CONCEPTS & SYNTHESIS

EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

Necrobiome framework for bridging decomposition ecology of autotrophically and heterotrophically derived organic matter

M. Eric Benbow,[1,2,3,11] Philip S. Barton,[4] Michael D. Ulyshen,[5] James C. Beasley,[6] Travis L. DeVault,[7] Michael S. Strickland,[8] Jeffery K. Tomberlin,[9] Heather R. Jordan,[10] and Jennifer L. Pechal[1]

[1]*Department of Entomology, Michigan State University, East Lansing, Michigan 48824 USA*
[2]*Department of Osteopathic Medical Specialties, Michigan State University, East Lansing, Michigan 48824 USA*
[3]*Ecology, Evolutionary Biology and Behavior Program, Michigan State University, East Lansing, Michigan 48824 USA*
[4]*Fenner School of Environment and Society, Australian National University, Canberra, Australian Capital Territory 2601 Australia*
[5]*USDA Forest Service, Southern Research Station, Athens, Georgia 30602 USA*
[6]*Savannah River Ecology Laboratory and Warnell School of Forestry and Natural Resources, University of Georgia, Aiken, South Carolina 29802 USA*
[7]*U.S. Department of Agriculture, National Wildlife Research Center, Sandusky, Ohio 44870 USA*
[8]*Department of Soil & Water Systems, University of Idaho, Moscow, Idaho 83844 USA*
[9]*Department of Entomology, Texas A&M University, College Station, Texas 77843 USA*
[10]*Department of Biological Sciences, Mississippi State University, Mississippi, Mississippi 39762 USA*

Abstract. Decomposition contributes to global ecosystem function by contributing to nutrient recycling, energy flow, and limiting biomass accumulation. The decomposer organisms influencing this process form diverse, complex, and highly dynamic communities that often specialize on different plant or animal resources. Despite performing the same net role, there is a need to conceptually synthesize information on the structure and function of decomposer communities across the spectrum of dead plant and animal resources. A lack of synthesis has limited cross-disciplinary learning and research in important areas of ecosystem and community ecology. Here we expound on the "necrobiome" concept and develop a framework describing the decomposer communities and their interactions associated with plant and animal resource types within multiple ecosystems. We outline the biotic structure and ecological functions of the necrobiome, along with how the necrobiome fits into a broader landscape and ecosystem context. The expanded necrobiome model provides a set of perspectives on decomposer communities across resource types, and conceptually unifies plant and animal decomposer communities into the same framework, while acknowledging key differences in processes and mechanisms. This framework is intended to raise awareness among researchers, and advance the construction of explicit, mechanistic hypotheses that further our understanding of decomposer community contributions to biodiversity, the structure and function of ecosystems, global nutrient recycling and energy flow.

Key words: biodiversity; carrion; community assembly; decomposition; detritus; ecosystem; interactions; litter; microbial ecology; nutrient cycling; organic matter.

INTRODUCTION

Decomposer organisms are highly efficient at consuming and transforming dead organic matter, and they play a critical role in shaping ecosystem structure and function. The impact of decomposition on ecosystems is demonstrated by the relatively small accumulation of the estimated 150–200 g of carbon·m^{-2}·yr^{-1} (Fierer et al. 2009) generated by plant net productivity, especially considering that 90% of plant biomass is not consumed by herbivores (Cebrian 1999, Gessner et al. 2010). Early research demonstrated the importance of detritus in communities and energy flow of both terrestrial and

aquatic ecosystems (e.g., Forbes 1887, Summerhayes and Elton 1923, Lindeman 1942, Teal 1962, Odum 1969, Swift et al. 1979, Wallace et al. 1999). The detrital pool has significant impact on the structure and function of ecosystems by increasing system stability and persistence, and the fate of such "dead plant," "decaying matter," "dung," or "litter" has been described for many ecosystems (Moore et al. 2004). Dead plant biomass, defined here as autotrophically derived decomposing organic matter, is not the only form of detritus that is recycled with important ecosystem function. Another often overlooked decomposition component in ecosystems is carrion, defined here as heterotrophically derived decomposing organic matter, or the carcasses of animals and other organisms that do not harvest energy from the sun but still contribute to the global detritus budget. These two forms of decomposing biomass may also include transitional forms of decaying organic matter, such as dung or frass, excreted organic molecules and dissolved and particulate forms that reflect the once living, and are the partially digested, exuded, and egested biomass of plants and animals.

