Reticulated channels in soil food webs

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ABSTRACT

Soil food web research has long recognized that real webs include a number of complexities often hidden in research focused on aboveground grazing webs. These complexities include nutrient recycling, omnivory (consuming more than one prey item) and multiple reticulated channels through which energy and resources flow. Increasing evidence in real and modeled food webs suggests a critical complexity of all webs is the presence of multi-channel feeding. Multi-channel feeding, or multi-channel omnivory, occurs when a consumer feeds across two energy channels: such as a consumer that eats both roots and detritus or bacteria and fungi. As growing empirical research has documented that multi-channel omnivores are the most common type of consumer in real webs, modeling studies have also highlighted that such omnivory can be stabilizing. Here I briefly review the evolving paradigm of multi-channel feeding in food webs and outline several major areas of research that could advance predictions of how common multi-channel feeding should be in soil food webs and its impacts on stability and trophic dynamics.

Simple models of food webs have been under attack for as long as such models have been proposed (e.g., Lindeman, 1942; Park, 1946). This is especially true of research over the last 30 years as debates about food chain length (Pimm, 1982; Post, 2002) and the prevalence of dynamics triggered by the bottom versus top of such chains (Shurin et al., 2002; Hairston and Hairston, 1993) have existed alongside a continuing outcry of researchers stressing complexity over simplicity, omnivory in place of carnivory and reticulation over linearity (Polis, 1991; Polis and Strong, 1996; Moore et al., 2004; McCann, 2012). In contrast to a world of simple linear food chains, separated neatly into compartmentalized channels, exists a reality of complicated chains where herbivores may also be saprophages and consumers prey across divergent resources.

Such a world is one dominated by multi-channel feeding (Odum, 1969; Polis and Strong, 1996; Moore and Hunt, 1988)— feeding across separate energy channels such as detrital and grazing channels. Over time a growing body of literature has documented that multi-channel feeding of upper trophic levels is the norm, rather than the exception (de Ruiter et al., 1995; Digel et al., 2014; Ward et al., 2015). Alongside this growing empirical research, theoretical work has shown how multichannel feeding may be critical to the structure and stability of real food webs (Moore and Hunt, 1988; Rooney et al., 2006; Wolkovich et al., 2014; Wollrab et al., 2012). While this research has occurred across systems (e.g., Vadeboncoeur et al., 2005; Ward et al., 2015), it is particularly applicable to soil food webs, where living plant matter and detritus almost always make up the two major basal resource pools and many species are well documented as multi-channel omnivores such as earthworms (Curry and Schmidt, 2006), omnivorous nematodes (Bongers and Bongers, 1998) and mesostigmatid mites (Moore and Hunt, 1988).

Here I outline the evolving paradigm of multi-channel feeding to show why it is critical to modern soil food web research and to highlight major questions in the field. I begin by briefly reviewing how food web paradigms have shifted over time. Then I discuss how multi-channel feeding may control the structure and function of soil food webs. I close by outlining the current major questions in this area. These questions, if addressed, could greatly advance both our understanding of soil food webs and related ecosystem structure and functions.

1. Evolving paradigms of multi-channel feeding in soil food webs

Simple versions of soil food webs generally include two basal

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levels conceptualized as live plant material (including roots and shoots), on which a 'grazing' feeding channel is structured, and detritus (usually made up mainly of plant detritus), on which a detrital feeding channel is built (see Fig. 1a). While each channel shares similarities in their structures they are disparate in their dynamics. In grazing webs plants may be the major determinant of the size of the consumer pools above it (called donor or bottom-up control) or, in contrast, upper trophic levels may determine the size of lower pools (top-down control). Detrital webs are generally considered to be donor-controlled (Bengtsson et al., 1996)—with consumer density determined by the size of the detrital pool. Further, increases in the detrital pool are independent of the size of the pool because, in contrast to plants, detritus can neither reproduce, grow or otherwise directly control its pool size. The detrital pool does, however, have a critical influence on plant growth and hence—indirectly—the size of the pool through plant litter and other detrital materials.

Continuing with our simple example (Fig. 1a), the two basal levels are united by a common resource pool, often conceptualized as nitrogen in soil food webs. This nitrogen pool is lost to uptake by plants but grows via inputs from mineralization of detritus and excretion of consumers. An additional connection occurs between these pools and the detrital pool: sloppy feeding and certain waste products also unite each pool to the detrital pool. Thus, even in a food web with no multi-channel feeding (Fig. 1a) the brown and green channels are inherently linked through resource recycling (Clarholm, 1985; Moore et al., 2012). This link allows a suite of complex united dynamics including allowing the grazing channel to influence nutrient recycling—and possibly even increase plant growth (de Mazancourt et al., 1998). Further, models that consider both the limiting nutrient and carbon suggest detrital webs may critically control plant nutrient limitation (Cherif and Loreau, 2007, 2009). This linkage between simple brown and green channels via nutrient recycling can stabilize food webs with inherently unstable grazing webs (DeAngelis et al., 1989; Moore et al., 1993). Grazing channels are often unstable due to the tight dynamics controlling death and reproduction of each pool by each adjacent pool, while the donor-control of detrital channels produces weaker

interactions and greater stability—resulting in an overall increase in stability when the two channels are connected (Moore et al., 2004).

