

# 5

## *Carrion Effects on Belowground Communities and Consequences for Soil Processes*

Michael S. Strickland and Kyle Wickings\*

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### 5.1 Introduction: The Soil Environment

Soil is both a chemically and biologically complex environment of great ecological importance. It is the primary store of terrestrial carbon (C) and is one of the most actively cycling pools of carbon (Schlesinger 1997; Manzoni and Porporato 2009). Additionally, it is a reservoir for plant nutrients, which fuel primary production (Epstein and Bloom 2005). Yet, not all soils are equal regarding their chemical and physical properties. For example, the underlying parent material of a soil can greatly impact its properties (e.g., pH, clay type, and soil texture). Additionally, soil mineralogy influences cation exchange capacity, which is an important determinant of traits such as soil fertility (Evangelou and Phillips 2005).

Humans can also have a marked impact on soil properties, and many soil characteristics are sensitive to land-use and management intensity. For example, conventional cultivation leads to a depletion of organic matter and soil fertility, requiring inorganic inputs of fertilizers to maintain plant biomass (Lal 2008). Intensive cultivation can also lead to long-term shifts in plant litter decay rates and patterns of litter chemistry over the course of decomposition (Grandy and Robertson 2007; Wickings et al. 2011).

Differences in the physical and chemical attributes of soil represent the prime determinants of the size and structure of belowground food webs. Soil microbial and invertebrate communities are heavily shaped by a legacy of resource quality, nutrient availability, soil pH, texture, and porosity (Petersen and Luxton 1982; Behan-Pelletier 1999; Callaham et al. 2006; Fierer and Jackson 2006; Salamon et al. 2006; Lauber et al. 2008, 2009; Strickland et al. 2009b; Wickings and Grandy 2011). Yet, the relationship between soil organisms and soil properties is bidirectional and involves numerous feedbacks. Although existing soil traits determine microbial and invertebrate community structure, differences in community structure can have significant functional consequences for soil attributes and processes. For example, change in soil microbial communities and the presence or absence of microarthropods can influence both rates of carbon cycling and decomposition (Strickland et al. 2009a, 2012; Wickings and Grandy 2011). Structural changes in soil food webs can also impact the chemistry of organic matter inputs, which may have long-term implications for soil organic matter (SOM) formation and stability (Wickings et al.

\* The authors contributed equally to this work.

- Q1** 2012). Soil organisms also shape soil structure. For example, macroinvertebrates, including earthworms, ants, and termites, alter soil porosity, organic matter distribution, and soil aggregates (Lavelle et al. 1997).

Organic matter inputs serve as the basal resource for the soil food web, and it is well recognized that the quality of these inputs can affect the size and structure of soil biological communities (Haynes 1999). Recent studies have also shown that the quality of organic matter inputs is an important constraint on the function of soil microbes and invertebrates (Smith and Bradford 2003; Strickland et al. 2009b; Yang and Chen 2009). Carrion represents a very high-quality input to soil and may have substantial effects on soil processes that are mediated by soil biota. Historically, the potential importance of these inputs has been overlooked as a very ephemeral resource pulse, with no long-term consequences for soils or ecosystems (but see Putnam 1978). Yet, there is a growing awareness that high-quality inputs such as carrion may play an important role in long-term soil processes such as the formation and stability of SOM (Barton et al. 2013; Cotrufo et al. 2013).