Dead organic matter of any type is defined as detritus (Petersen et al. 1918; Odum and de la Cruz 1963) but has been primarily perceived in the literature as organic matter resulting from plant death, with some, but few, instances of dead animal organic matter (or carrion) referred to as detritus (e.g., Swift et al. 1979, Moore et al. 2004). In the current literature, the majority of references to detritus describe decomposing plant biomass, reinforcing a separation with other widely ubiquitous forms of biomass with relatively higher turnover, such as carrion and dung/feces. With this understanding we propose to facilitate broader recognition of the commonalities and differences of dead organic matter of any type, defined in this paper as necromass, a term previously used in the literature (e.g., Coûteaux et al. 2005, Lomstein et al. 2012), but understood to be synonymous with the holistic definition of detritus as summarized by Moore et al. (2004).

Necromass takes a wide range of shapes, sizes, and quality (Swift et al. 1979, Carter et al. 2007). It forms the basis of many food webs and consequently has significant bottom-up importance for ecosystem function (Gessner et al. 2010). It also forms the focal point for interactions and behaviors among decomposer species comprising complex communities influencing ecosystems across temporal and spatial scales (Yang et al. 2010); and in freshwater habitats, decomposition is considered a fundamental ecosystem process that contributes to watershed biodiversity (Woodward et al. 2012). Despite the importance of decomposer communities, there exists no standard framework to conceptualize their complex and dynamic interactions across both plant and animal necromass. This lack of a framework is significant because it limits a comprehensive understanding of the community ecology of decomposition and has implications for defining and testing paradigms related to nutrient recycling, gene flow, population dynamics, and other ecosystem processes at the frontier of ecological research.

There has been a recent expansion of knowledge about both micro- and macro-scale processes structuring decomposer communities and contributing to the species interactions (e.g., Burkepile et al. 2006, Gessner et al. 2010, Wilson and Wolkovich 2011, Metcalf et al. 2016); however, much is still unknown. To date, ecological theory describing decomposition processes has included succession theory (Payne et al. 1968, Michaud et al. 2015), meta-population theory (Hanski 1987), and aggregation and coexistence theory (Ives 1991). Carrion and dung, in particular, have been useful systems to test and develop these theories and mechanistic hypotheses having relevance to many other areas of ecology (see Box 1). However, a new synthesis is required to integrate existing knowledge with the new discoveries occurring in the animal and plant decomposition disciplines. We propose an expansion of a recent framework to facilitate this synthesis in a way that encompasses all forms, functions, and ecological dynamics of organic matter decomposition: the necrobiome (Fig. 1).

The necrobiome was originally defined as "...the community of species (both prokaryotic and eukaryotic) associated with decomposing remains of heterotrophic biomass, including animal carrion and human corpses" (sensu Benbow et al. 2013; Benbow et al. 2015c). While the original development of this term was focused on vertebrate carrion, we argue it can be expanded to include any form of necromass (e.g., leaves, wood, dung). We also suggest the necrobiome framework is relevant to both plant (i.e., autotrophically derived) and animal (i.e., heterotrophically derived) necromass decomposition by highlighting the fundamental similarities and differences in the processes that define decomposition. In this paper, we take a conciliatory approach to more fully develop the necrobiome framework as a unifying construct for guiding research in decomposition, regardless of how the life form was derived (Fig. 2).

All life is terminal and the remaining nutrients and energy are ultimately recycled within and across ecosystems (Polis et al. 1997). Some aspects of this ecological process are universal across all forms of necromass, such as disintegration, dispersal, and microbial activity. In contrast, other aspects, such as community dynamics and decomposition rates, and specific decomposer taxa, are distinct across different forms of necromass. The major similarities and differences in necrobiome structure and function have yet to be synthesized in detail but are influenced by the overall composition and quality of the specific necromass, and the associated decomposer species that have evolved to exploit the resource.

In this review, we provide an overview of the similarities and differences among decomposer communities associated with plant and animal necromass. We suggest plant and animal necromass research findings illustrate a broader generality to the processes structuring decomposer communities across a range of substrates that,

Box 1. Shared ecological theory across studies of plant and animal decomposition.

