Carrion Decomposition

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Contents

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Introduction

Life concentrates biologically limiting resources. Primary producers harness relatively diffuse solar energy and earth elements to produce tissues that feed the vast array of herbivores globally. Herbivore tissue in turn, as a resource, increases in nutritional value and feeds a diversity of predators across multiple trophic levels. In death, animal tissues are consumed or re-enter the cycle via decomposition. In this way, death disperses biologically limiting resources. This simplification of global resource cycling via biological pathways highlights the fundamental importance of dead animal matter (carrion; e.g. vertebrate carcasses) in maintaining biodiversity and ecological processes, especially in terrestrial ecosystems. Carrion occurs in all biomes and can be conceptualized as a bottleneck in the vital flow of energy and limiting nutrients with profound ecological and evolutionary consequences. Until mortality, consumers temporarily concentrate and sequester energy, nutrients, and moisture in their standing biomass. As a result, carrion constitutes a critical resource for a variety of communities and it strongly affects scavenger guilds, the maintenance of biodiversity, and life-sustaining ecological processes (Barton et al. 2013a).

Carrion decomposition is a fundamental ecological process involving the breakdown of dead animals and the recycling of their embodied nutrients and energy through other organisms and their environment. The decomposition process involves a combination of physical and biological degradation and breakdown of a carcass into smaller fragments and its constituent biochemical components. This occurs through the combined action of intrinsic (e.g. enzymatic and internal microbial processes), and extrinsic processes (e.g. fragmentation and consumption by organisms). All of these processes are strongly moderated by a wide variety of abiotic (e.g. temperature, moisture), and biotic factors such as vegetation and inter-specific competition among scavengers. In this chapter, we have taken a broad perspective of carrion decomposition to include all biotic and abiotic processes that affect the breakdown of an animal carcass. Subsequent chapters give greater detail on the specific taxa (see chapter “Invertebrate Scavenging Communities”) and processes (see chapter “Ecological Functions of Vertebrate Scavenging”). We outline the decomposition process, the role of different groups of organisms, and key moderating abiotic and environmental factors. We conclude with a discussion of some future research directions that highlight how different technologies and interdisciplinary collaboration can yield greater understanding of this important process.

Carrion Decomposition

Animal Carrion as a Distinct Resource

Carrion is a distinctive form of detritus in ecosystems when compared with other forms of detritus, such as animal dung, fruiting fungal bodies, or the many kinds of plant detritus, like litter, dead wood, or fruit (Barton et al. 2013a; Finn 2001). It is important to highlight three key attributes of carrion that affects its decomposition. First, the remains of animals are generally rare and comprise only a fraction of the organic biomass in ecosystems (Barton et al. 2013a; Parmenter and MacMahon 2009). In contrast, plant litter is ubiquitous in many ecosystems, from terrestrial grasslands to marine kelp forests. Although the occurrence of different forms of plant detritus can vary (e.g. leaves vs. branches), the availability of plant detritus is generally not as limited as carrion. Second, carrion is very rich in nutrients, whereas plant litter is comparatively nutrient-poor with low concentrations of key macronutrients such as nitrogen and phosphorus (Moore et al. 2004; Swift et al. 1979). The nitrogen content of carrion can be up to five times higher, and moisture up to 10 times higher, than several kinds of plant litter (Carter et al. 2007). Third, carrion decomposes orders of magnitude faster than plant litter (Parmenter and MacMahon 2009), and is only available as a resource to other organisms for a brief window of time. These factors combine to make carrion spatially patchy in occurrence, very nutrient rich, and ephemeral. These distinctive features of carrion not only make it a unique resource in ecosystems, but also strongly affects how it decomposes.

The Decomposition Process

The processes responsible for the decomposition of an individual carcass have been described as creating a ‘cadaver decomposition island’ (sensu Carter et al. 2007). This decomposition island is a very localized and intense ‘hot spot’ and ‘hot moment’ of chemical and biological activity that ultimately leads to the breakdown and recycling of the energy and nutrients in a dead animal through other organisms and the wider environment. This occurs through both chemical and biological processes. The intrinsic chemical processes, such as autolysis and putrefaction, are not covered in detail in this chapter. Briefly, after death of the animal, cells no longer receive oxygen or nutrients, and they are unable to maintain normal functioning. This leads to uncontrolled enzymatic and biochemical activity, which leads to cell death, autolysis and the breakdown and leakage of cell membranes. A more in-depth coverage of this aspect of decomposition can be found elsewhere (e.g. Carter et al. 2007; Dent et al. 2004; Forbes and Carter 2015). The extrinsic biological drivers of decomposition are largely due to other organisms, and is initiated by the rapid proliferation of bacteria present in the digestive tract and on the epidermal surface. These microbes release their own enzymes that further break down the animal’s cells. Together with the intrinsic chemical activity, the early stages of decomposition are characterized by the release of gases, which act as cues that attract early insect colonizers of carrion that specialize on carrion as a food resource (see chapter “Invertebrate Scavenging Communities”), and in turn begins the physical break down of the animal carcass through consumption of internal fluids and tissues. Further physical decomposition of carrion is facilitated by vertebrate scavengers that disarticulate carcasses and consume large portions of tissue (see chapter “Vertebrate Scavenging Communities”). This results in fragmentation of the carcass into smaller parts as pieces are physically moved apart and scattered by animals. The net product of these chemical, biological and physical processes leads to the decomposition and disintegration of a carcass.