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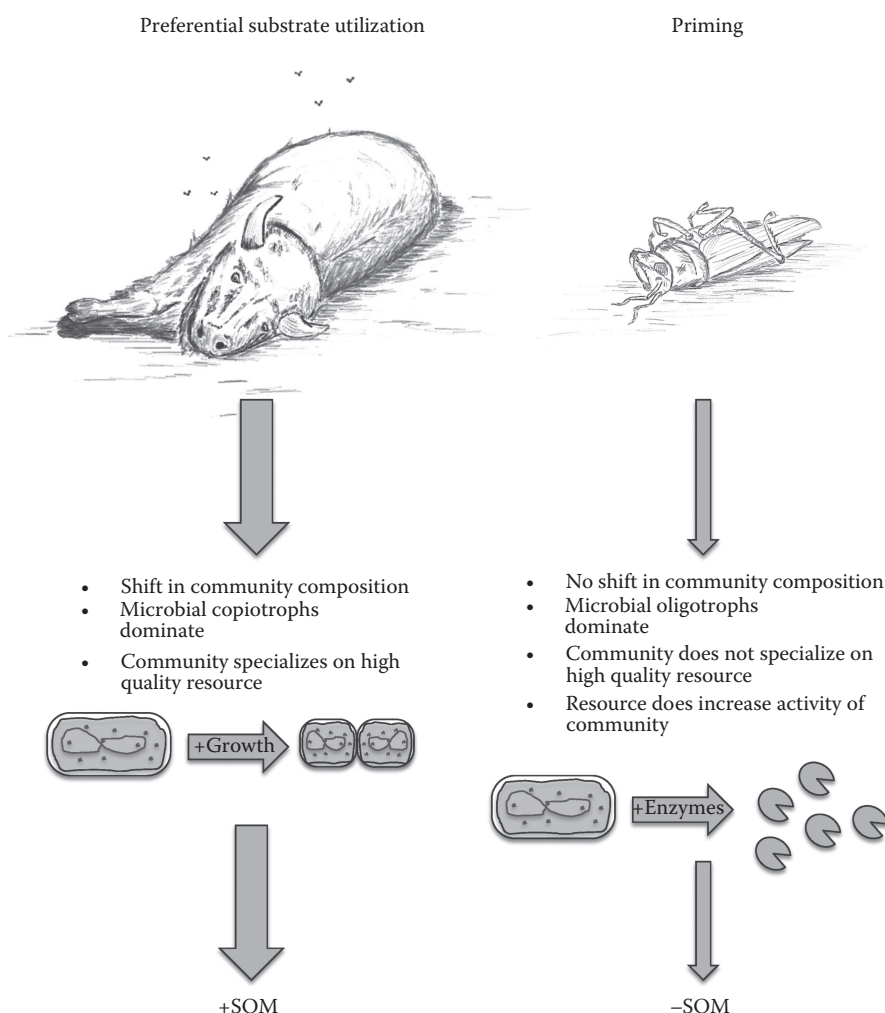
## 5.2 Carrion as a Resource Input

The bulk of inputs entering soil is plant-derived, consisting of both leaf litter and root-derived inputs (Swift et al. 1979; Lavelle et al. 1993; Aerts 1997; van Hees et al. 2005). These inputs contribute the most to SOM formation and fuel the bulk of biological activity in soil (Aerts 1997; van Hees et al. 2005; Pollierer et al. 2007). The chemical quality of plant-derived resources is, under similar climate, a major determinant of their decomposition rates. Often, this is graded using lignin: nitrogen or carbon: nitrogen ratios, with a greater ratio either indicative of a more recalcitrant input or slower breakdown rate.

Animal-derived inputs, however, have often been overlooked. The rationale is that such inputs decompose very rapidly, represent a relatively small input to any system, and likely have little-to-no long-term effect on soil processes (Parmenter and MacMahon 2009). Although this may be true, there is little-to-no empirical evidence supporting this view and recent studies are beginning to challenge this idea (Barton et al. 2013; Macdonald et al. 2014). Additionally, although such inputs are rapidly decomposed, this does not indicate that they are unimportant or that their impacts are ephemeral. In fact, recent research indicates that the more labile an input is the greater its long-term influence on soil properties such as soil organic carbon (Yang and Janssen 2002; Strickland et al. 2010; Bradford et al. 2013; Cotrufo et al. 2013).

This idea is termed the microbial efficiency-matrix stabilization (MEMS) framework (Cotrufo et al. 2013) and is based on the microbial assimilation efficiency of a given compound. The more efficient the assimilation, the more likely the resource will be converted into microbial biomass and/or metabolites (Yang and Janssen 2002; Cotrufo et al. 2013). These microbial products are then more apt to lead to the formation of stable SOM (Yang and Janssen 2002). Alternatively, such labile compounds may actually stimulate microbial activity and subsequently the loss of SOM (Dalenberg and Jager 1981; Fontaine and Barot 2005; Bradford et al. 2008). This is commonly referred to as priming (Dalenberg and Jager 1981). The possibility that priming occurs is often dependent on the amount of labile compounds entering a system. If labile compounds represent a small input relative to more recalcitrant inputs, then priming is likely to occur (Fontaine and Barot 2005; Bradford et al. 2008). Alternatively, if labile compounds represent a relatively high input, then preferential substrate utilization (akin to MEMS) will occur (Wu et al. 1993; Fontaine and Barot 2005). Often, the balance between these two processes is dependent on the resource quality and availability of the site in question.