Both plant and animal necromass has been used extensively as model systems to test and develop ecological theory, and while historically often operating independently, these areas of study are where ecologists on both sides of the decomposition "divide" have done well to learn from each other. This is perhaps due to the implicit recognition by theorists of the similarities in fundamental processes occurring during decomposition. There has been research that included both autotrophically and heterotrophically derived necromass in food web studies (Polis and Hurd 1996, Polis et al. 1997, Nakano et al. 1999), but comparisons and similarities in processes, community ecology, and mechanisms has received less attention in the literature. *Community succession* of carrion has a long history (Mégnin 1894, Schoenly and Reid 1987, Michaud et al. 2015), and has many important similarities with community succession on dead plant matter, such as leaf and fruit litter and dead wood (Ulyshen 2016). Indeed, succession theory is one of the most widely used theories relating to decomposition, especially with regard to the study of the diversity and structure of arthropod communities (Richards and Goff 1997, Hobischak et al. 2006), and more recently for microbial communities (Pechal et al. 2013, Metcalf et al. 2016). *Meta-population* and *meta-community* theory has been tested using animal carcasses and dung pads as model resource patches to simulate the focal points of insect assemblage aggregation and dispersal (Hanski 1987). This work has led to validation of competitive exclusion and dispersal limitation as mechanisms underpinning population dynamics (Hanski and Gilpin 1991) but could also be tested using decaying plant material. *Aggregation and coexistence theory* has been tested using fly communities at carrion (Ives 1991, Fiene et al. 2014), as well as mushrooms and rotting fruit (Heard 1998, Finn 2001). The theory predicts that if the distribution of a competitively superior species is spatially aggregated, this frees other patches to be colonized by competitively inferior species, thus leading to differences in community composition and greater overall diversity across multiple patches (Kouki and Hanski 1995, Woodcock et al. 2002). *Resource subsidy theory* describes the spatial movement of energy and nutrients between two spatially disjunct ecosystems (Polis et al. 1997, Leroux and Loreau 2008, Gravel et al. 2010). This theory has been effective at integrating plant and animal necromass into one resource pool (Moore et al. 2004), and at demonstrating links between terrestrial and aquatic systems (Polis and Hurd 1996). For example, the mass emergence of cicadas from forest ecosystems can lead to the deposition of animal necromass into ponds, increasing pond productivity and altering their communities (Nowlin et al. 2007). Measurement of marine-derived plant and animal necromass washing up on islands has also been shown to underpin island terrestrial arthropod biomass (Polis and Hurd 1995). *Landscape heterogeneity theory* has emerged as a way to link patterns and processes occurring at individual patches to large-scale consequences for landscapes (Wiens 1995). For example, two patches of dead wood or carrion at different temporal decay stages or spatial locations will support a greater range of species than two of the same resource patches at the same decay stage or location. Ultimately, the state of the resource has consequences for supporting overall biodiversity (Barton et al. 2013a), driving soil nutrient heterogeneity (Harmon et al. 1986, Bump et al. 2009a), and generating novel combinations of species (Bump et al. 2009b, Barton et al. 2013b). Application of other landscape ecology principles, such as patch composition vs. configuration theory (Tscharntke et al. 2012), has the potential to yield further insights into the large-scale role of necromass in ecosystem structure and function (Barton 2015). Our necrobiome framework can act as a catalyst for further testing and synthesis of theory describing the interactions among organisms and their environment. Especially, for interactions and processes with clear temporal or spatial components in saprotrophic communities as resource substrates degrade over time, such as dispersal of insects or microbes among patches and the succession of necrophagous communities.

CONCEPTS & SYNTHESIS

cumulatively, have large-scale ecosystem-level effects. We synthesize the key similarities and differences among these decomposer communities and place them into a broadened conceptual model of the necrobiome. We then provide details of the biotic structure of the necrobiome, the different ecological functions each part performs, and the key interactions occurring among the decomposer organisms. Further, we explore how the necrobiome provides a useful way to conceptualize how decomposition delivers nutrients, energy, genomes, and communities across space and time with ultimate responses in ecosystem biodiversity and function. By presenting a new synthesis of decomposer communities that continues the approach developed by Moore et al. (2004), we aim to provide an integrative perspective to the key concepts used by researchers that are separated

into plant or animal decomposition disciplines. Rather than continuing to consider each necromass type in isolation, we stress the importance of synthesizing this knowledge to develop a holistic understanding of nutrient cycling and food web dynamics across scales.

