottom of the food chain is perhaps no longer the most dangerous place to be.

Food web theory, but little space for parasites

FOOD WEBS are fundamental models in ecology around which much of our understanding of ecosystems and community ecology has been based. The early days of food web ecology were characterised by a hunch that stable ecosystems tended to be diverse and complex [1, 2], a hunch that survived theoretical and empirical investigation to remain the consensus among ecologists today [3]. Understanding the relationship between food web complexity and ecosystem stability is increasingly important in a world of biodiversity loss, invasive species and climate change. This ominous backdrop supports calls for parasites, as the majority of species on Earth [4], to be integrated into food web ecology [5,6]. The pioneering attempts to achieve this, particularly by David Marcogliese and colleagues, have shown that parasites are an important component of food webs [7-10], but that comprehensive field data are lacking. Overcoming this barrier to include parasites in food webs presents substantial logistical and analytical challenges, because i) the amount of fieldwork needed to collect such data requires considerable time and expertise, ii) visualizing parasites in food webs adds dizzying complexity to model systems that is difficult to visualise (Figure 1) and iii) many important food web models simply cannot incorporate parasites because they assume that organisms only consume others smaller than themselves [11,12], an assumption that effectively disqualifies parasites.

Good data, sound knowledge and a striking result

Undaunted by this challenge, Lafferty et al. [13] included as much of their impressive understanding of the ecology and parasitology of their study system as possible, gained by thorough study of the food web of Carpinteria Salt Marsh in California [14]. This included both micro- and macro parasites for which a host-parasite association was confirmed, ranging from viruses to helminths. Lafferty et al. [13] then used simple metrics of food web structure, such as CONNECTANCE and NESTEDNESS, to observe the effects on food web structure of including parasites. This involved two novel approaches. Firstly, the authors used sub-classes of food webs, or ‘sub-webs’, (Figure 2) to examine the familiar predator-prey and parasite-host sub-webs known from previous studies, and introduced new predator-parasite and parasite-parasite sub-webs. These latter two sub-webs account for predators that consume parasites in their prey or consume free living parasite stages and parasites that consume each other (e.g. intraguild predation between larval trematodes). Secondly, they realised that previous studies of parasites in food webs [7,8,10] had miscalculated connectance in such a way that it would be inevitably underestimated.

Lafferty et al.'s new approach showed that when parasites were added to their Carpinteria food web, the resulting increase in connectance was 93% higher than that calculated using previous methods. Nestedness increased by over 400%, and connectance was 11% higher with the adjusted calculation - even if the new parasite-parasite and predator-parasite subwebs were excluded. Parasites may therefore be of much greater importance to food web structure than was previously thought.

Parasites are entangled in food webs, but so what?

If parasites have such a marked effect on simple food web statistics, are parasites as important to food web function and stability? Food webs with higher connectance are thought to be less prone to extinction [15], so parasites may be of considerable importance to ecosystem stability if they are responsible for a significant proportion of food web connectance. Lafferty et al. found that the connectance of parasite-host and predator-parasite subwebs was much higher than that of predator-prey and parasite-parasite subwebs, so this may well prove to be the case. Of course it may be possible that parasites, despite being intricately entangled in food webs, are involved in relatively trivial interactions compared to classic predator-prey food interactions. However, when one discovers that the turnover of parasite biomass in 70ha of Carpinteria Salt Marsh is estimated in thousands of kilograms per year [16], one realises that the food web energy flows involving parasites are certainly far from trivial, at least in this study system. Even if energy flows are small, parasites are well known to influence host behaviour [17], and affect host life history sufficient to regulate wild populations [18], offering the potential for strong food web interactions between parasites and hosts. Furthermore, even if the majority of parasite interactions in food webs are weak, the linking of different trophic levels by parasites with complex life cycles and multiple hosts may make ecosystems more stable (Dobson et. al., in press, cited in [14]). The mechanistic approach to understanding the influences of parasites on food web structure are complemented by empirical observation, which suggests that biodiversity and production are enhanced by parasites [19]. Healthy ecosystems, therefore, may typically have diverse parasite faunas.

The middle man in everyone's sights

A surprising consequence of Lafferty et al.'s novel examination of four sub-webs was that when concentrating their attention on the parasite-host subweb, species at high trophic levels (e.g. fish-eating birds such as Great Blue Herons *Ardea herodias*) were most at risk of parasite infection, as one might expect. However, the risk of exposure to predators varied differently, such that when considering the whole food web to examine the vulnerability of a species to both predators and parasites (i.e. all natural enemies), Lafferty et al. found that species at middle trophic levels (e.g. fish further than one level below top predators, such as California killifish *Fundulus parvipinnis*) were most vulnerable to attack, due to the combined attentions of a range of predators and a range of parasites. This contradicts previous models based on classical predator-prey food webs, which predict that vulnerability should decline with increasing trophic level [11] and that species at the lowest trophic level of a food web should be most vulnerable to attack, due to the attentions of so many predators.

