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1 **RESEARCH FOCUS:**

2

3 **Parasites entangled in food webs**

4

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7

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9

10 **Abstract:**

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

16

17 *Food web theory, but little space for parasites*

18 FOOD WEBS are fundamental models in ecology around which much of our understanding  
19 of ecosystems and community ecology has been based. The early days of food web ecology  
20 were characterised by a hunch that stable ecosystems tended to be diverse and complex [1, 2],  
21 a hunch that survived theoretical and empirical investigation to remain the consensus among  
22 ecologists today [3]. Understanding the relationship between food web complexity and  
23 ecosystem stability is increasingly important in a world of biodiversity loss, invasive species  
24 and climate change. This ominous backdrop supports calls for parasites, as the majority of  
25 species on Earth [4], to be integrated into food web ecology [5,6]. The pioneering attempts to

26 achieve this, particularly by David Marcogliese and colleagues, have shown that parasites are  
27 an important component of food webs [7-10], but that comprehensive field data are lacking.  
28 Overcoming this barrier to include parasites in food webs presents substantial logistical and  
29 analytical challenges, because i) the amount of fieldwork needed to collect such data requires  
30 considerable time and expertise, ii) visualizing parasites in food webs adds dizzying  
31 complexity to model systems that is difficult to visualise (Figure 1) and iii) many important  
32 food web models simply cannot incorporate parasites because they assume that organisms  
33 only consume others smaller than themselves [11,12], an assumption that effectively  
34 disqualifies parasites.

35

### 36 *Good data, sound knowledge and a striking result*

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

51 Lafferty et al.'s new approach showed that when parasites were added to their  
52 Carpinteria food web, the resulting increase in connectance was 93% higher than that  
53 calculated using previous methods. Nestedness increased by over 400%, and connectance was  
54 11% higher with the adjusted calculation - even if the new parasite-parasite and predator-  
55 parasite subwebs were excluded. Parasites may therefore be of much greater importance to  
56 food web structure than was previously thought.

57

58 *Parasites are entangled in food webs, but so what?*

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

76 understanding the influences of parasites on food web structure are complemented by  
77 empirical observation, which suggests that biodiversity and production are enhanced by  
78 parasites [19]. Healthy ecosystems, therefore, may typically have diverse parasite faunas.

79

#### 80 *The middle man in everyone's sights*

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

93

#### 94 *A call for more muddy boots*

95 The work of Lafferty et al. may represent a breakthrough in food web ecology akin to  
96 that made by Anderson and May in 1978 [20,21], which made an important leap from  
97 modelling predator-prey interactions to parasite-host interactions. Future advances in  
98 molecular genetics could increase the taxonomic resolution of food webs, further improving  
99 the reliability of modelling approaches to understanding food web ecology: DNA barcoding  
100 [22] offers alluring dreams of the automated identification of all the species present in a

101 bucket of estuarine mud, or of all the parasite species contained within one isolated host. Such  
102 advances may reveal hidden complexity due to the underestimation of some host-parasite  
103 associations, particularly microparasites.

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

111

## 112 **Glossary**

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

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

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

125

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128 helpful comments on earlier versions of the manuscript.

