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Effects of increasing carrion biomass on food webs

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ABSTRACT

Carrion has well-documented effects on ecosystem processes, but how those effects change with increasing biomass, particularly with extreme amounts of carrion occurring during mass mortality events, is relatively unstudied. Traditional food web theory predicts basal resource availability is linked to bottom-up effects, which may support higher primary consumer biomass and food web diversity. Recycling efficiency increases with primary consumer diversity through niche differentiation and facilitation or potentially a sampling effect of having more species and functional groups. As carrion biomass increases, however, the carrion food web expands to include a more diverse community of secondary consumers that prey upon carrion obligates. With increases in vertical diversity of food webs, basal resource depletion generally decreases because primary consumers are preyed upon. Here we present empirical and previous literature evidence that indicates ecological interactions indeed change in response to increasing carrion biomass by increasing primary and secondary consumer diversity of species participating in carrion recycling. Our observations also indicate that rare and novel interactions emerge with extreme amounts of carrion. We pair previous literature with our observations to develop a theoretical basis for developing hypotheses and predictions concerning the relationship between carrion food webs and increasing biomass.

1. Introduction

In nutrient cycles within ecosystems, organisms can be conceptualized as temporary storage pools of nutrients. At the moment of death, stored nutrients begin mobilizing again in the cycle. Because carrion releases resources that are otherwise unavailable to consumers, death elicits bottom-up effects in food webs. Hereafter, when discussing bottom-up effects of carrion it is in the context of consumers using resources that originate from carrion (i.e. carrion-based food web). While it is widely accepted that carrion is an important resource in ecosystems, and some of the bottom-up effects on scavengers are well documented (e.g. Meehan et al., 2005; Carter et al., 2007; Beasley et al., 2012; Barton et al., 2013; Macdonald et al., 2014), less attention has been paid to how increasing carrion biomass affects the strength of bottom-up and top-down forces. In this paper, we will focus on three important predictions from traditional food web theory about how increasing resource availability and consumer diversity affects food webs from the bottom-up and top-down: 1) increasing resource availability strengthens the bottom-up effects on diversity of primary consumers and across trophic levels (Pace et al., 1999; Shurin et al., 2002; Gessner et al., 2010); 2) increasing primary consumer diversity strengthens top-down control of resource availability (Jonsson and Malmqvist, 2000; Hooper et al., 2005; Srivastava et al., 2009; Hector et al., 2009; Tiunov and Scheu, 2005); and 3) increasing vertical diversity (i.e. across trophic levels) weakens primary consumer top-down control on resource availability (Wyman, 1998; Lecerf et al., 2005; Greig and McIntosh, 2006; Schmitz et al., 2008). More directly as it relates to the carrion food web, increasing carrion biomass is predicted to increase scavenger abundance and diversity, and increasing abundance and diversity of scavengers should increase the efficiency of carrion recycling. However, once carrion biomass increases to a level that increases the vertical complexity of the food web, predators of scavengers should decrease the speed of carrion recycling. We acknowledge the importance of the nutrient cycle of carrion for soil bacteria and plants. However, topics regarding soil-based food webs are beyond the scope of this manuscript.

2. Does increasing carrion biomass affect food web diversity?

Previous carrion-based food web studies support the prediction of strengthened bottom-up effects with increasing resource availability (Abrams, 1993; Kaunzinger and Morin, 1998). To study bottom-up effects, differences in carrion biomass inputs can be generated by manipulating carcass size or quantity, but almost all studies manipulate carcass size. Those studies report that larger carrion size invokes higher scavenger diversity or abundance and lengthens the duration of resource availability (Müller et al., 1990; Nagano and Suzuki, 2007;

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Selva and Fortuna, 2007; Sutherland et al., 2013). For example, a study on scavenger assemblages in South Africa detected more species feeding on large (i.e. >100 kg) carcasses than smaller carcasses (i.e. <10 kg; Moleón et al., 2015). They surmised that specialized scavengers were able to quickly capitalize on the smaller carcasses that were available for a shorter period of time, while both specialized and facultative scavengers colonized larger carcasses that persisted longer and were likely easier to detect for less specialized species. Similarly, microbial communities also tend to be more diverse as carcass size is increased (Fontaine and Barot, 2005; Bradford et al., 2008). As such, carrion food web studies support that increasing carrion biomass indeed strengthens bottom-up effects by increasing the scavenger diversity.

While the longer persistence of the resource may contribute to the diversity of consumers by increasing colonization of less specialized species, the decrease in decomposition rate reported in several studies (e.g. Simmons et al., 2009; Spicka et al., 2011; Sutherland et al., 2013) seems to indicate that the increase in consumer diversity did not result in increased recycling efficiency. This pattern is dissimilar to reports in detrital decomposition from aquatic and terrestrial systems, where increasing detritivore diversity increases the efficiency of detrital decomposition (Jonsson and Malmqvist, 2000; Srivastava et al., 2009; Hector et al., 2009; Tiunov and Scheu, 2005). Although carrion and leaf detritus are different kinds of resources that attract different consumers, the processes that regulate resource depletion through competition or facilitation among consumers should be similar. So why the different pattern in decomposition rate with increasing consumer diversity in the two systems?