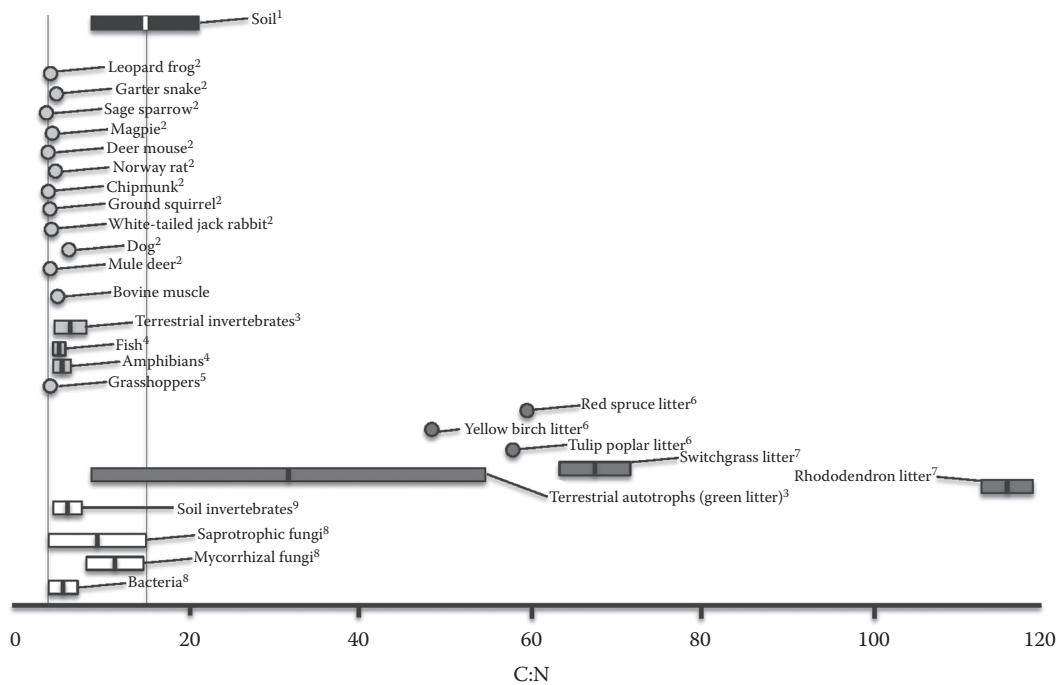
These recent hypotheses related to SOM formation might aid us in better understanding the influence carrion inputs potentially have on soil ecosystems. For instance, the quality of most carrion inputs is high when compared with most plant-derived inputs (Figure 5.1). These inputs are stoichiometrically similar to microbial biomass (Figure 5.2) and should lead to high biological assimilation efficiency (Guggenberger et al. 1999; Sterner and Elser 2002). The amount of input and the context of the surrounding resource quality are then likely to strike the balance between priming and preferential substrate



**FIGURE 5.1** Effects of carrion inputs on soil communities and ecosystem processes. Large quantities of carrion inputs may lead to a shift in soil microbial community composition toward copiotrophic organisms. These organisms specialize on labile substrates and decompose little SOM. As these organisms grow and die, their biomass forms the precursors for stable SOM, leading to an increase in SOM. In contrast, small quantities of carrion inputs are not likely to lead to a change in the microbial community but may alleviate the energy demands on the current, oligotrophic community. This may then lead to increased extracellular enzyme production by that community, which induces a priming effect and subsequent loss of SOM.

utilization (Bradford et al. 2008). For instance, a bison carcass is likely to represent a large labile input, relative to the dominant recalcitrant plant litter, and leads to a marked shift in the soil community (discussed subsequently) toward organisms that primarily consume that carcass. This occurrence could result in preferential substrate utilization and potentially an increase in SOM. In contrast, small carrion inputs, such as arthropod carcasses, may induce a priming effect in the community. Dispersal of the carrion by scavengers (see Chapter 6 on Scavengers) or mass die-offs (see Chapter 13 on Ecosystems) may alter these outcomes. That is, spreading a large carcass across a landscape may lead to a shift from preferential substrate utilization to priming.

The impacts that carrion have on soil processes are likely to vary over time (Putnam 1978; Parmenter and MacMahon 2009; Metcalf et al. 2013; Macdonald et al. 2014). Initially, changes to the soil environment should be relatively minor, with low carrion inputs entering the soil during the fresh and bloat



**FIGURE 5.2** The carbon:nitrogen ratios of decomposer organisms (white symbols), plants (dark gray symbols), animals (light gray symbols), and soil (black symbol). Bars represent the mean (solid line) and standard deviation. Circles represent single point estimates for a given organism. Vertical dotted lines indicate the range of C:N ratios associated with decomposer organisms. The data were sourced from the following publications with corresponding numbers: <sup>1</sup>(Fierer, N. et al. 2009. *Ecology Letters* 12: 1238–1249), <sup>2</sup>(Parmenter, R.R. and J.A. Macmahon. 2009. *Ecological Monographs* 79: 637–661; Note: %C was assumed to be 45%), <sup>3</sup>(Elser, J.J. et al. 2000. *Nature* 408: 578–580), <sup>4</sup>(Vanni, M.J. et al. 2002. *Ecology Letters* 5: 285–293), <sup>5</sup>(Hawlena, D. and O.J. Schmitz. 2010. *American Naturalist* 176: 537–556), <sup>6</sup>(Keiser, A.D. et al. 2011. *Biogeosciences* 8: 1477–1486), <sup>7</sup>(Strickland, M.S. et al. 2009a. *Ecology* 90: 441–451, Strickland, M.S. et al. 2009b. *Functional Ecology* 23: 627–636), <sup>8</sup>(Strickland, M.S. and J. Rousk. 2010. *Soil Biology and Biochemistry* 42: 1385–1395), <sup>9</sup>(Ferris, H., R.C. Venette, and S.S. Lau. 1997. *Soil Biology and Biochemistry* 29: 1183–1194).