Temporal Progression of Carrion Decay

A key aspect of carrion decomposition is its temporal component, involving the progressive breakdown of tissues through time. In their detailed review, Michaud et al. (2015) noted that carrion decomposition is often viewed as a series of steps or stages by many researchers, and this step-wise description is pervasive in both the entomological and forensic literature. This view, of course, serves as a useful way to differentiate between assemblages of species or qualitative features of a carcass at different points in time. This approach is further perpetuated by sampling and observation methods, which are often necessarily restricted to points in time, thus leading to clear distinctions when making comparisons among samples and observations. Nevertheless, it is important to reiterate (with the above-mentioned methodological constraints in mind) that little evidence exists of substantive step-changes in decomposition, and that the process (mostly) occurs gradually through time. The description of decay 'stages' should therefore be considered as phases of decomposition through which a typical carcass passes gradually and not abruptly, and care should be taken in focusing on discrete stages where there is a continuum of change.

A typical classification scheme of temporal decay stage includes fresh, bloat, active, advance, and dry decay. A *fresh* carcass lasts for only a few minutes to hours after death, depending on temperature, before it enters a bloat stage whereby internal bacteria proliferate inside the gut, and leak into the lymphatic system and other tissues. The *bloating* is caused by the gases released by the bacteria and decaying tissues, and include methane, hydrogen sulfide, and carbon dioxide (Forbes and Carter 2015). The release of gases during the bloat stage is often the trigger for colonisation by carrion insects, such as blowflies, with gases acting as an important cue for species to search and locate the carcass (see chapter "Invertebrate Scavenging Communities"). *Active decay* of an animal carcass is characterized by the putrefaction and liquefaction of carcass tissues, and the release of a complex array of volatile organic compounds (Forbes and Carter 2015). A rapid loss of carcass mass occurs due to the consumption of tissues by scavenger organisms, both vertebrate and invertebrate (see chapters "Invertebrate Scavenging Communities" and "Vertebrate Scavenging Communities"). Moisture is also lost from the carcass into the environment via evaporation and leakage of fluids into the soil. Vertebrate scavengers can play a role in disarticulating and moving larger carcasses, and local weather conditions such as wind and rain, may play a role in spreading the components of a carcass such as bones, skin fragments and fur/feathers. Progression into *advanced decay* involves the final breakdown of soft tissues and the appearance of the skeleton. *Dry decay* occurs over a much longer time frame, and depending on the environment, the recalcitrant parts of a carcass, particularly the ligaments, nails, hair, and skeleton, may persist for many months and years.

The Contribution of Organisms to the Decomposition Process

A diverse range of taxa are involved with the decomposition process, with several being critical to the rate and/or completeness of decay through either the direct consumption of carrion, or preying on other organisms that do. Experimental exclusion or removal of different components of the necrobiome have also demonstrated their importance in accelerating mass loss from a carcass (Lauber et al. 2014; Pechal et al. 2014a). Below we outline the role of three broad groups of organisms—microbes, invertebrates and vertebrates—in the decomposition process. We focus only on the most important taxa, with further and more comprehensive details on succession and species-specific roles of invertebrates and vertebrates given in other chapters.

Microbial Decomposers

Microbial decomposers (bacteria, archaea, fungi, protists) have a critical role in the decomposition of carrion (Carter et al. 2008; Crippen et al. 2015; Lauber et al. 2014; Metcalf et al. 2015). The diversity of the microbial community found at carrion is impressive, with many thousands of taxa found both in and on carcasses (Crippen et al. 2015; Pechal et al. 2013, 2014b). The primary mode of action of both bacterial and fungal decomposers is the secretion of enzymes to breakdown complex organic molecules into smaller ones that are then metabolized for their growth and rapid proliferation. Microbes, primarily bacteria, are present in great numbers both in the gut of animals and on the surface of the skin. Gut bacteria have a particularly important role in the decomposition of animals, and can influence the rate of decay (Lauber et al. 2014), as well as the appearance and odour of carcasses. The main aerobic bacteria include several taxa from the Firmicutes and Bacteroidetes phyla, and anaerobic bacteria include the commonly known *Lactobacillus*, *Streptococcus*, and *Staphylococcus* that play a role in the fermentation of various organic compounds in carrion (Forbes and Carter 2015). Fungi may become more abundant on older carcasses as conditions become drier and more hostile for bacteria (Carter and Tibbett 2003). Importantly, microbial communities play a critical role in accelerating decomposition rates, and can drive the decomposition process in the absence of all other eukaryotic organisms. It has been established through experimental work, for example, that decomposition rates of mice carcasses occurred at twice the rate in soil with intact microbial communities compared with sterile soil (Lauber et al. 2014). The importance of microbes to decomposition lies in their ability to produce a broad array of degradative enzymes, and their ability to colonise and use a broad range of carrion substrates, including all internal tissues and organs, as well as keratinous hair and skin, and even bone.

Arthropods

Arthropods comprise both primary and secondary consumer trophic roles at carcasses, and their presence at a carcass can accelerate the decomposition process through consumption of the different components of a carcass. Surprisingly few experimental tests have been performed to directly assess the role of arthropods, but these few studies have identified important contributions (Farwig et al. 2014; Payne 1965; Pechal et al. 2014a). A detailed overview of the different arthropod taxa present at carrion is given in chapter "Invertebrate Scavenging Communities", and here we focus on their functional roles.