A call for more muddy boots

The work of Lafferty et al. may represent a breakthrough in food web ecology akin to that made by Anderson and May in 1978 [20,21], which made an important leap from modelling predator-prey interactions to parasite-host interactions. Future advances in molecular genetics could increase the taxonomic resolution of food webs, further improving the reliability of modelling approaches to understanding food web ecology: DNA barcoding [22] offers alluring dreams of the automated identification of all the species present in a bucket of estuarine mud, or of all the parasite species contained within one isolated host. Such advances may reveal hidden complexity due to the underestimation of some host-parasite associations, particularly microparasites.

The key to Lafferty et al.'s food web data, however, is a sound knowledge of the natural history of their system: disentangling the complex interactions between hosts, parasites, predators and prey. This is knowledge largely won the old-fashioned way with muddy boots, muddy hands and dissecting microscopes. With the seductions of the impressive technological advances in biology, is there a danger that such fundamental skills may be lost? [23]. As Hannah Glasse's aprocryphal 1747 recipe for roasted hare begins, "First, catch your hare" [24].

Glossary

FOOD WEB: A model of the flow of energy through an ecosystem, a paradigm of ecology in whch organisms are grouped into trophic levels, based on the levels of separation from primary producers (typically plants or algae). Topological food webs examine the pattern of links between the organisms in a food web.

CONNECTANCE: The proportion of potential links between organisms in a food web that are realised. A robust metric for examining high-resolution food webs: higher connectance is thought to make an ecosystem more resistant to extinction.

NESTEDNESS: A further food web metric examining the asymmetry of interactions between the organisms in a food web, i.e. certain subsets of organisms are linked only with certain other subsets. Higher nestedness results from more 'cohesive' food webs that are organised around a central core of interactions. Nestedness is also thought to render food webs more resistant to extinction

Acknowledgements

Thanks to Kevin Lafferty for assistance with figures, and to four anonymous referees for their helpful comments on earlier versions of the manuscript.

Figure 1.

A food web diagram of Carpinteria Salt Marsh

Lines connect a consumer with a consumed species. Free-living species are arranged horizontally, with trophic level increasing along the y-axis. Blue arrows connecting predators to their prey at different trophic levels. Red arrows link parasites, arranged on the right axis, and their hosts, including parasites on an arbitrary right vertical axis, illustrating the complexity added to traditional food webs by the addition of parasites. Reproduced with permission from [19].