stages of decomposition, although colonization of the carrion by soil organisms at the soil–carrion interface is likely to accelerate input rates.

Once active decay (and the process of putrefaction) begins, a flush of resources enters the soil, leading to the greatest alterations in soil processes and the soil community. It is likely, during this stage, when the balance between priming and preferential substrate utilization is struck. It is also during this time when changes in the soil physiochemical environment are the most dramatic, with rapid increases in soil moisture and pH (due to carrion fluids) (Metcalf et al. 2013). These changes probably continue through to the dry stage of decomposition, with an overall decrease in soil community activity. Although there is little empirical evidence for such temporal effects, Metcalf et al. (2013) demonstrated that soil microbial community composition and soil pH tended to follow this pattern for mouse carcasses and Vass et al. (1992) found that soil solution characteristics also followed this pattern for human cadavers.

The effects of carrion inputs on the soil, though, are likely to be long lasting, with either gains or losses of SOM and most likely increased soil nutrients (Towne 2000; Macdonald et al. 2014). The long-term consequences of these inputs are relatively unknown (Barton et al. 2013), but research has demonstrated that carrion inputs can alter future processes, such as leaf litter decomposition, in soil ecosystems (Hawlena et al. 2012).

### 5.3 Carrion Inputs: Soil Microbial Community Dynamics

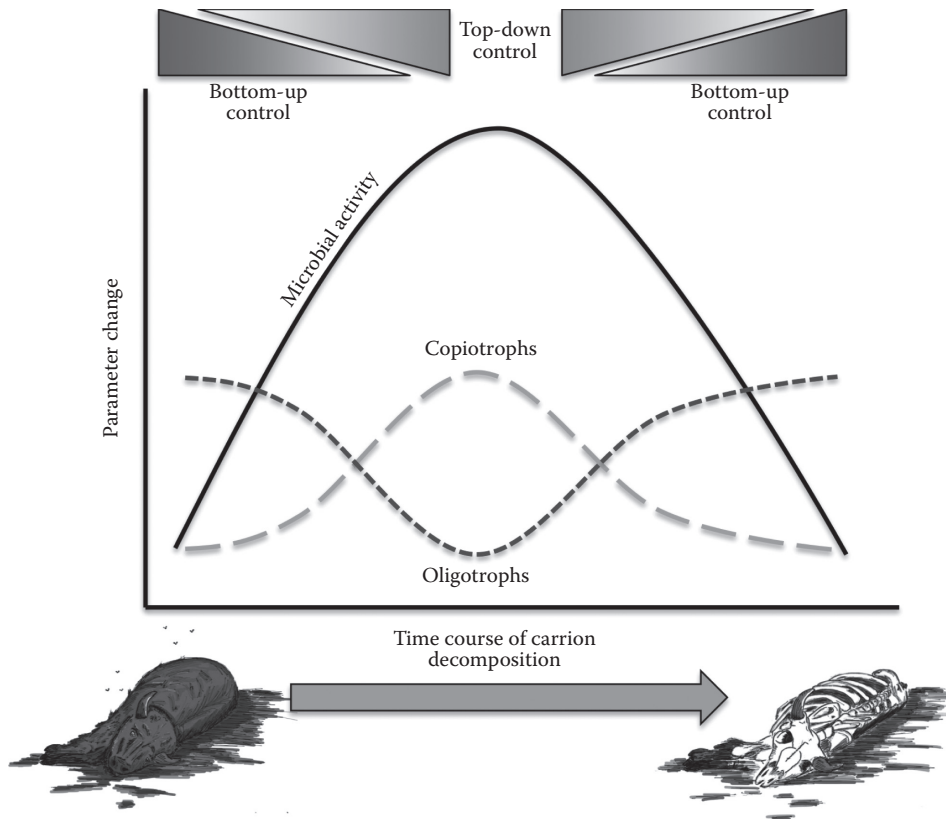
Microbes (see Chapter 3 on Microbial Communities) constitute the dominant heterotrophic biomass in soil, and they are responsible for the bulk of elemental cycling in terrestrial ecosystems (Zak et al. 2006; Fierer et al. 2009). Microbial communities vary with regard to the potential influence that they have on these processes as well as how they respond to alterations in resource inputs (Strickland et al. 2009a, b). Although carrion inputs represent a short-term pulse of a high-quality resource, this input potentially leads to shifts in the function of soil microbial communities.