Braack (1987) provided a useful classification scheme of the functional role of different arthropod groups by synthesizing his research on the arthropod fauna at carcasses in Africa. Not all functional groups may be present at a carcass in other parts of the world, or indeed at different carcasses in the same biome. For example, the rumen contents and large horns of an antelope attract a different set of fauna than a small carnivore carcass where these elements are absent. The relationship between the taxa that make up these functional groups (Fig. 1) shows that some taxa may feed on more than one carcass component, and therefore perform more than one functional role. This also applies to adults and larvae of the same species, which may each specialize on a different component. Such variation highlights varying

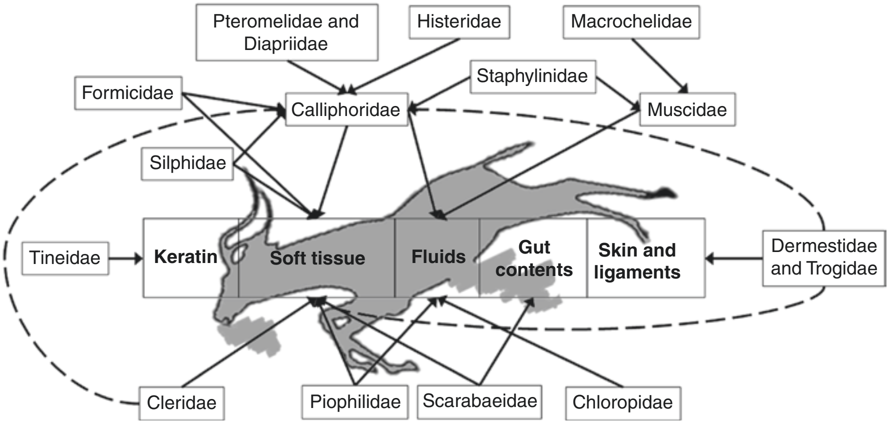

Fig. 1 A food web of the main arthropod taxa associated with an impala carcass in southern Africa (re-drawn from Braack 1987). Different carrion-associated taxa specialize on different components of the carcass (shaded grey), but there can be overlap between components of the carcass. Credits: the chapter authors

degrees of functional redundancy and complementarity among species at different carcasses in different biomes. The *sarcophagous* component feeds on carcass soft tissues, including muscle and body fluids, and is dominated by various fly taxa (e.g. Calliphoridae, Muscidae). Several taxa have a minor role, including Diptera: Piophilidae, Chloropidae, Coleoptera: Silphidae, Cleridae, Scarabaeidae, or Hymenoptera: Formicidae. The *coprophagous* component are most relevant to herbivore carcasses and are attracted to and feed on the gut contents. Typically dominated by the Scarabaeidae, but other taxa typically found at dung pads will also be found at carcasses. The *dermatophagous* component feed on the skin, and is dominated by the beetle taxa Dermestidae and Trogidae. The *keratophagous* component is a highly specialized fauna that feed on horns, nails, hair and hooves, and include the Tineidae and Trogidae. The *detritivore* component is a more generalized fauna that feed on various organic material, but is distinct from the Sarcophagous component by being opportunistic rather than specialists. The detritivore component includes many taxa, including those species that specialize on other components, such as the Formicidae, Dermestidae and Trogidae. The *predator* component is a large and diverse group of taxa that feed predominantly on the abundant fly larvae and eggs, but may also feed opportunistically on other arthropods. The predator component includes the Formicidae, the beetle taxa Histeridae, Silphidae, Cleridae, Staphylinidae, and the mite taxa Macrochelidae and Parasitidae. Spiders will also opportunistically prey upon arthropods on carcass. The *parasitic* component includes several wasp species that are parasitoids of fly larvae. Many mites at carcasses disperse via phoresy, but are technically not parasites of their fly or beetle hosts. The predator and parasitic functional groups may play a role in decomposition by moderating the abundance or activity of other consumer groups.

Vertebrates

Vertebrates involved with decomposition are typically termed ‘scavengers’ (see chapter “Vertebrate Scavenging Communities”). They play a key role in the consumption and fragmentation of large carcasses, and can be responsible for consuming the majority of carrion in some ecosystems (DeVault et al. 2003; Wilson and Wolkovich 2011). Small carcasses can be entirely consumed by scavengers, but larger carcasses may only be partially consumed, resulting in disarticulation and dispersal of carcass material through the landscape. The importance of vertebrates in carrion removal varies among ecosystems, but it is clear that vertebrates generally accelerate carrion decomposition rates where they occur (DeVault et al. 2003; Ogada et al. 2012; Parmenter and MacMahon 2009). This may depend, in part, on the size and composition of the scavenger guild (Sebastián-González et al. 2016; Moleón et al. 2015). Some scavenger guilds are more diverse than others, with some guilds dominated by only a few large facultative scavenger vertebrates, such as dingos and raptors in arid Australia (Read and Wilson 2004), whereas other ecosystems have a relatively large and diverse guild with both facultative and obligate scavengers, such as lions, hyenas, jackals and several vulture species in the Serengeti of Africa (Hunter et al. 2007). Importantly, many vertebrate predators will opportunistically scavenge on animal remains, and so also fill an important role in carrion consumption and carcass removal (Mateo-Tomás et al. 2015; Moleón et al. 2014; Moreno-Opo and Margalida 2013).