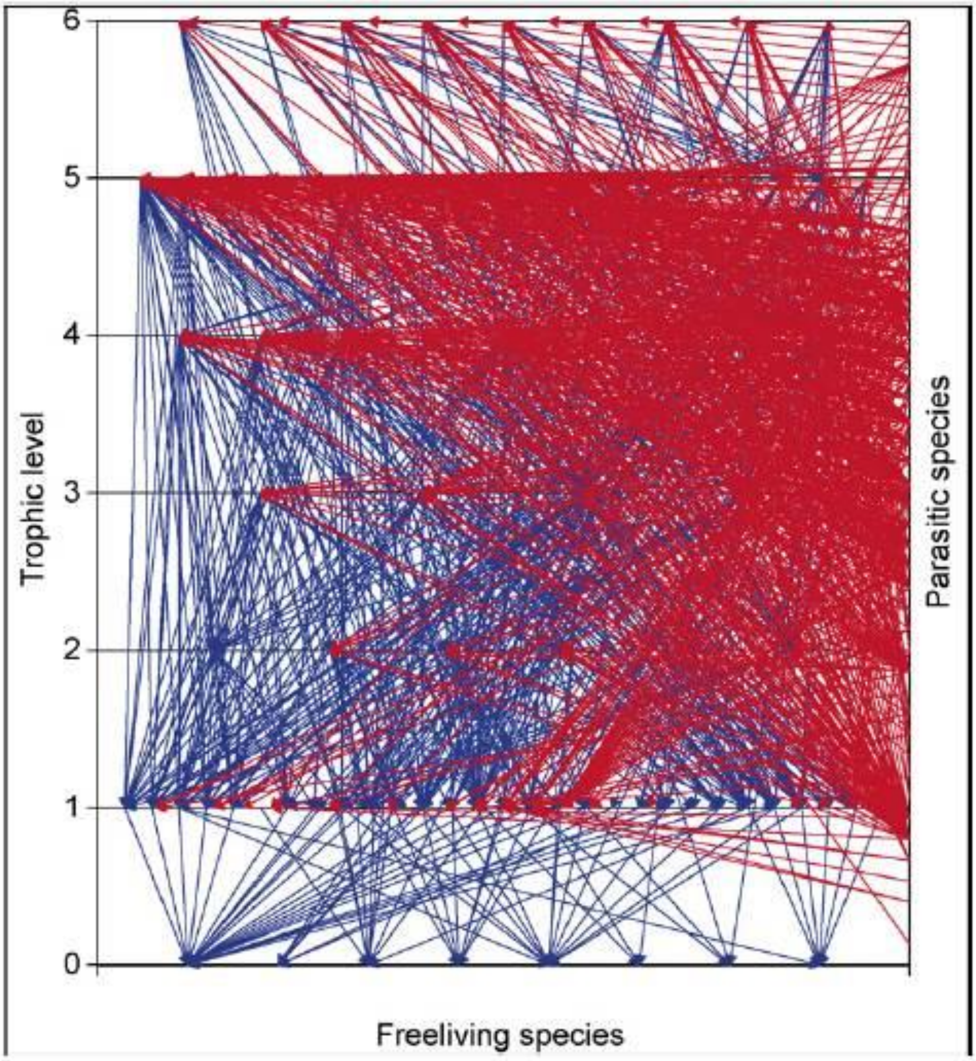
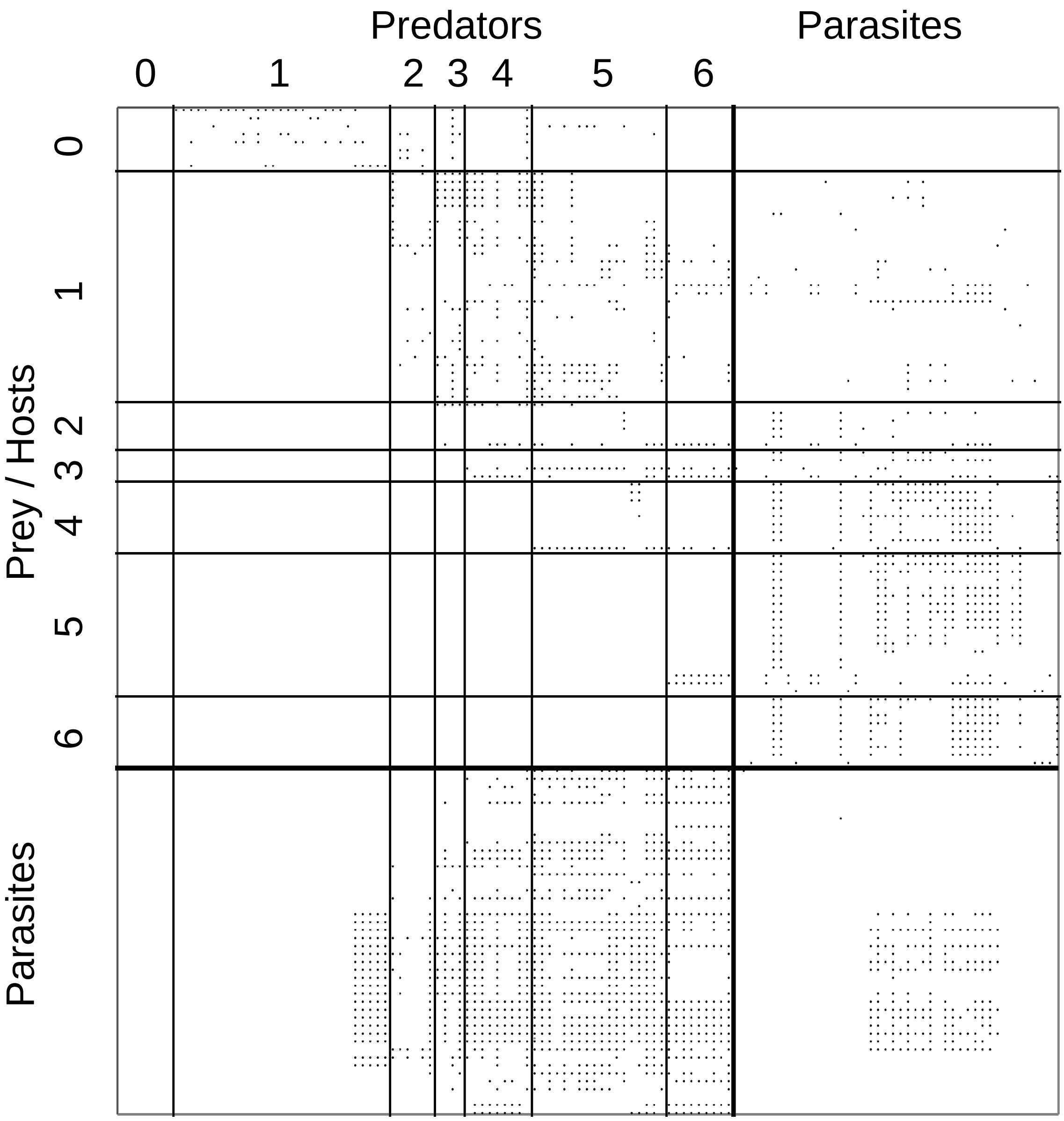


Figure 2.

A food web of Carpinteria Salt Marsh divided into four subweb matrices

Columns represent consumer species as predators or parasites, rows represent the same species as prey or hosts. Dots indicate a link in the food web. Subwebs allow both the ecology and parasitology of interacting species can be taken into account. Upper left quadrant: predator-prey subweb (or classic food web). Upper right quadrant: parasite-host subweb. Lower left quadrant: the predator-parasite subweb, where predators eat parasites in their prey and free living parasite stages. Lower right quadrant: the parasite-parasite subweb, where parasites consume each other. Reproduced with permission from [13].


Predators
Parasites
0
1
2
3
4
5
6
Prey / Hosts
0
1
2
3
4
5
6
Parasites

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