Typically, the expectation is that soil microbial communities in bulk soil are dominated by oligotrophic organisms (Fierer et al. 2007). Oligotrophs are organisms that tend to have slow growth rates and high substrate affinities, meaning that they are adapted to low-resource environments (Koch 2001). But, these communities are punctuated by copiotrophic organisms around high-resource sites (e.g., roots). Copiotrophs are organisms that grow rapidly when resources are plentiful and have low substrate affinity (Koch 2001). This dichotomy is akin to the well-known ecological definition of life-history trait ecology (i.e., r- vs. K-strategists) (Fierer et al. 2007). Although this differentiation only highlights two extremes in life history, it does provide a useful metric for testing hypotheses regarding the functional implications of carrion inputs.

For instance, carrion inputs of significant quantity are likely to lead to a more copiotrophic community. Metcalf et al. (2013) found evidence that this occurs with a decrease in the relative abundance of Acidobacteria, a primarily oligotrophic phylum in soil, and an increase in Proteobacteria, a primarily copiotrophic phylum in soil, under decomposing mouse carcasses. Under this scenario, microbial activity is likely to increase during the course of carrion decomposition and then decrease as the carrion substrate is depleted (Carter et al. 2007, 2008; Pechal et al. 2013). That is, microbial activity with time potentially elicits a unimodal response (Figure 5.3). Additionally, the shift in functional groups within the microbial community may follow a pattern in which copiotrophs increase in dominance up to the peak of activity and subsequently decline, being replaced by more oligotrophic organisms (Figure 5.3). Such changes in the functional attributes of the microbial community have been proposed during litter decomposition but not for carrion decomposition (Moorhead and Sinsabaugh 2006). However, the expectations should remain the same but at a much shorter time scale.

Shifts between copiotrophic and oligotrophic life histories have implications for soil ecosystem functioning (Fierer et al. 2007). Oligotrophs tend to degrade more recalcitrant SOM but are often energy (i.e., C) limited in this endeavor. Thus, carrion inputs may alleviate this energy demand and lead to increased SOM decomposition. This occurrence is likely to happen during the initial or later stages of carrion decomposition if carrion input is of relatively large quantity and high quality and when copiotrophs are less abundant. If the carrion input is initially of low quality, then copiotrophs may never increase in abundance and oligotrophs will utilize the carrion input to subsidize SOM decomposition, potentially leading to declines in SOM. Of course, gradients in the carrion effect on SOM may occur. For example, Hawlena et al. (2012) added grasshopper carrion, which varied in quality (C:N of 4.00 and 3.85), to soils and then subsequently determined how this input altered leaf litter decomposition. In both instances, an increase in litter decomposition was found, but this effect was much greater for the higher quality grasshopper carrion. This suggests that fine-scale gradation in the quality of carrion inputs, brought about by factors such as stress, has marked impacts on ecosystem function.

Another metric used to assess the function of soil microbial communities is the ratio of fungi to bacteria. In many ways, this metric resembles the copiotroph–oligotroph dichotomy, with bacteria largely described as the former and fungi the latter (Guggenberger et al. 1999; Strickland and Rousk 2010). However, one key distinction is the potential difference in stoichiometry and growth form between fungi and bacteria (Strickland and Rousk 2010). Based solely on stoichiometry, bacteria are likely to dominate the decomposition of most carrion but fungi may be important decomposers of many invertebrate species, due to greater stoichiometric similarity and may also dominate during the latter stages of decomposition (Figure 5.2). Additionally, most large vertebrate carrion inputs are associated with an increase in soil pH, which is known to favor bacteria over fungi (Rousk et al. 2010). However, although carrion inputs are apt to favor the bacterial community, fungi may play an important role as well. Because of



**FIGURE 5.3** (See color insert.) Change in soil community parameters during the time course of carrion decomposition. Microbial biomass and activity are likely to increase until active decay at which point it will begin to decrease. During this time, the typically oligotrophic soil community will give way to a more copiotrophic one until carrion decomposition begins to slow. Finally, regulation of the microbial community will also change during carrion decomposition, with bottom-up regulation being more important during the early and later stages and top-down regulation being more important during active carrion decay.

the mycelial growth form, fungi may relocate nutrients derived from carrion to locations throughout the mycelial network potentially stimulating decomposition across a much larger area (Strickland and Rousk 2010). In the case of mycorrhizal fungi, translocation is likely to stimulate plant growth (Sagara 1995). The overall zone of influence that carrion inputs have on soil microbial communities and processes is unknown; however, soil fungi may play an important role in extending the carrion footprint beyond its direct contact with soil.