Factors Affecting Decomposition

Temperature and Moisture

Temperature and moisture are the two most important abiotic factors affecting the rate of decomposition of carrion. Temperature is critical in determining rates of chemical reactions driving autolysis and putrefaction, the metabolic activity of microbes, and development rates of fly larvae. Moisture is also critical in providing a substrate for effective enzymatic activity and bacterial proliferation, as well as preventing desiccation of carrion tissues and larvae of flies. The temperature-dependence of many processes in the natural world has led to the development of the ‘accumulated degree days’ (ADD) principle. This principle uses variation in daily temperature and the total time taken for a process to occur (Simmons et al. 2010). ADD has been examined widely in the forensic sciences (Megyesi et al. 2005; Michaud and Moreau 2009) to generate predictions for post-mortem interval. This is often based on the developmental rates of key insect taxa such as flies. The development of fly larvae (and other holometabolous insects) through their instar stages requires a minimum threshold temperature. Above this threshold (and if sufficient food resources are available), higher temperatures will result in faster development and faster progression through instar stages until an upper threshold is reached and survival is reduced. By summing daily minimum and maximum temperatures at a carcass, and relating this to larval instar stage, it is possible to accurately determine the time the larvae were first deposited at the carcass, and therefore the age (or time of death) of the carcass. Temperature and moisture are closely linked, with very low temperatures preserving carcasses for extended periods by reducing moisture availability. For example Musk ox (*Ovibos moschatus*) carcasses in the arctic circle have been shown to have extended effects on the localized environment, perhaps for over 10 years and due in part to lower temperatures (Danell et al. 2002). Conversely, extreme high temperatures can also reduce moisture availability, and can increased likelihood of mummification of carrion tissues, thus slowing decomposition.

Vegetation and Habitat

Vegetation can affect decomposition by moderating the abiotic environment (i.e. through provision of shade), as well as by providing habitat to different species involved with decomposition. Many studies have compared arthropod communities from different habitats and found important differences. For example, differences in carrion arthropods between grassland or forest habitats (de Almeida and Louzada 2009), and urban, farmland and forest habitats (Kavazos and Wallman 2012) have been reported. These differences in species occurrence have the capacity to alter decomposition rates.

Vegetation structure can also impede access by large vertebrate scavengers. For example, consider that carrion initially attracts scavengers from a relatively local area. If the amount of carrion is small it will be consumed by competitively dominant scavengers that arrive first. However, if the amount of carrion is greater than is swiftly consumed locally, then it is reasonable to expect scavengers to continue to recruit from increasingly distant areas. Some scavengers, especially avian species, are more capable of recruiting to or discovering carrion more rapidly than others (Wilmers et al. 2003). However, the increased feeding radii of avian scavengers is dependent upon the visibility of carrion. If carrion is sufficient obscured from visual detection by vegetative or other habitat characteristics then it is reasonable to expect that differences in decomposition can occur due to varying degrees of carrion use and disarticulation.

Burial and Soil

Burial can alter decomposition by moderating temperature and moisture, limiting the external microbial fauna that comes into contact with the carcass, and preventing access by carrion-feeding arthropods and vertebrates (Carter and Tibbett 2008; Payne et al. 1968; VanLaerhoven and Anderson 1999). Burial therefore typically slows decomposition. Large carcasses may also produce an adipocere—a fatty layer that forms around a carcass following biochemical decomposition and hydrolysis of tissues. This can act as a barrier to nutrient and microbial movement away from the carcass and may prolong the decomposition process (Dent et al. 2004; Forbes et al. 2005).

Submersion

The decomposition of carrion in aquatic and marine environments is fundamentally different from that in terrestrial systems (Beasley et al. 2012; Parmenter and Lamarra 1991; Wallace 2015). The vast majority of research on carrion decomposition has been conducted in terrestrial environments rather than aquatic environments (freshwater or marine), and this has influenced much of our understanding of the process. Some key points of difference between decomposition in terrestrial and aquatic environments were synthesized by Beasley et al. (2012). These include the overarching effect of water acting as a medium through which organisms and nutrients must move through to go towards or away from the decomposing carcass. This can have an effect on which animals are attracted to a carcass via movement of chemical cues downstream or with currents. Another critical effect of water is the moderation of temperature, which is a major determinant of decomposition rate. Carrion in shallow water can experience fluctuations in temperature extremes, whereas in deep water temperature is more constant. In marine systems, ocean depth can determine the composition of the scavenger community and the decomposition process. Deep sea abyssal biomes (Smith and Baco 2003), for example, have very different scavenger assemblages than shallow marine environments (Moore and Howarth 1996), and oxygen concentrations may have a role in which species are able to colonize carcasses (Anderson and Bell 2014). The decomposition of carcasses in marine and freshwater environments is also affected by faunal colonization and succession (see chapter "Invertebrate Scavenging Communities"). Key points of difference between freshwater and marine systems is the absence of insects in the marine environment (replaced largely by crustacean arthropods), and the comparative lack of carrion specialists in freshwater environments. Whether a carcass is completely submerged, floating at the surface, or in contact with the bed/floor of the water column, can affect what taxa is able to colonize and how rapidly the carcass may be consumed.

Carcass Size

The size of a carcass has important implications for how it decomposes, including its rate of decomposition and what organisms might use the carcass as a food resource. The size of a carcass affects how it moderates internal and ambient temperatures, which is critical to decomposition rate. Large carcasses can contain more than 210,000 fly larvae (Braack 1987), and this generates heat that increases internal temperatures. This can accelerate microbial and intrinsic decay processes relative to smaller carcasses that cannot accommodate such large maggot masses. For example, Hewadikaram and Goff (1991) showed that 15 kg pig carcasses had higher internal temperature relative to 8 kg carcasses. Further, they showed that the internal temperature of small pig carcasses more closely matched that of ambient temperatures.

