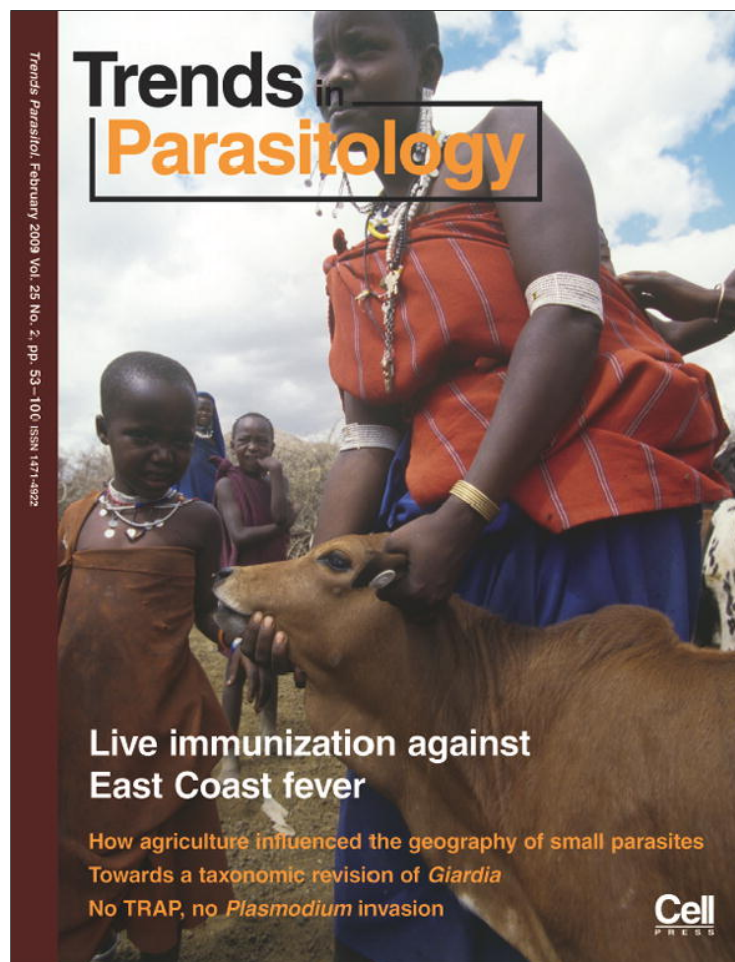


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Research Focus

Including parasites in food webs

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Growing evidence indicates parasite inclusion in food-web analyses is a logical default. Comparisons of food webs including and excluding host–parasite interactions demonstrate the influence of parasites on community dynamics. Although including parasites is undoubtedly informative, the necessary level of detail exists for only a handful of systems. In a recent *Ecology Letters* article, Lafferty *et al.* pose many good questions to catalyze discussions for determining when and how parasites should be incorporated into food-web analyses.

The case for the inclusion of parasites

Here's an interesting thought experiment: which activity did more to propel humans to the top of all natural food webs, the removal or extinction of top predators through direct hunting and habitat modification or the advent of the cooking of meat for human consumption? Conventional wisdom would indicate the removal of predators is of utmost importance. However, Lafferty *et al.* [1] would probably contend that by eliminating food-borne parasites, cooking meat was equally influential and has been overlooked, largely because of the conspicuousness of predatory events in relation to the common, but unseen, process of parasite transmission. If the authors are correct, then surely we must better engage parasites in food-web theory, construction and analysis. But what exactly is to be gained by adding parasites into food-web theory? Furthermore, operationally, can parasites be tagged onto existing webs, or do food webs require wholesale restructuring and analysis? In short, what are the criteria for deciding when to incorporate parasites, and how do we do it?

Food webs have long been used by ecologists to discern key linkages between species and processes that govern ecosystem stability, functioning and biological diversity. Food-web analyses have enabled ecologists to identify strong and weak interactors [2], discern key foundational concepts in ecology such as keystone species [3], quantify

energy flow among trophic levels [4], and even hypothesize why the world is green [5]. Especially as infectious and emerging diseases are coming into the spotlight, the inclusion of parasites in this fundamental ecological tool might galvanize insights about the roles and interrelationships of parasites in ecological communities. These insights could include a better understanding of the relationship between parasites and host diversity or the extent to which parasites affect conservation concerns that involve interactions among species, such as biodiversity loss, invasive species impact and the recovery of endangered species.