Another important consideration is the relationship between the extant microbial community and the carrion-derived community. Soil is a very different environment from carrion itself and, although there are broadly similar groups of microbes living in both environments, it seems unlikely that the carrion community could survive in soil for an extended period of time. However, this does not mean that the carrion community does not influence the soil community. In fact, during active decay, a huge influx of carrion-derived microbes enters the soil. These organisms will possibly survive for a period of time, but will ultimately be replaced by extant soil microbes. It is probable that the carrion resource, potentially due to the introduction of novel organisms or genes, may have a marked influence on the function of the soil community in the future. In fact, Metcalf et al. (2013) found that some taxa of bacteria (e.g., Rhizobiales) increase in abundance in response to carcass inputs.

Resource history of soil microbial communities has been shown to have a marked influence on community function (Ayres et al. 2009; Strickland et al. 2009a, b). One well-recognized example is the



home-field advantage hypothesis, which states that soil microbes are better able to degrade a resource that they have had historical exposure to (Gholz et al. 2000; Ayres et al. 2009). This has been well documented in the leaf litter decomposition literature (Ayres et al. 2009). In fact, Carter and Tibbett (2008) observed a similar occurrence during the decomposition of skeletal muscle tissue. In the context of carrion decomposition, this may mean that systems that are frequently exposed to carrion inputs may be geared toward their decomposition. Examples of such systems may be grasslands, in which annual die-offs of grasshoppers are common. Such systems likely maintain a community capable of rapidly utilizing carrion pulses. If this is the case, then there may be implications to the overall function of the system. For example, Strickland et al. (2009a, b) found that systems that tended to be more fertile also tended to decompose labile compared with recalcitrant leaf litter more rapidly. If carrion improves site fertility, then this ephemeral resource may have long-term consequences for microbial function.

Soil microbial communities also interact with other soil organisms and form the base of the decomposer food web. Typically, these organisms are expected to be bottom-up regulated with the overall low quality of plant-derived inputs expected to control total microbial biomass (Hairston et al. 1960; Allison 2006). However, carrion inputs may remove this bottom-up control, making top-down control (i.e., microbivory) a more important mechanism. If this is the case, then microbivores, such as microarthropods, nematodes, and protists, should flourish (Bonkowski 2004). Increased predation will stimulate microbial turnover and mobilization of soil nutrients, making these nutrients available for plant uptake and/or loss from the system (Bonkowski 2004). Top-down control would be strongest during active decay of the carrion and bottom-up control would be strongest during the fresh and dry stages of decomposition.

Although little is known regarding the effect carrion has on the soil microbial community, current theory related to resource acquisition strategies of the microbial community may provide some of the foundational hypotheses to begin understanding these effects. Once carrion was thought as an insignificant, ephemeral input to soil (Swift et al. 1979), but now it is being realized that the legacy of vertebrate carrion inputs can markedly impact microbial community function (Hawlena et al. 2012). Future research in this realm should not just employ short-term measures of a changing microbial community but also assess the long-term functional implications of carrion inputs.

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#### 5.4 Carrion Inputs: Soil Invertebrate Community Dynamics

Invertebrates (see Chapter 4 on Arthropod Communities) play diverse and important roles in the decomposition of organic matter, including carrion. Invertebrate contributions to carrion decay have been recognized for centuries, and, today, invertebrates are a critical component in modern forensic diagnostics. When it comes to soil invertebrates, however, the knowledge of the invertebrate–carrion relationship is scarce. Past research emphasizes the direct colonization of the carrion resource, and only a handful of studies have focussed on how carrion inputs affect invertebrates in bulk soil (Braig and Perotti 2009).

