Fear and below-ground food-webs

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ABSTRACT

Predator induced trait mediated indirect interactions (TMIIs) are likely the dominant facet of trophic interactions in aboveground food-webs. New research is beginning to show that TMIIs are also important in revealing how soil food-webs (SFWs) regulate biogeochemical processes. We suggest that TMIIs can modify SFW functions by (a) regulating the quantity and nutritional quality of plants and animal production known to drive the SFW, (b) inducing defense phenotypes in soil-organisms, and (c) changing soil environmental conditions. Currently, very few studies have explored the role TMIIs play in shaping SFW functions, especially the cascading effects on SFW dynamics. Much theoretical and empirical research is needed before we can successfully incorporate the non-consumptive effects of predation into SFW models.

1. Main text

Food-webs are networks of consumer-resource interactions that shape ecological processes from the individual to the ecosystem levels. Conventionally, food-webs are viewed in terms of direct feeding interactions that trickle down and affect not only community composition but also important ecosystem functions, such as nutrient cycling (Vanni, 2002; Wardle and Bardgett, 2004). Growing evidence shows that natural enemies can additionally regulate ecosystem functions via trait-mediated indirect interactions (TMIIs) (Schmitz et al., 2010).

Far from being helpless victims, prey can reduce their probability of being killed by predators by altering phenotypic expressions of behavioral, morphological, physiological and life-history traits (Lima and Dill, 1990; Tollrian and Harvell, 1999; Preisser et al., 2005). Implementation of such inducible defense strategies may interfere with non-emergency functions, and alter the prey’s role in conveying energy and elements up and down the food-web (Hawlena and Schmitz, 2010a). We posit that predator induced TMIIs can shape soil food-web (SFW) functions by 1) altering the nutritional-elemental composition of plant- and animal-derived organic inputs to soils, 2) inducing defense phenotypes in soil-organisms, and 3) changing soil conditions (Fig. 1 Pathways 1–3, respectively).

Nutritional-elemental content of organic inputs to soils is an important determinant of SFW structure and function (Wardle et al., 2004; Hattenschwiler et al., 2005; De Deyn et al., 2008). The majority of these inputs are comprised of senesced, uneaten plant-litter, roots, and root exudates (Cebrian, 2004; Pollierer et al., 2007; Pangesti et al., 2013; Jackrel and Wootton, 2015). Thus, it is widely assumed that herbivores primarily affect the way SFWs regulate biogeochemical processes by altering the quantity and quality of plant-derived organsics inputs to soils (Bardgett and Wardle, 2010). When threatened by predators, herbivores use defensive behaviors that constrain their dietary choices (reviewed in Brown and Kotler, 2007). Herbivores may also change their diet to consume a higher proportion of digestible carbohydrates needed to fulfill stress induced nutritional demands (Hawlena and Schmitz, 2010a, b). Consequently, predators can regulate the SFW function by causing differential herbivory on various plant species (Fig. 1 Pathway 1a-b).

PREDATOR INDUCED DIETARY DEVIATIONS MAY SELECT FOR PLANT COMMUNITIES WITH DIFFERENT CHARACTERISTICS, ALTERING THE ELEMENTAL COMPOSITION OF PLANT-DERIVED ORGANIC INPUTS TO SOILS (Fig. 1 Pathway 1a). For example, grasshoppers reared under chronic risk of spider predation alter their diet and consume more of the dominant forb Solidago rugosa, whose litter is recalcitrant to decomposition. This dietary change allows other plants to proliferate, increasing plant diversity and increases the detritus nutritional quality and rates of N-mineralization (Schmitz, 2006, 2008).
Herbivores’ dietary changes in response to predation can additionally regulate the elemental quality of plant-derived organic inputs by altering plant physiology and by inducing chemical and mechanical defenses (Chen, 2008) (Fig. 1, pathways 1b). For instance, grasshoppers stressed by predation enhance plant carbon uptake and slow carbon loss via ecosystem respiration and reallocation of carbon among plant aboveground and belowground tissues. Consequently, fear of predation leads to increased carbon retention (Strickland et al., 2013).

It is believed that animal waste materials and carcasses merely induce a localized ephemeral effect on SFWs, with little or no effect on ecosystem functioning (Bardgett and Wardle, 2010). This classical view requires revisions (Barton, 2015). Animal carcasses and waste material are rich in protein-N. Protein inputs to soils allow microbial communities to grow and produce extracellular enzymes that catalyze the decomposition of complex substrates into bioavailable products (Schimel et al., 2007). Therefore, animal-derived organic inputs to soils may accelerate mineralization of subsequent inputs of much larger quantities of low-quality plant-litter biomass (Hawlena et al., 2012). By doing so, animal carcasses and waste material may generate a mosaic landscape of soil communities that differ in function.

