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Current Opinion

Current opinions: Zeros in host–parasite food webs: Are they real?

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ABSTRACT

As the data have poured in, and the number of published food webs containing parasites has increased, questions have been raised as to why free-living species consistently outnumber parasites, even though most general reviews on the subject of host:parasite species richness suggest the contrary. Here, I describe this pattern as it exists in the literature, posit both real and artifactual sources of these findings, and suggest ways that we might interpret existing parasite-inclusive food webs. In large part, the reporting of free-living species devoid of any associated parasites (termed here in the coding of food web matrices as "zeros") is a consequence of either sampling issues or the intent of the study. However, there are also several powerful explanatory features that validate real cases of this phenomenon. Some hosts appear to authentically lack parasitism in portions of their geographic ranges, and parasites are often lost from systems that are either in early phases of community re-colonization or are compromised by environmental perturbation. Additionally, multi-stage parasite life cycles and broad host spectra allow some parasite species to partially saturate systems without providing a corresponding increase in parasite species richness, leading to low parasite species richness values relative to the free-living community. On the whole, the existing published food webs are sufficient to, at least in principle, determine basic patterns and pathways associated with parasite establishment and persistence in free-living communities because (1) for the purpose of those features, species rarity is roughly analogous to absence and (2) the existing data seem to suggest that the addition of more parasite taxa would reinforce the patterns already observed. This is particularly true for helminth parasites, in which our understanding and the resolution of our work is most robust.

1. Introduction

At a recent meeting of the American Society of Parasitologists (Anchorage, AK, 2011), an important, though largely ignored, question was raised at the conclusion of my oral paper discussing the patterns of parasitism in a riverine food web; where are all the parasites? Specifically, the discussion centered around the apparent paucity of parasites in published food webs relative to free-living taxa, and spawned a recent review offered by my mentor and co-author on the paper (Sukhdeo, 2012). While the review was successful in framing the relationship between ecologists studying food webs and those of us attempting to use food webs to explain basic patterns of parasitism (and the concerns and issues therein), little attention was given to explaining why food webs typically contain far fewer parasites than free-living species. From the outset, most food webs containing parasites match (or surpass) the resolution of those containing only free-living species, and are often studies that augment (and build from) already well-established food webs. But, as a demonstration of the problem, consider a laundry list of recent parasite-to-free-living ratios in published food webs (note, I have removed micropredators as parasites where applicable); 25:88 (Huxham et al., 1995), 11:62, 40:83 (Lafferty et al., 2006a), 16:122 (Rossiter and Sukhdeo, 2011), 13:37 (Amundsen et al., 2009), 35:161 (Zander et al., 2011), 15:48 (Preston et al., 2012) and 21:100 (Rossiter and Sukhdeo, in review).

At best, we see a 1:2 ratio of parasite-to-free-living taxa, and this sits in stark contrast to the case that parasitologists have been making to the larger scientific community (that parasites are more abundant than free-living taxa and are crucially important; e.g. Poulin, 1997; Dobson et al., 2008; Lafferty et al., 2008). For example, it is frequently stated that parasitism is the most common and abundant feeding strategy in nature (Price, 1980). Parasites are present in nearly every animal group, and can make up as much as 75% of the interactions observed in biological systems (Lafferty et al., 2006b). It is now thought that we are losing many species of parasites with the extinction of each free-living species (Dunn et al., 2009). Those working with particular host–parasite systems will no doubt be able to ramble off numerous parasites associated with their favorite host species. For example, work on mummichogs (*Fundulus heteroclitus*) along two rivers in New Brunswick,

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Canada, produced more than 20 associated parasite species (Blanar et al., 2011). In a recent survey of the ectoparasites of 45 species of marine fishes, only one had fewer than three associated parasite species, with an average of 5.36, suggesting that parasites should be much more prevalent in our community-wide studies (Gotelli and Rhode, 2002). The same pattern emerges when considering the parasites of the gastrointestinal tracts of marine fishes (Poulin and Luque, 2003). An earlier large-scale review of parasitism across vertebrate taxa yielded an average of 10.53 (±8.39) parasite species per host (Poulin, 1997). Taken as a whole, it is estimated that there may be as many as 300,000 parasite species residing in just the 57,000 vertebrate taxa on the planet, and while the full culmination of the existing data suggest just 1.53 helminth taxa per host species (neglecting all protozoans, bacteria and viruses; Dobson et al., 2008), we still get the idea that there are many more parasites than free-living taxa in natural communities.