Although it is difficult to make generalizations about them as a whole, soil invertebrate communities may exhibit some predictable responses to carrion inputs in the landscape. Soil invertebrates, such as microbes, are generally thought to be nutrient-limited due to the low nutritional quality of dead plant matter serving as their basal resource (Hairston et al. 1960; Allison 2006). Carrion inputs have drastic effects on soil nutrient availability and may serve as resource islands (Carter et al. 2007), ultimately dampening the negative consequences of nutrient limitation on soil invertebrate communities. Although nutrient effects on soil invertebrates have not been studied extensively, some fairly consistent responses can be found within the existing literature. In particular, detritivorous and microbivorous soil invertebrates have been shown to decrease in density in response to nutrient additions, whereas predator and herbivore densities often increase (Throop and Lerdau 2004; Gan et al. 2013; Grandy et al. 2013). The positive effect of nutrient addition on herbivores is well recognized and is typically attributed to improved plant nutrition (Mattson 1980). Similarly, positive predator responses to nutrient amendment may be driven by shifts in prey abundance. The opposing response of decomposers and microbivores to nutrient addition, however, may be related to the importance of microbes in the interaction between arthropods

and detritus. Soil invertebrates commonly rely on microbes for deriving nutrition from low-quality plant tissues. They accomplish this via many routes, the most common of which is microbivory, or the direct feeding on microbial cells. Soil invertebrates also benefit from soil microbes indirectly, by feeding on plant detritus that has undergone extensive microbial decay. Whether direct or indirect, invertebrates benefit from soil microbes via the same mechanism: harnessing the ability of soil microbes to access and degrade recalcitrant organic matter. Thus, changes in decomposer and microbivore density in response to nutrient addition reflect changes in microbial biomass and/or enzyme production. Past studies have shown that microbial biomass and activity in soil are sensitive to carrion inputs (Benninger et al. 2008), suggesting that carrion may have strong indirect effects on microbivorous invertebrate populations.

Thus, taken solely as a nutrient pulse, carrion may have substantial effects on soil arthropod communities. However, carrion differs from other nutrient inputs in many ways, and its impacts on soil invertebrates may not be as predictable as those derived from inorganic nutrient additions, which have been the focus of past work. For example, in addition to the mineralized nutrients released from carrion during decay, many labile organic molecules are also released into soil (Macdonald et al. 2014). Additionally, compared with plant detritus, particulate organic matter from carrion may be directly assimilated by soil invertebrates. Past studies support this assertion, showing that some soil invertebrates will feed on cadaver tissue (Rusek 1998; Von Berg et al. 2012). This behavior has been attributed to the overall nutrient quality of carrion combined with the high degree of opportunistic feeding that occurs in soil food webs and suggests that carrion can potentially serve as a significant food source for soil invertebrates.

Carrion may also have many effects on soil invertebrate communities related to shifts in climatic and physical factors. For example, fresh carrion has high water content and can serve as a significant moisture source for soil food webs. Large cadavers may also provide a shading effect on soil, decreasing water loss, and attracting cryptic invertebrate taxa that prefer shaded, moist environments. In addition to moisture, carrion inputs can cause a significant increase in the temperature of nearby soil during the initial stages of decomposition (Wilson et al. 2007). Soil tunneling by carrion-inhabiting fly larvae seeking pupation sites also changes the physical pore structure of soil below and around carrion, which can have marked effects on soil invertebrate communities (Nielsen et al. 2008). These changes in physical and climatic factors due to carrion inputs may lead to increased soil invertebrate abundance and activity.

Carrion can have many other effects on soil chemistry. Past studies have shown changes in soil pH below decomposing carrion corresponding with the activity of carrion-feeding larvae and a flush of nutrients from cadaver to soil, and more recent work suggests that the impact of carrion on soil pH varies over the course of decay (Carter et al. 2008). This shift in soil pH is likely driven by changes in the form of available nitrogen over the course of decay; however, its magnitude may vary with soil type. Soil invertebrates typically exhibit a negative response to increasing soil pH; however, the response varies based on the type of substrate causing the change (e.g., fertilizer, wood ash, and insect waste) and can be site-dependent (Liiri et al. 2002). Carrion also introduces many other compounds to soil during its decay, including cadaverine, putrescine, various acids, and phenolic compounds. Although few studies have explored relationships between cadaver-derived compounds and soil invertebrates in the field, it is recognized that these, and other related, compounds can suppress the density and activity of invertebrates in soil (Neuhauser and Hartenstein 1978; Katase et al. 2009; Asplund and Wardle 2013; Dekeirsschieter et al. 2013).

Shifts in pH and the introduction of repellent or toxic compounds in soil beneath decomposing carrion are assumed to have a negative impact on soil invertebrate communities, and past studies have observed that during active decay the soil faunae are substantially reduced (Bornemissza 1957). This finding, however, is not always consistent, and, in a recent review, Braig and Perotti (2009) highlight studies showing an enrichment of soil invertebrate communities under decomposing cadavers. Additional studies are needed to better understand these conflicting reports.