Predators can regulate SFW function by altering the nutritional composition of animal-derived organic inputs to soils (Fig. 1 Pathway 1c). Prey physiological stress responses to predation often involve allocation of resources from growth and reproduction to higher energy consuming emergency functions (Hawlena and Schmitz, 2010b). Prey can also allocate resources to develop and support new defense morphologies (e.g., larger tail muscles, and shell or exoskeleton fortifications; Tollrian and Harvell, 1999). Both physiological and morphological defenses can alter the nutritional composition of prey body and waste materials (e.g., Hawlena and Schmitz, 2010a; Dalton and Flecker, 2014; Guariento et al., 2015; Janssens et al., 2015). When decomposed, carcasses and waste materials of stressed animals may affect the SFW differently from those of non-stressed prey (Fig. 2). For instance, grasshoppers stressed by spiders have a higher body carbon-to-nitrogen ratio than do non-stressed grasshoppers. This change in elemental content does not slow grasshopper decomposition but alters SFW function by decelerating the subsequent decomposition of the much bigger biomass (~140 times more) of plant-litter by 62% (Hawlena et al., 2012).

Another way by which predators can affect SFW functions is by inducing defense responses in soil organisms (Fig. 1 pathway 2). Termites respond to ant predation risks by reducing detritus removal rates (Korb and Linsenmair, 2002). Similarly, under risk of spider predation, collembolans decrease their activity, resulting in lower soil N content, and lower soil CO₂ flux (Sitvarin and Rypstra, 2014). These effects are, in part, attributed to cascading effects on microbial respiration and the activities of N-fixers, possibly via mediation of nutrient release from detritus and by consumption of other soil organisms. Interestingly, the collembolans alter behavior in response mostly to pheromones of dead conspecifics (i.e., necromones; Sitvarin et al., 2015), a response that is presumably common to many soil detritivores (Yao et al., 2009). Experimental evidence implies that soil–predator induced TMIIs can substantially affect processes such as N₂O emissions from soil (Thakur et al., 2014). For example, the risk of predation can induce bacterial defenses (for review see Jouset, 2012) that may subsequently alter important ecosystem functioning such as decomposition, pollutant degradation and plant productivity. Yet, to the best of our knowledge, the non-conservative effects of soil-predators on decomposers, and their implications for SFW dynamics and function, have never been specifically explored.

Soil food-web structure and function are also regulated by the soil chemical and physical conditions such as soil compaction, pH and water content (Bråthen and Hansen, 1996; Zak et al., 1999; Rousk et al., 2010). Soil organisms can modulate these conditions by engineering the environment (Anderson, 1995). Thus, attempts of soil organisms to escape predation by shifting their activity to a different habitat domain may alter soil conditions and affect SFW dynamics (Fig. 1 Pathway 3a). For instance, anecic earthworms (Phoretima aspergillum) evade predation by shifting their activity deeper into the soil. This behavioral shift leads to increased soil porosity, and soil-soluble N and total P (Zhao et al., 2013). Similarly, coprophagous beetles respond to elevated predation risk by increasing their tunneling depth, decreasing soil bulk density and increasing water content and soil soluble N, ultimately increasing plant biomass by 28% (Wu et al., 2014, 2015). Plant traits are known to be important determinants of soil conditions including moisture, light, and temperature. Thus, another indirect way by which predators can regulate soil conditions is by controlling plant community composition via herbivore risk-induced dietary deviations (Fig. 1 Pathway 3b). Control over the organic inputs to soils is the
third mechanism by which predation can regulate soil environmental conditions (Fig. 1 Pathway 3c).

A decade ago, Preisser et al. (2005) demonstrated that intimidation costs, traditionally ignored in predator–prey ecology, may actually be the dominant facet of trophic interactions in above-ground food-webs. Emerging research indicates that TMIIs are also important in explaining SPW functions. We provide a general framework by which TMIIs can be incorporated into existing SPW concepts. Testing this framework will pose great challenges, requiring scaling individual responses to ecosystem level processes. Moreover, in almost all studies linking TMIIs to ecosystem functioning, the SPW was treated as a black box. This opens the way for exciting new research that could explore how TMIIs trickle through the SPW. Such exploration may force us to adopt a detailed functional approach in an attempt to better understand SPW dynamics and functions. We hope that in ten years, enough data will be available to conclude whether and how TMIIs shape SPW functions.

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References