More than a decade ago, Marcogliese and Cone [6] sounded a plea for incorporating parasites into food webs. Few previous efforts had attempted this [7]. But in subsequent years, several efforts have begun to address topics foundational to this plea [8–14]. Some of the more tangible elements demonstrated by these studies were that webs contain many more host–parasite links than predator–prey links [11]; that food-web connectance might not respond to increasing species richness as rapidly in host–parasite webs as in predator–prey webs because of strong co-evolutionary constraints [12]; and that parasites can alter hosts that have crucial functional roles in systems, in turn affecting community composition, structure and energy flow [13,14]. Although these studies demonstrate that data and appropriate attention have been mounting, they have seemingly stemmed from only a handful of parasite-minded researchers; clearly, the concept of full parasite inclusion in community webs has been slow to catch on among general ecologists.

Lafferty *et al.* [1] convey to a broad ecological audience the growing consensus among ecological parasitologists that community and food-web theory needs to embrace more fully a holistic food-web theory that includes parasites. The ubiquity of parasites across systems would seemingly warrant this. Kuris *et al.* [15] recently documented that parasite biomass in three salt-marsh systems can exceed that of top predators. But how generalizable are the patterns in hand? That is, do well-studied sites (e.g.

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Carpinteria salt marsh in southern California [11,15]) typify the ecological roles played by parasites in food webs? Understanding the prominence of parasites within systems is important for determining how often or in which specific cases one needs to incorporate parasites into a food web. Such incorporation, obviously, greatly increases the complexity of a food web, from data collection through to analysis and interpretation. So, for which systems and to what extent should parasites be incorporated into food webs? Certain systems might be more likely to be high in parasite diversity and influence (e.g. aquatic systems with snails) and should perhaps include parasites in web construction as standard practice. Although, as Lafferty *et al.* [1] argue, it might be prudent to always begin food-web construction with parasites included and, if necessary, exclude them later.

Does parasite inclusion change food-web dynamics?

It seems well accepted that parasites change descriptive parameters, such as connectance, looping and linkage density, of food webs [6,11,16]. However, from a broader perspective, the more challenging yet important question might be to address whether incorporating parasites changes emergent properties and dynamics of food webs such as energy flow, stability and mass balance. Several theoretical studies have indicated such properties might be altered once parasites are incorporated in food webs. For example, including parasites can preclude trophic cascades based strictly on relative body size [16], increase model ecosystem stability [17] and either increase or decrease system stability, depending on the type of parasite [18]. One proposed mechanism that could cause webs that include host–parasite links to differ is that host–parasite interactions tend to be asymmetric. That is, specialist parasites (i.e. those with few links) are more frequently associated with hosts that harbor many parasite species (i.e. species with many links) [19,20]. Initially, it was thought that such asymmetric webs might respond differently to traditional, symmetrical webs (in which each species can potentially feed on every other species). However, so far theoretical [21] and empirical work [22] indicate that both asymmetrical and symmetrical webs exhibit similar properties and, thus, might not differ fundamentally in their behavior and emergent characteristics. These early findings could surely benefit from being tested on a wider variety of host–parasite webs.

Perhaps the most straightforward way for parasitologists to aid resolution of this issue is to generate food-web datasets on their systems, or to fit their data into already-quantified systems, and analyze these webs with and without parasites [9,23]. A variant of this approach is to parameterize a food-web model and conduct sensitivity analyses to demonstrate the relative contribution of parasites to system responses [24]. In a mass-balance approach of a coral reef ecosystem analyzed with and without parasites, when parasites were added, the number of interactions and pathways between species increased [23]. This seems an inevitable finding if any type of species is added (see, for example, Ref. [11]) but, intriguingly, most properties of mass flow did not change when parasites were added. This general comparative approach was also used to examine how adding parasites with simple versus complex

life cycles to webs influences dynamics [18]. To date, comparative work on empirical data indicates that parasites affect web dynamics minimally, although clearly, we have only scratched the surface of this issue. These comparisons, especially if they demonstrated significant differences in food-web dynamics, would go a long way to convincing ‘macroscopic’ ecologists to collaborate with parasitologists.