The functional significance of shifts in soil invertebrate communities is still poorly understood among soil ecologists. Hence, predicting how carrion-induced changes in soil invertebrate communities will influence belowground processes is a difficult task. Still, past studies assessing the influence of substrate quality on soil invertebrate function may prove insightful. Osler and Sommerkorn (2007) provide a framework for predicting the impact of soil invertebrates on carbon and nitrogen cycling based on stoichiometric differences between microbivorous invertebrates and their prey. Invertebrates with high



assimilation efficiency (e.g., bacteria feeders) are predicted to contribute greatest to nitrogen availability, whereas those with low assimilation efficiency (e.g., detritivores and fungivores) should contribute greatest to the availability of dissolved organic matter. Although this framework remains to be tested in the field, past studies confirm that resource quality constrains the influence that soil invertebrates exert over soil processes such as decomposition (Smith and Bradford 2003; Yang and Chen 2009). Ultimately, changes in microbial communities (e.g., between fungal and bacterial dominance) in response to carrion inputs may modify the role of invertebrates in soil carbon and nutrient cycling. Invertebrate contributions to soil processes under decomposing carrion may also be highly sensitive to successional changes in compounds introduced to soil during decay.

Finally, it is worth considering the potential direct contribution of soil invertebrates as a carrion input. Although invertebrate biomass is dwarfed by microbial biomass (Fierer et al. 2009), soil invertebrate carrion constitutes a substantial organic matter input to soil. In their comprehensive paper, Petersen and Luxton (1982) report total soil invertebrate biomasses from different habitats ranging from roughly 2 to 8 g dry wt. m<sup>-2</sup>. In extreme cases, total invertebrate biomass can reach over 20 g dry wt. m<sup>-2</sup> (Paoletti and Bressan 1996; Lavelle et al. 1997). Within this range, soil macrofauna (large earthworms, millipedes, centipedes, predatory beetles, fly larvae, spiders, snails, and ants) comprised anywhere from 5% to 80% of all biomasses, whereas soil mesofauna (mites, collembolans, and enchytraeid worms) comprised anywhere from 2% to 62%. Given their low C:N ratio (Figure 5.2), and the fact that many taxa have high turnover rates, soil invertebrates may represent a significant carrion input (Barton et al. 2013).

It is clear that carrion inputs to soil can influence the biomass and composition of soil invertebrates. However, to date, the effects of carrion on soil invertebrate communities and their role in soil processes have received limited attention. Although the responses of soil invertebrates to carrion in previous studies have been mixed, recent work suggests that carrion-induced changes in soil invertebrate communities may persist well beyond the physical input of carrion itself (Salona et al. 2010). Improving our understanding of soil invertebrate responses to carrion inputs will require interdisciplinary studies of soil microbe and invertebrate interactions during, and well after, carrion decay. These studies must also identify the underlying chemical and physical drivers of biological responses across different decay stages.

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## 5.5 Conclusions: Do Carrion Inputs Affect Soil Processes?

Do carrion inputs influence soil processes? The answer to that question is likely yes. In the short term, carrion effects can be quite dramatic: from a rapid increase in soil pH to increased available soil nitrogen (Benninger et al. 2008). However, whether carrion inputs can have marked influence on long-term soil processes and/or at the ecosystem scale is a topic that has only recently begun to be discussed in depth (Barton et al. 2013).

Depending on what is considered long term, there is evidence that carrion effects can have lasting impacts on soil properties for months (Benninger et al. 2008; Macdonald et al. 2014). Additionally, changes in the availability of carbon due to carrion inputs may also have long-term impacts on SOM. For instance, priming may elicit a rapid loss in soil carbon that may take years to decades to regain. The possibility of this and the balance between SOM formation and loss due to carrion inputs have yet to be tested.

Additionally, the ecosystem level implications of carrion inputs as they relate to soil processes are not well known (see Chapter 13 on Ecosystems). The marked increase in nutrients associated with carrion can ultimately stimulate primary production and a shift in plant community composition (Yang 2004). Additionally, carrion inputs, depending on quality and quantity, are likely to accelerate litter decomposition (Hawlena et al. 2012). Such impacts on processes may simply equate to point disturbances (i.e., carrion decomposition island) in the case of organisms for which death is a spatially and temporally random event (Carter et al. 2007). However, the death of other organisms may equate to a pulse of more evenly distributed resources and may have more widespread ecosystem consequences (Hawlena et al. 2012). Yet, even the former of these two types of carrion inputs may contribute to the heterogeneity in soil properties and process.

In the future, research needs to address the potential ecosystem scale consequences of carrion inputs on soil processes. It must also determine how the quantity, quality, and distribution of carrion inputs influence soil properties and communities. Although carrion inputs have often been thought to be of little significance, there is a growing realization that this may not be the case. Furthermore, contemporary theory in soil ecology, while not focussed explicitly on carrion, also suggests that carrion inputs may play a significant role in structuring soil communities and the processes that they drive, especially legacy effects. All that is left to do is explore this possibility.

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