When we compared the systems, we realized differences may result from a confounding factor in the study design of manipulating carrion biomass by altering carcass size. That is, manipulating carrion biomass by increasing carcass size may actually decrease per capita access to carrion by scavengers because of the decreasing surface area to volume ratio of the resource. Empirical evidence that increasing detritivore diversity leads to more efficient decomposition of leaf litter comes from studies that manipulated the litter biomass by changing the number, not the size, of the leaves (Gessner et al., 2010). Also, explicit empirical tests of the top-down effects of consumer diversity come from manipulating access by some detritivores. Thus, a parallel comparison for decomposition rates in carrion food webs would incorporate manipulations of carcass number, instead of size, and scavenger access. To our knowledge only one such data set has been reported, Lashley et al. (2018a) increased carrion biomass by adding carcasses and also had a partial scavenger exclusion treatment. They concluded carrion recycling became more efficient as carrion biomass increased given that time to full decomposition was relatively similar across the gradient in biomass. In other words, the larger the carrion biomass the faster it had to decompose to reach full decomposition in the same time. Also, their data indicate that efficiency was in part linked to scavenger diversity because excluding vertebrate scavengers consistently delayed decomposition time. Thus, when carrion size is consistent among treatments, results from Lashley et al. (2018a) and various detrital studies suggest similar patterns in the effect of resource biomass and primary consumer diversity on recycling efficiency via facilitation from some organisms providing transportation or access for other organisms to the resource.

The previously observed increases in efficiency associated with scavenger abundance and diversity may be influenced by several mechanisms (e.g. Moreno-Opo and Margalida, 2013; Moleón et al., 2014; Abernethy et al., 2016). First, increasing the abundance of scavengers may accelerate decomposition rate simply by attracting more scavengers. Secondly, increasing the diversity of scavengers may increase niche complementarity in the decomposition process. The separation of specialties in decomposing different parts of the same carcass facilitates higher efficiency than would increasing the abundance of a single functional group. For example, dermatophagous species such as skin beetles (Dermestidae) specialize in decomposing skin whereas sarcophagous species such as blowfly larvae specialize in decomposing flesh (Braack, 1987). Having the same abundance of decomposers, but with both functional groups represented, would increase efficiency of fully decomposing both skin and flesh. Similarly, another mechanism of efficiency involves indirect effects from species interacting in the carrion food web. For example, vertebrate scavengers facilitate colonization or access of invertebrates or microbes to carrion by providing transportation or by creating openings to penetrate the epidermis (Meehan et al., 2005). It should also be noted that some authors have reported neutral or negative effects of primary consumer diversity on resource depletion efficiency (McKie et al., 2008; Creed et al., 2009). This normally happens when diversity includes a relatively inefficient species that is dominant because of their activity, density, or aggressive behavior, but could also result from other antagonistic interactions (Gessner et al., 2010).

In most cases, traditional food web theory predicts increases in vertical diversity by adding primary consumer predators should decrease the efficiency of consumers through behavioral- or density-mediated mechanisms (Wyman, 1998; Lecerf et al., 2005; Greig and McIntosh, 2006; Schmitz et al., 2008). Increasing carrion biomass increases predators of scavengers (Braack et al.1987), affecting depredation rates and generating other indirect effects (Cortés-Avizanda et al., 2009a, 2009b; Steinbeiser et al., 2017; Lashley et al., 2018a). However, there is, to our knowledge, no empirical evidence of a consistent relationship between predator diversity or abundance and carrion recycling efficiency. In other food webs, increasing vertical diversity may enhance or depress resource exploitation depending on different factors (Gessner et al., 2010). If the predator decreases the abundance or activity of an efficient consumer, or one that is essential in facilitation of other consumers, the predator decreases carrion recycling (Mulder et al., 1999; Schmitz et al., 2008). Alternatively, predators of scavengers could increase recycling efficiency by numerically or temporally regulating competitive dominance of an inefficient consumer in the decomposition process (Duffy et al., 2007) or if the predator is also an efficient scavenger itself.

3. What happens when biomass is abnormally high?

Recent literature has raised concern over increasing occurrences of mass mortality events (MMEs), which are catastrophic die-offs that differ from background mortality levels in both magnitude and temporal scale (Fey et al., 2015). Depending on cause, MMEs can take place in a relatively short time (e.g. Scorolli et al., 2006) or over several months (e.g. Rijks et al., 2016; Kock et al., 2018), and the number of deaths is widely variable, with some events including hundreds of thousands of individual deaths (e.g. McDowell et al., 2017; Kock et al., 2018). Not only can MMEs be catastrophic to the species affected, but they also generate a unique context in carrion food webs because of the extreme input of resources. Little empirical data are available to evaluate how ecosystem processes are affected by these events but some work suggests that MMEs can have long-lived effects on the productivity of ecosystems (Subalusky et al., 2017). Based on the idea that extreme resource abundance potentially increases consumer diversity, MMEs could cause a food web expansion to include species that are rarely or not previously documented as participating in the carrion food web.

Lashley et al. (2018a) describe several rare species interacting in the carrion food web, which increased in occurrence with carrion biomass. Thus, MMEs could alter interactions in the carrion food web simply by adding to the number of species interacting. For example, Lashley et al. (2018a) demonstrated this where increasing carrion biomass had a nonlinear exponential increase in soil perturbations from armadillo foraging for blow fly larvae. Also, MMEs may change interaction strength between species by changing the relative importance of scavengers in the decomposition process (Tomberlin et al., 2017). Another unique consequence of MMEs is due to the fact that there is a finite number of consumers in the ecosystem, and those consumers vary markedly in feeding rates and reproductive capability. Because of