What does adding parasites entail? What are the obstacles?

Given the increasing evidence for parasite abundance in systems and thus their warranted inclusion in food webs, what are the ramifications for web construction, analysis and interpretation? Recently, there has been a trend to add more realism to food webs – including cannibalism, omnivory and intraguild predation and now, parasites. However, although such realism is beneficial for thorough understanding of systems, the cost of all these additions is increasing complexity. However, there are model systems that could be used to help understand the added complexity parasites bring to food-web analyses. For example, parasitoids and micropredators (e.g. fleas, mosquitoes and leeches) are already considered in many webs because parasitoids are lethal and micropredators are large (compared to parasites), external and more readily visible. These species perhaps serve as good segues into full embracement of parasites into webs because although micropredators typically attack more than one host, they usually affect hosts in an intensity-dependent manner, similar to parasites [1].

Typically, internal parasites cannot fully be treated separately because they are dependent upon a host for survival and their effects on the community must be directly through the infected hosts (see, for example, Ref. [12]). Thus, on a simple level, one might like to treat parasites as a modifier of host dynamics and handle this by splitting a host species into two boxes – one for uninfected and one for infected hosts. Such tracking would provide a level of detail similar to tracking two separate life stages of a species (e.g. if a species undergoes an ontogenetic shift). However, complications with this simplified approach enter quickly. For example, accounting for the dynamics of the parasite independent of the host is necessary if multiple hosts are used by parasites. In essence, the food-web analytic framework required becomes vastly more complex upon consideration of the myriad parasite life histories including such facets as parasites serving as prey, lack of host specificity and hyperparasitoids.

Initial efforts to incorporate parasites looked only at effects of parasites on hosts (see, for example, Refs [7,9]). However, Lafferty *et al.* [1] remind us that it is important to consider and include two other ways in which parasites contribute to food webs: parasite–parasite interactions (i.e. parasites prey on or parasitize other parasites) and predator–parasite interactions (i.e. parasites are food). These links are important because they can substantially boost food-web connectance, yet existing data on these interactions are sparse.

For the time being, food-web models with parasites might need to be formulated *ad hoc* to incorporate the idiosyncratic details of various parasite life histories – each with different implications on how they should be modeled

and incorporated. Perhaps as more community webs incorporating parasites are quantified, more generalizations can be made across systems and more ready-made food-web model templates will become available that fit the life cycles of particular parasites in the system under inspection. Food-web development has always been somewhat *ad hoc*, anyway – rarely is an entire ecosystem included in the model because potential connectance (and, thus, inter-linked dynamics) scales with the square of each species included. Rather, the important focal components are isolated, including as many contributing species as the data and analysis will make tractable. An initial similar approach seems reasonable with parasites.

Concluding remarks

Lafferty *et al.* [1] and a few previous related studies [6,7,10,11] collectively make a strong case that incorporating parasites into food webs should be standard procedure in the future. Determining when parasite inclusion is prudent must surely depend on the questions being asked, but given the ubiquitous effects of parasites, surely one omits them at his or her peril. However, how we go about inclusion is hard to say because we are in the early stages of wholesale incorporation, and the specifics and complexities of parasite life histories in a given system can necessitate an *ad hoc* approach. Lafferty *et al.* [1] give a few ideas for fruitful inroads (e.g. allometric scaling and niche modeling) but fall somewhat short of explicating specifically how to add parasites without sacrificing other important elements of the web. But their biggest contribution is to convincingly shift the burden onto food-web practitioners who choose to exclude parasites to justify their decision. Food webs, like any modeling approach, are only as good as the data that feed into them, and probably in many cases, parasite data will be lacking. In systems in which parasite parameterization is possible, analyses of webs with and without parasites to isolate their effects will continue to be particularly illustrative [7,11,23,25].

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Letters

Dogs, vaccines and *Echinococcus*

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Control of echinococcosis is an important issue, although it is not always straightforward. The potential use of a vaccine in dogs is a welcome development because such a vaccine

could cause a considerable reduction in the biomass of *Echinococcus granulosus* in endemic areas. Therefore, the review by Zhang and McManus [1] is important.

However, a close inspection of the data of the research reviewed indicates there are substantive issues in the

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