In contrast to this simple example, many food web models acknowledge that multi-channel omnivory may occur, especially at higher (see Fig 1b) consumer levels (e.g., Hunt et al., 1987; Rooney et al., 2006). Linkages of separate energy or nutrient channels through multi-channel feeding can produce a suite of far more complex dynamics that may explain a number of observed patterns. In particular such omnivory allows apparent competition (Holt and Lawton, 1994), where the dynamics of the two prey groups become united through their shared predator. Perhaps the best studied version of this is the apparent trophic cascade (Polis and Strong, 1996), where a trophic cascade on one food chain can be explained by support for the top predator—that drives the cascade—from the other channel (Polis and Hurd, 1996; Ward et al., 2015). This apparent trophic cascade has been discussed most often in united grazing and detrital chains (Polis and Strong, 1996; Ward et al., 2015), but applies to all energy channels linked by a common predator, including the often-conceptualized separate fungal and bacterial chains (Hunt et al., 1987; Moore et al., 1988).

As multi-channel feeding has become better established in the literature research has turned to understanding its stabilizing and destabilizing features to food webs. Research to date is united in showing that how much the multi-channel omnivore unites the two channels—that is how much energy or nutrients the omnivore derives from each channel—is critical to whether it engenders stability or instability (Rooney et al., 2006; Wolkovich et al., 2014). Yet beyond that research still seems too inchoate to offer many generalizations. Modeling studies show that multi-channel feeding can be stabilizing when linking channels of different 'speeds' (where nutrients move through one channel distinctly faster than the other, see Rooney et al., 2006). Other studies suggest that how much multi-channel feeding engenders stability depends on the exact dynamics of the system. For example, recent research has found that the trophic level at which a multi-channel omnivore unites the channels impacts the omnivore's affect on stability (Wollrab et al., 2012).
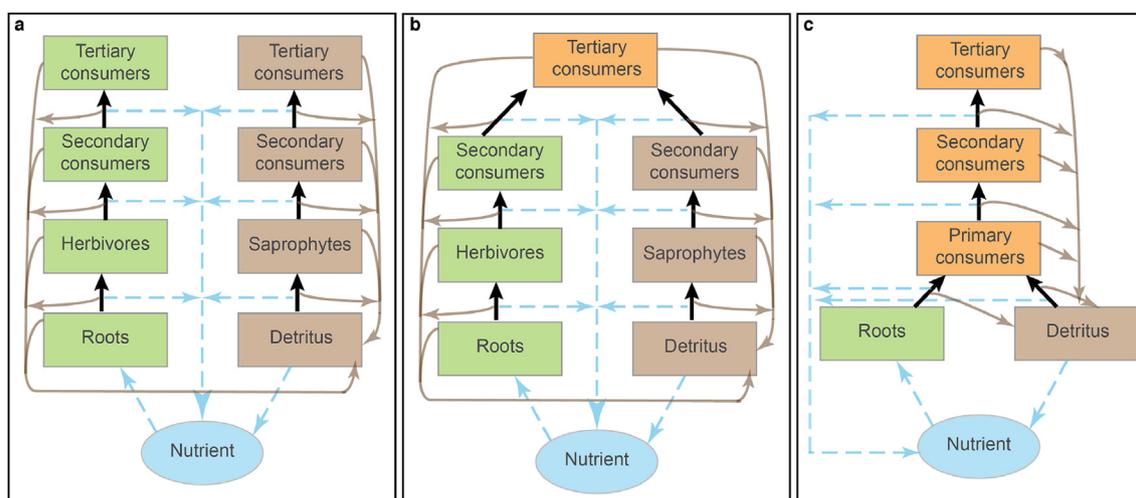

Fig. 1. Models of soil food webs have often highlighted the complexity of connections between differing channels (here shown as a grazing channel based on living roots and a detrital channel) via recycling directly to the nutrient pool (dashed blue lines) or indirectly via recycling to the detrital pool (light brown lines, for simplicity closed systems are shown). Yet over time growing empirical evidence has highlighted that few consumers actually feed (black arrows) only on one channel (as shown in a) and instead often unite channels. While such omnivory was thought to occur most often at upper trophic levels (b), growing evidence suggests it is prevalent at the lowest consumer level and throughout the upper levels (c). These models, however, are still extreme simplifications and models that further consider carbon highlight how critical detrital webs may be to plant growth and nutrient limitation (e.g., de Mazancourt et al., 1998; Cherif and Loreau, 2007). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The trophic level at which multi-channel feeding occurs in food webs seems a fulcrum point where models and empirical data have yet to converge. Increasing evidence from soil foods—as well as many other systems (Wolkovich et al., 2014; Scheunemann et al., 2015; Ward et al., 2015)—suggests multi-channel feeding occurs at the lowest possible trophic level, primary consumers. While previous encapsulations of food webs have imagined chains united by multi-channel feeding at only the very top level, increasing empirical evidence shows that many consumers of lower trophic levels feed across what had previously been considered separate channels, including grazing and detrital (Wolkovich et al., 2014) or bacterial and fungal. In contrast to most current models (e.g., Rooney et al., 2006; Wollrab et al., 2012), a realistic model of a soil food web would include multi-channel omnivory at most or all consumer levels (see Fig. 1c).