The ecological study of carrion has been conducted on many kinds of carcasses (Barton et al. 2013a), including bison (Towne 2000), pigs (Mądra et al. 2015), kangaroos (Macdonald et al. 2014), rabbits (De Jong and Chadwick 1999), rats (Carter et al. 2008), and even slugs (Woodcock et al. 2002) to name but a few. This has resulted in a wide range of separate studies involving different carcasses. Due to the requirements of proper scientific method, samples are typically replicated across the same kind of animal carcass. This has meant that few studies have explicitly compared decomposition among different carcass types to see how this attracts different sets of organisms (but see Moleón et al. 2015; Parmenter and MacMahon 2009). One way to understand the effect of carcass size is to view each carcass as a food particle (Moleón et al. 2015). When viewed this way, the size of a carcass will determine what organisms will use it as a food resource, and therefore the fate of the carcass and its nutrients. To illustrate this point, carcasses of very small animals (i.e. insects, small rodents) are typically consumed whole by scavenging animals such as birds or other small vertebrates (DeVault and Rhodes 2002). Very large carcasses (e.g. ungulates) can often be larger than any of their predators or potential scavengers. In these instances, each carcass may support multiple species of scavenger organism (Selva et al. 2005), and this introduces new factors such as species interactions that may affect decomposition. A study by Moleón et al. (2015) found that scavenger assemblages were more species rich at larger carcasses, and that this was largely due to the presence of facultative scavengers (i.e. mammal carnivores) rather than obligate scavengers (i.e. vultures). A consequence of this size-driven assemblage difference was that decomposition rate, expressed as percentage biomass consumed, was negatively associated with carcass size, indicating that rate of decay was slower for bigger carcasses.

Ecological Theory Underpinning Carrion Decomposition

The study of carrion decomposition has been informed by several important theories relating to populations and communities of carrion-associated organisms. Most work on carrion decomposition has been dedicated to case studies and detailed field observations, with less emphasis on hypothesis testing and development of theory (Michaud et al. 2015). The ecological attributes of carrion are well known, and include its (relatively) predictable decay pattern (Payne 1965; Schoenly and Reid 1987) and its unpredictable patchiness and ephemeral occurrence (Barton et al. 2013a; Braack 1987; Doube 1987; Finn 2001). These ideas capture much of the theory describing faunal communities involved with carrion decomposition, including succession, competition, and coexistence and aggregation. Other processes link carrion to ecosystems at larger scales, including carrion-based subsidies of communities and resource pulse dynamics (Oro et al. 2013; Polis and Hurd 1996; Yang 2006), as well as predators decoupling carrion distribution from live-prey distribution (Bump et al. 2009a).

Succession

The succession (i.e. the sequenced arrival and departure) of different organisms at a carcass through the decomposition process is very well documented (Bornemissza 1957; Matuszewski et al. 2011; Mégnin 1894; Payne et al. 1968; Schoenly and Reid 1987). Succession theory is one of the most widely used theories relating to carrion decomposition, especially with regard to the study of the diversity and structure of arthropod communities (Barton et al. 2014; Benbow et al. 2013; Hobischak et al. 2006; Richards and Goff 1997), and its application to the estimation of postmortem interval for forensic purposes (Archer 2014; Pechal et al. 2014b; Schoenly 1992;

Schoenly et al. 1992). Indeed, there is evidence that the concept of succession was first formalized by forensic entomologists working with human cadavers in the late 1800s (Mégnin 1894), which contrasts with the history of succession theory usually attributed to plant ecologists in the early 1900s (Michaud et al. 2015). Succession theory as it relates to carrion, however, differs somewhat from how it is applied to other ecological phenomena such as plant colonization and community development following disturbance (Turner et al. 1997). This is because carrion decomposition does not lead towards a 'climax' community where species and resources reach equilibrium. Rather, carrion is a finite resource that rapidly reduces in quality and quantity until depleted.

The processes driving succession relate to the change in carrion quality through time, including changes in the moisture and nutrient content, as well as the mix of volatile organic compounds released from the carcass. A fresh carcass is fundamentally different to dry remains in this regard, and this determines which specialists, generalist scavengers, and higher predators, will be attracted to a carcass at different points in time. Indeed, the temporal change in the 'signature' of chemicals released from a carcass may be an important mechanism driving insect succession, although his has not been explicitly tested (Michaud et al. 2015). Another key mechanism behind succession is *facilitation* (Connell and Slatyer 1977). It occurs when species present at a carcass have a role in modifying the resource after its arrival, thus preparing the carcass for colonization by another species. Although suggested by some (Schoenly and Reid 1987; Smith and Baco 2003), it has not been explicitly tested (Michaud et al. 2015).

Competition

The rare occurrence of carrion, and its high nutrient content, produces intense competition among species for the limited resources available at carcasses (Braack 1987; Kneidel 1984). This has led to the selection of key traits of species to enable them to rapidly disperse, locate, colonize, and feed on the carrion for growth and development of offspring (Tomberlin et al. 2011). Any species that can perform these tasks faster or more efficiently than others can potentially monopolize the resource and have a competitive advantage. Direct competition, however, should lead to the evolved specialization of species to reduce overlap in their resource requirements. It is evident that niche specialization exists among scavenger communities, especially for diverse arthropod assemblages (Bessa et al. 2014; Braack 1987) and obligate vertebrate guilds (DeVault et al. 2003). However, there are other mechanisms that also underpin competitive dynamics, such as resource partitioning, population aggregation, and chemically mediated interactions.