Given their apparent ubiquity, it is odd that every published food web containing parasites also contains many free-living species that do not act as a host for any parasites. Here, I refer to these as “zeros,” in that the coding of non-interactions in food web matrices is typically “0”. But, are these zeros real? If so, why do they exist? If not, what biases give rise to this phenomenon? I argue that nearly all zeros are artifacts of sampling biases (both unavoidable and intentional). However, some well-known patterns help make sense of real absence data in many systems, and there is some anecdotal evidence that some zeros are completely authentic. These sources of absence data in parasitological studies are summarized in Table 1. I then address how this might impact our interpretation of the existing literature in this area, and offer suggestions for future work.

2. Sources of zeros

2.1. Taxonomic resolution and sampling effort

For anyone working in the field of ecology (or parasitology for that matter), it would be hard to miss the fact that food webs have become a (if not the) prominent way for biologists to study the structure and function of natural communities. However, assembling reliable measures on entire ecological communities is an incredibly daunting task (Brown and Gillooly, 2003; Woodward et al., 2005). This is also the case for those attempting to incorporate parasites into food webs. Where studies that hone in on a particular host species might discover many associated parasites, the sampling necessary to flesh out such high-resolution data is almost impossible at the community level. Beyond the simple logistics of sufficiently sampling a system and the shear manpower necessary, whole-community studies typically rely on collaborative efforts among many biologists, each specialized in their respective floral or faunal groups. For this reason some groups are more resolved than others in food web studies. As an anecdotal example, almost no authors even attempt to resolve plankton in their systems (unless they are explicitly performing a study centered around planktonic species), instead simply calling large groups of organisms “phytoplankton” or “zooplankton,” and occasionally explicitly naming relevant ostracods or copepods (see references herein). In a recent study of the Raritan River food web in central New Jersey, I incorporated “morphospecies” of phytoplankton and zooplankton, which resulted in 12 additional organismal units in the lower trophic levels of the food web (Rossiter and Sukhdeo, in review). Still, a detailed review of 67 river systems revealed an average phytoplankton species richness of 126 (Rojo et al., 1994), suggesting that a more resolved plankton survey would more than double the size of most food aquatic food webs! The same patterns exist for microbes, unionids, and other animal groups in these systems. Likewise, it is this absence of resolution (and appropriately skilled specialists) that initially led to the lack of parasites in early food webs, the absence of which was addressed by Marcogliese and Cone (1997) among others. This situation has been fully acknowledged and evaluated in the literature (e.g. Paine, 1988; Martinez, 1991, 1993), with the general feeling being that having poorly resolved guilds or groups can impact some, though certainly not all, of the general patterns observed (Thompson and Townsend, 2000; Dunne et al., 2002; Woodward et al., 2005).

Another related and entirely unavoidable problem is the bias of sampling effort among organismal groups (taxonomic, trophically defined, or otherwise). One reason is that some habitat types are more amenable to sampling than others. For example, even at small spatial scales in lotic systems, deep and fast moving waters represent a different set of difficulties than do slower moving pools. Runs are difficult to traverse, even harder to sample benthos in (when deep), and are almost always undersampled when trapping or electroshock methods are being used. Ironically, many of us in the field have focused on wetland and marsh systems, expanses of which are nearly impossible to access, let alone sample. Likewise, sampling the epipelagic portions of seas or large lakes is expensive, labor intensive and seasonally inclement. While I'm emphasizing aquatic examples, the basic point is that some

Table 1

General description of the sources of “zeros” in food webs containing parasites, where I discuss them, whether the zeros are real or artifact, and the relative frequency in which each type of zero is observed. Frequency categories are: very common, common, less common, and rare, where very common sources are present in nearly all studies and rare sources represent anomalous observations.

Source of zero		Section	Type	Relative frequency
Numerical biases	Undersampled or ignored groups	2.1	Artifact	Very common
	Differences in taxonomic resolution	2.1	Artifact	Very common
	Host or parasite abundance or rarity	2.1	Artifact	Common
	Absence or limits on destructive sampling of hosts	2.1	Artifact	Very common
	Intent or goal of the study	2.1	Artifact	Very common
Spatial or temporal	Spatial scale or system size	2.2	Valid	Common
	Cumulative vs real-time surveying	2.2	Artifact	Common
	Duration of study	2.2	Artifact	Common
Ecological	Parasite life history	2.2, 2.3	Valid	Common-rare[a]
	Host local and geographical distribution	2.2	Valid	Less common-rare
	Environmental constraints or perturbation	2.2	Valid	Less common[b]
	Community (or food web) structure	2.2, 2.4	Valid	Very common

[a] Commonly, broad host spectra, along with multi-host life cycles, allow many free-living species to serve as hosts even when there are few parasite species. More rarely, the absence of one host in the life cycle prevents the establishment of a parasite in other would-be hosts in a study system.

[b] Because constraints and perturbations are so diverse, it is difficult to estimate how frequently they limit parasitism in communities.