2. Major questions in multi-channel feeding in soil food webs

For soil food webs increasing evidence has established that multi-channel feeding is the norm for consumers rather than the exception, and that such omnivory plays a major role in food web dynamics. The challenge to researchers now is organizing current findings and further research into a useful framework for (1) identifying the attributes across systems that predict the prevalence and trophic positions of multi-channel omnivores and (2) understanding how different attributes of multi-channel feeding impact system dynamics.

Across systems three major attributes appear to be useful predictors for the prevalence and importance of multi-channel feeding to food webs: productivity, the degree to which resource inputs come from inside or outside the system, and heterogeneity (Polis et al., 1997; Moore et al., 2012; Ward et al., 2015). Ecologists have long studied how productivity impacts the structure, feasibility (i.e., whether all pools in the model are positive at equilibrium, sensu Roberts, 1974) and stability of food webs with higher productivity generally making complex webs more feasible but also making most webs comparatively less stable (Moore et al., 2004). We may thus expect the same for systems with multi-channel feeding. There has been relatively little work on this, however, and it seems a critical area for more modeling studies (for empirical work see Ward et al., 2015). Productivity can then be divided into whether it originates from inside (autochthonous) or outside (allochthonous) the system. Allochthonous detritus can stabilize food webs (Polis and Hurd, 1996; Polis et al., 1997; Moore et al., 1993) and thus should be an important component to measure and model in soil food web conceptualizations. However, a key attribute of allochthonous detritus in most studies to date is that it is temporally homogeneous when compared to autochthonous resources: thus the regular input of detritus from outside stabilizes a food web where the natural temporal heterogeneity of the autochthonous inputs alone would produce instability (Polis et al., 1997; Moore et al., 2004). This highlights the important role of heterogeneity in driving the structure and stability of webs. This is particularly important in soil food webs where both temporal and spatial heterogeneity are often very high (Porazinska et al., 2003; Austin, 2011). Such high heterogeneity should favor multi-channel feeding by allowing omnivores to take advantage of resources that shift in space and time. This also means that at the narrowest spatial and temporal scales multi-channel omnivores become effectively specialists and reticulate networks approach simple models.

Two other aspects of food webs with multi-channel feeding appear critical to understanding how such feeding may structure food web dynamics: the level at which multi-channel omnivores link distinct channels and, relatedly, how energy flows through multichannel feeding. Almost all research into food webs currently suggests multi-channel omnivory begins lower in food webs than previously suspected. While some consumers certainly focus on one energy channel (Wolkovich et al., 2014), the majority appear to link previously-considered 'distinct' channels. Models examining impacts on system stability have examined multi-channel omnivores that prey on two consumers or—one trophic level down—prey on both plants and detritus (e.g., Rooney et al., 2006; Wolkovich et al., 2014) but have not directly examined how the location of the omnivore impacts stability. Given other differences in these models (e.g., parameters, functional response of the omnivore) it becomes impossible to judge how the trophic level of the multi-channel feeding impacts the results. Research designed specifically to examine this would be ideal and should consider how the presence of multi-channel feeding at multiple consumer levels impacts results. Studies on stability suggest a key additional aspect will be how strongly the consumers unite the two (or more) energy channels (Rooney et al., 2006): this includes how much the multi-channel omnivores attack prey from differing channels but also, critically, how well they can assimilate each prey item and produce new biomass from it.

3. Conclusions

A slew of literature has now empirically documented multi-channel feeding across diverse webs and established that it plays a critical role in trophic dynamics. In soil food webs improved methods and new research have continually shown that many hypothesized divisions between disparate energy channels—grazing and detrital or bacterial and fungal—are generally false. The challenge to soil food web research in this area now is two-fold. First, a major goal is to better understand and predict when and to what degree such omnivory occurs in different webs, and the role it plays in driving the stability and trophic dynamics of soil food webs. Models examining one or a couple omnivores uniting simplistic channels will most likely be vital to useful insights. Yet such models must heed the other major goal: to always remember the complexity of real soil food webs, where channels are never truly separate entities but simplifications to help our understanding, and where the flow of energy and nutrients is reticulate and dynamic across habitats, resource pools and time (Dilly and Irmler, 1998; Moore et al., 1988).

Acknowledgements

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