Partitioning of carrion resources among species can occur within and among individual carcasses. Different combinations of species of arthropods and vertebrates have been shown to utilize different kinds and sizes of carcasses (Hewadikaram and Goff 1991; Moleón et al. 2015; Sebastián-González et al. 2016) and this represents a kind of resource partitioning *among* different carcasses. Nestedness in species-rich vertebrate scavenger assemblages has been reported from carcasses in Spain (Sebastián-González et al. 2016) and in Poland (Selva and Fortuna 2007), and is thought to be a consequence of competition among species-rich assemblages. This non-random occurrence of species among carcasses is evidence of partitioning among carcasses. However, partitioning is best known *within* carcasses where different species utilize different parts of a carcass (e.g., Fig. 1). For some species, competition may have resulted in niche differentiation, such as among flies competing for moist tissues and fluids (e.g. Calliphoridae, Muscidae; (Hanski 1987b). For other species, partitioning may represent an adaptation to an available niche where there is low competition. The tough, keratinous horns and hooves of some animals, for example, is exploited by tineid moths or trogid beetles and few other arthropods (Braack 1987), likely due to low competition for this challenging substrate.

Interactions between competitively superior and inferior species can affect levels of coexistence among species seemingly sharing the same patchy resource. The 'aggregation model of coexistence' for a community of species sharing a single resource proposes that if the distribution of a competitively superior species is spatially aggregated, i.e. clumped at patches, then this frees other patches of resource to be colonized by competitively inferior species (Atkinson 1985). This model has been examined in detail for communities of carrion flies (Hanski 1987a; Ives 1991), and has shown a general tendency for increasing aggregation to lead to increasing levels of coexistence among species competing for the same carrion resource. Factors such as carcass size and habitat quality have also been shown to affect species aggregation and levels of species coexistence (Woodcock et al. 2002). Another consequence of competition among species for a patchy resource is the evolved capacity for rapid location, colonization, and exploitation of the resource patches (Barton et al. 2013b; Ruxton and Houston 2004). The early arrival of a species prior to a competitor, may confer a competitive advantage by providing a window of opportunity to consume the resource unencumbered by other species. Such 'priority effects' are another potential mechanism underpinning patterns of succession and coexistence among species competing for the same resource (Alford and Wilbur 1985; Brundage et al. 2014).

Competitive interactions among decomposers and scavengers can be mediated by chemicals. For example, the interactions between microbial decomposers and vertebrate carrion consumers has been known for some time (DeVault et al. 2003; Janzen 1977). However, it is only more recently that examples have been documented for the competitive exclusion of arthropods by bacteria (Burkepile et al. 2006; Tomberlin et al. 2012) and bacteria by arthropods (Hoback et al. 2004; Rozen et al. 2008). This competitive dynamic might have significant implications for rates of carrion decomposition if rapid consumption by flies, for example, is prevented. Further implications for ecosystems may include diversion of nutrients into the soil decomposer system where they are metabolized in the soil by bacteria and fungi at the site of a carcass.

Top-Down Versus Bottom-Up Effects on Carrion Communities

The study of foodwebs often focuses on a plant-herbivore-predator perspective of trophic interactions and community structure, but this overlooks the importance of detritus (both plant and animal) as an alternative resource base (Barton 2015; Moore et al. 2004). The role of carrion resources in structuring scavenger communities is poorly understood, although this is growing for some vertebrates (DeVault et al. 2003; Wilson and Wolkovich 2011). Further details on vertebrate scavenger communities is given in chapter "Vertebrate Scavenging Communities". Theory suggests that carrion resources may underpin a larger amount of energy and nutrient flow than consumption of live prey (Wilson and Wolkovich 2011).

Carrion can have an important role in structuring food-webs via top-down (i.e. predator-based) regulation of lower trophic levels and bottom-up (i.e. resource-based) regulation of higher trophic levels (DeVault et al. 2003; Dyer and Letourneau 2003; Mateo-Tomás et al. 2015). Although the top-down vs. bottom-up dichotomy is a useful way to conceptualize trophic interactions, recent evidence has shown that predators often have multiple links to other components in a foodweb. For example, many predators (arthropods and vertebrates) will consume carrion when the opportunity arises (Moleón et al. 2014; von Berg et al. 2012; Wilson and Wolkovich 2011). This suggests that a compartmentalized view of trophic levels is simplistic, and that the role of predators in structuring carrion-centered food webs are more complicated and warrant further study.

There are several examples of bottom-up control of scavenger communities, particularly in island or cave ecosystems (Polis and Hurd 1996; Schneider et al. 2011). Such systems often lack primary production, and may be entirely dependent on external detrital resources, including carrion, as a source of energy and nutrients. For example, work by Polis and Hurd (1995) examined the role of carrion on oceanic islands. They revealed a causal relationship between marine-derived carrion and terrestrial foodweb dynamics of islands. Another example involves work by Schneider et al. (2011) and the manipulation of amounts of carrion in a series of caves. They showed that carrion-associated arthropod communities in these caves were profoundly affected by carrion addition and removal, thus revealing the extent to which these cave biota are dependent upon outside carrion subsidies (Schneider et al. 2011).

Decomposition Linkages Between Ecosystems

The movement of carrion within and across ecosystems can underpin the functioning of some food webs and ecosystems by subsidizing detritus resources (Polis et al. 1997). For example, many small or young islands have very limited autochthonous biomass production due to limited soils or unfavorable growing conditions. In these environments, carrion from nesting birds, or fish, bird and seal carcasses washed in from the sea, can supplement the resource base for the island food web. This has been demonstrated by Polis and Hurd (1995) on islands in the Gulf of California, where they measured invertebrate densities on a range of islands of different size. Carrion inputs were shown to be critical to these ecosystems, and supported high abundances of scavenger invertebrates and their spider predators.