129

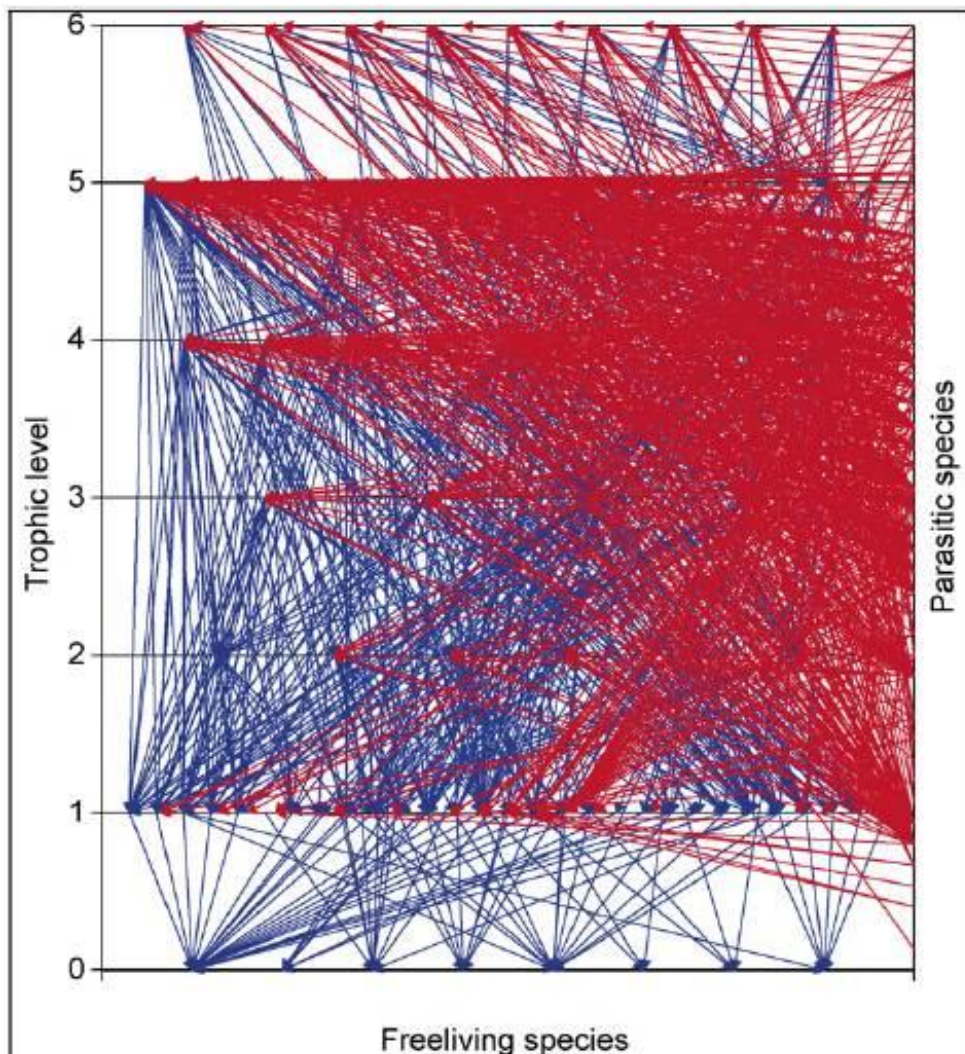
130



131 **Figure 1.**

132 **A food web diagram of Carpinteria Salt Marsh**

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

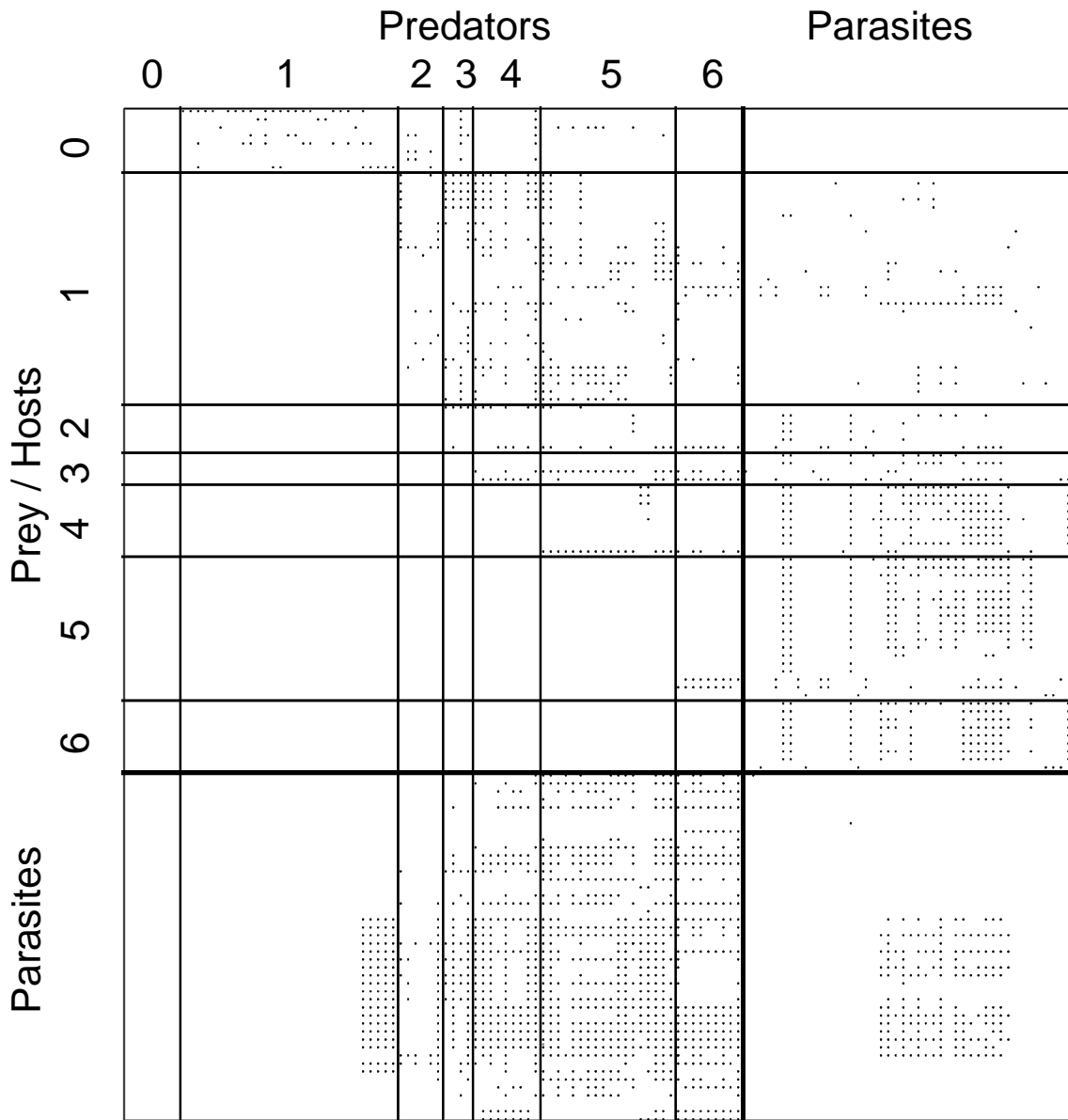


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141

142 **Figure 2.**  
143 **A food web of Carpinteria Salt Marsh divided into four subweb matrices**  
144 Columns represent consumer species as predators or parasites, rows represent the same  
145 species as prey or hosts. Dots indicate a link in the food web. Subwebs allow both the ecology  
146 and parasitology of interacting species can be taken into account. Upper left quadrant:  
147 predator-prey subweb (or classic food web). Upper right quadrant: parasite-host subweb.  
148 Lower left quadrant: the predator-parasite subweb, where predators eat parasites in their prey  
149 and free living parasite stages. Lower right quadrant: the parasite-parasite subweb, where  
150 parasites consume each other. Reproduced with permission from [13].



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152

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