The movement of carrion across ecosystems can also occur through the migration of live animals. A good example of this is the migration of anadromous salmon (e.g. *Salmo* spp. and *Oncorhynchus* spp.) up streams from the ocean as part of their annual spawning runs (Hocking and Reynolds 2011). This migration from marine to freshwater ecosystems, and the subsequent die-off of thousands of individuals results in the mass transfer of substantial quantities of salmon biomass, with benefits for many scavenger invertebrates (Hocking et al. 2009). A similar phenomenon has been documented for the mass emergence of aquatic insects and their dispersal to nearby riparian and terrestrial habitat (Dreyer et al. 2012, 2015). Although insect carcasses are small, this is made up for by their sheer quantity and high densities. Such carcass-mediated transfers of carbon and nitrogen can be substantial across ecosystem boundaries, and has the potential to affect ecological processes and nutrient cycling.

Patch Dynamics and Landscape Heterogeneity

The spatial and temporal patchiness of animal carcasses in the environment has been repeatedly found to influence the dynamics of species populations and assemblages at carrion (Barton et al. 2013a). Much of this work, however, has been at small scales with a focus on individual carcasses. This has helped to consolidate the dominant paradigm of the ‘ephemeral resource patch’, which provides an effective general framework for how resource patchiness can affect the spatio-temporal dynamics of species populations or communities (Finn 2001). It also draws conceptual parallels between carrion resources and other spatially discrete and temporary resources, such as dung pads (Doube 1987), fungal fruiting bodies (Heard 1998) and plant fruits (Sevenster and VanAlphen 1996). By contrast, scaling up this work to understand the role of carrion in landscapes and ecosystems has been rare (Bump et al. 2009a). Further, an outward perspective that questions the larger-scale role of carrion in nutrient cycling and landscape heterogeneity is lacking, despite there being some high-profile evidence of the large-scale impact of carrion (Hocking and Reynolds 2011; Yang 2004).

The patchiness of carrion can affect landscape heterogeneity in terms of biodiversity and ecological processes. For example, two carcasses at *different* decay stages will support a greater range of species than two carcasses at the *same* decay stage, and this has consequences for supporting overall biodiversity within landscapes (Barton et al. 2013a). Carcasses can also drive soil nutrient heterogeneity (Bump et al. 2009a), and can provide establishment opportunities for grasses (Barton et al. 2013b) and for trees (Barton et al. 2013b; Bump et al. 2009b). When in sufficient quantities, and multiplied across space and over time, the geographic location and turnover of carcasses can have significant effects on whole ecosystems (Bump et al. 2009a).

It was previously thought that well-consumed carrion did not contribute to ecological heterogeneity. We have learned, however, that in some cases even well consumed carrion can cause significant physical disturbances and nutrient pulses that alter mosaics of biogeochemical complexity, nutrient availability, microbial biomass, activity, and composition, and soil biodiversity. Consumptive activities disperse carrion resources beyond a discrete area. Carcass sites also concentrate other materials resulting from the activity of consumers. Initially, carcass sites receive resource inputs from predators and scavengers, including feces and urine. Enhanced plant quality and growth at carcass sites can attract herbivores and their predators, which also results in excretory inputs (Danell et al. 2002, 2006; Towne 2000). Insects and birds may also contribute significant inputs of chitin and keratin, respectively. Cumulatively, these inputs can extend the duration and quantity of energy and nutrient exchange at carcass sites, thereby producing positive feedbacks that prolong elevated levels of heterotrophic activity and ecological heterogeneity. These changes affect above ground biomass, community composition, foliar nutrient levels, and tree seedling establishment and sapling growth (Bump et al. 2009a, b; Towne 2000). The ability of carrion to alter steady-state edaphic and ecological properties represents a strong, reciprocal feedback between above and belowground communities. This occurs via mortality of above ground organisms, which leads to multiple effects on belowground communities that then alter aboveground ecological properties (Bardgett and Wardle 2010; Dreyer et al. 2015; Schmitz et al. 2010). As a consequence, this work is highly cross-disciplinary, spanning multiple scales of ecological inquiry.

Conclusions and Future Perspectives

Knowledge of carrion decomposition will continue to inform many aspects of ecology, biodiversity conservation, natural resource management, as well as the forensic medical sciences. The decomposition of carrion results from a complex series of chemical, biological, and physical processes that ultimately recycles the energy and nutrients embodied in an animal through other organisms and its environment. Understanding of carrion decomposition has been developed by specialists in chemistry, medical pathology, microbiology, soil science, entomology, and ecology, and the future of decomposition research will need to foster deeper interdisciplinary collaboration among these specialists.

Key emerging areas of carrion decomposition research will stem from advances in technology and the rapid reduction in costs of various forms of molecular analysis. Further advances will also come from multi-disciplinary research that integrates molecular and ecological perspectives. Emerging areas and advances in carrion decomposition will also benefit from increased spatial variance sampling that will allow researchers to determine under what circumstances carrion decompositions contributes to or diminishes environmental heterogeneity at multiple scales. At the macro scale, continued comparative investigation of controls (e.g. weather, disease, predation) of carrion distribution in space and time are necessary to predict how climate change will likely affect carrion availability and decomposition in ecosystems.

Molecular Tools and the Microbial Frontier

Rapid developments in technology, including improved instrumentation and computational power, is generating ever increasing amounts of biomolecular data. This is true for all aspects of the life sciences, and there is clear potential to apply this to understanding carrion decomposition. One example of this is the emergence of ecogenomics and the rapid assessment of diversity, composition and function of hyperdiverse microbial communities (Metcalf et al. 2015; Pechal and Benbow 2016; Pechal et al. 2014b). A particularly exciting area of research is the role of the microbiome in decomposition, and how this is influenced by other carrion-feeding organisms such as blowflies (Pechal et al. 2013). Although each carcass has its own community of microbes in its gut and on its skin, the effect of colonizing insects in bringing new bacteria to a carcass, and potentially altering decomposition patterns, remains poorly understood. The diversity and composition of the microbiome is likely to have important effects on carrion decomposition, and the rapid and accurate assessment of microbial diversity using molecular tools will be critical to this future research area (Crippen et al. 2015; Metcalf et al. 2015; Pechal et al. 2014b). Further, there is the unknown possibility of carrion gut microbiota ‘seeding’ soils, potentially increasing localised soil microbial diversity and broader spatial microbial heterogeneity.

Community Interactions

There is a renewed focus on understanding the dynamics and interactions among species associated with carrion, and which combine to form the ‘necrobiome’ (sensu Benbow et al. 2013). This includes all the microbial, arthropod, and vertebrate taxa that are part of the carrion foodweb and are responsible for the decomposition of carrion. An exciting and emerging area is the interaction between microbes and insects. As noted above, the microbiome of a carcass has a hugely important role in its decomposition (Metcalf et al. 2015), yet interactions among insect species and among insects and bacteria also have important implications for decomposition (Pechal et al. 2013; Tomberlin et al. 2012). Research into the complex interactions among species, within and among carcasses, and at multiple spatial scales, is emerging as critical to understanding the decomposition process (Benbow et al. 2015), and its role in driving biodiversity dynamics, nutrient cycling, and ecosystem functioning more broadly (Barton et al. 2013a).

Particular recent interest in vertebrate scavengers (e.g. Moleón et al. 2014; Wilson and Wolkovich 2011) stems from the decline of apex predators in many ecosystems worldwide (Estes et al. 2011) and subsequent functional replacement by a range of other predators. Apex predators, such as lions or wolves, generate carrion by leaving the un-consumed remains of kills (Bump et al. 2009a), which is used by other smaller predators and scavengers. However, many predator species increase their scavenging of carrion during times of low prey availability (Wilson and Wolkovich 2011). This can result in changed structure of food webs, and altered pathways of nutrient and energy flow through ecosystems. A research priority is therefore understanding how changes to carrion food webs, and their species interactions, might translate to changes in ecosystem functioning (Barton et al. 2013a; Tomberlin et al. 2011; Wilson and Wolkovich 2011). A significant barrier to this work, however, is the lack of studies that have compared communities of multiple taxa such as microbes, arthropods, birds and carnivores (but see Parmenter and MacMahon 2009; Read and Wilson 2004; Selva and Fortuna 2007; Tomberlin et al. 2012).

Despite the recent recognition of the ecological importance of carrion, the spatial and temporal dynamics of carrion distribution via large vertebrate carcasses is comparatively unexamined. Yet, it is of fundamental ecological importance because large vertebrate carcasses can facilitate niche provisioning and specialization, and alter resource competition dynamics for other species. For example, carcass-derived nutrients can shift competitive relationships among primary producers (Barton et al. 2013b; Bugalho et al. 2011; Towne 2000), serve as a disturbance mechanism (Danell et al. 2006), and carcass sites constitute specialized, critical habitat for obligate carrion feeders and reproducers (Selva and Fortuna 2007).

Decomposition and Global Change

Many aspects of global change have the potential to alter carrion dynamics and the decomposition process. This includes changes to land use and the habitat that supports carrion scavenger and decomposer communities (DeVault et al. 2011; Klein 1989), and the transmission of disease and the timing and magnitude of animal mass mortality events (Fey et al. 2015). The drivers of land use change include agricultural expansion and intensification, as well as urbanization. When changes to land use occur, some consumers of carrion may be lost, or their spatial or temporal distribution changed, with potential implications for decomposition processes and rates (Kavazos and Wallman 2012; Klein 1989). For example, loss of species may result in reduced functional complementarity and redundancy among carrion consumers. It is already known that many vertebrates will opportunistically scavenge on carrion (see chapter “Vertebrate Scavenging Communities”), and there is evidence that some intra-guild compensation occurs when dominant scavengers are removed or lost due to land use changes (Olson et al. 2012). Similarly, several species of blow fly (Diptera: Calliphoridae) typically co-occur at carcasses, but recent evidence suggests that urbanization affects fly community composition (Kavazos and Wallman 2012), and this is likely to change levels of inter-specific competition, and perhaps even carrion decomposition rates.

Far less is known about the potential impacts of global climate change on carrion decomposition. The strong temperature dependence of the decomposition would suggest this important process is highly vulnerable to temperature changes, with higher temperatures likely accelerating rates of decay. However, the impact of climate change on species of microbe or insect critical to decomposition, or their interactions, is unknown. An expected effect includes range shifts due to changes in optimal developmental envelopes (Chen et al. 2011; Walther et al. 2002), and this is likely to move species into new areas, and out of existing ones. This has implications for both the ecology of carrion decomposition and its application to forensic problems that depend on knowledge of species presence and development rates.

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