AUTOTROPHICALLY AND HETEROTROPHICALLY DERIVED BIOMASS: STANDING STOCKS, PRODUCTION, AND TURNOVER

Autotrophically derived necromass refers to the dead biomass produced from organisms that use energy from sunlight as energy (e.g., plants and algae) or chemical reactions (various prokaryotes) to produce organic compounds. Heterotrophically derived necromass, by contrast, refers to the dead biomass produced from organisms that obtain organic material through the consumption of other

(d) Habitat and ecosystem determines the substrate context, the species pool, and key abiotic moderating processes

Habitat and ecosystem

(b) Necrobiome structure

Internal microbial communities (endonecrotic microbiome)

External microbial communities (epinecrotic microbiome)

Substrate microbial communities (epigeic, soil, or water microbiome)

Saprophage communities (invertebrate and vertebrate consumers)

Saprophage community

External microbiome

Internal microbiome

Necromass

Substrate microbial community

(c) Necrobiome interactions and functions

1. Internal microbe and element translocation, molecular catabolism
2. External surface microbe and element translocation
3. Mixing of microbes and elements via trophic and physical pathways
4. Translocation of elements and microbes via invertebrate and vertebrate trophic pathways
5. Saprophage-mediated dispersal of microbes and elements into broader ecosystem
6. Microbe and element mixing across the necromass-substrate interface via trophic and physical pathways
7. Dispersal of microbes and elements into broader ecosystem via trophic and physical pathways

(a) Necromass qualities include the size, nutrient content, and digestibility of the resource
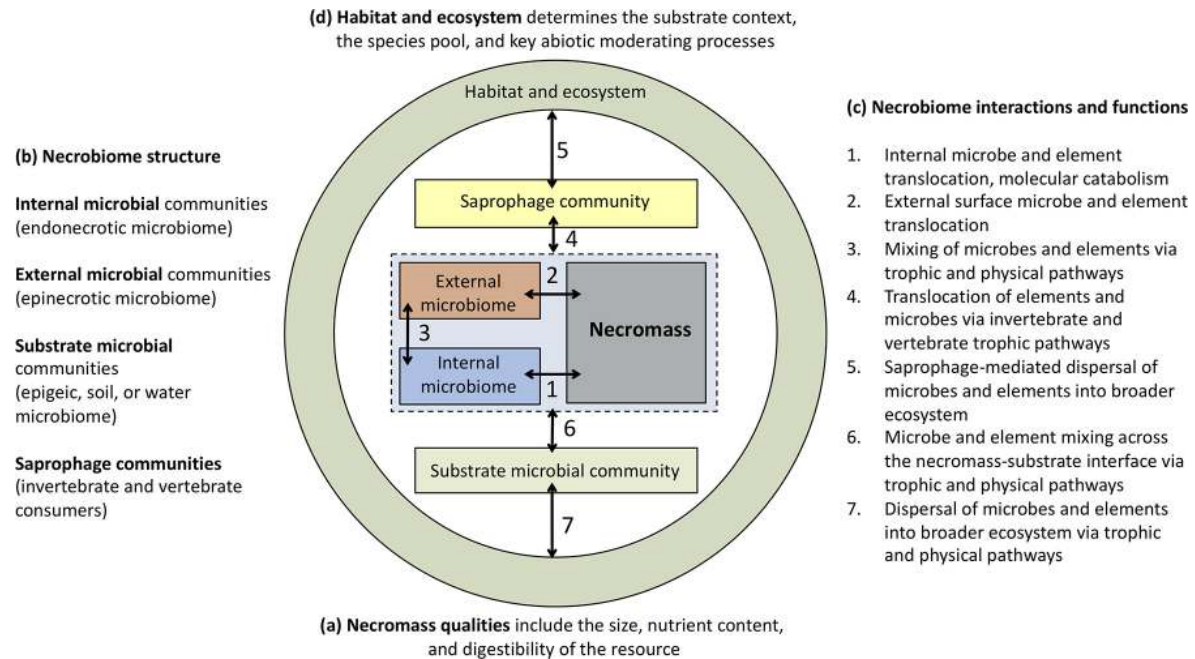
Fig. 1. The necrobiome is the community of organisms associated with necromass decomposition and includes their interactions with the necromass, with each other, and with their surrounding habitat and ecosystem. This concept is general across plant, fungi, dung/frass/feces, or animal necromass types, and in both terrestrial and aquatic realms. (a) Various qualities of necromass have strong controlling effects on its associated necrobiome. (b) The decomposing necromass is host to a microbiome while alive, both internal (endonecrotic) and external (epinecrotic), and these communities begin to change after death and during the course of decomposition. The changing microbiomes use the organic matter as habitat and for energy and nutrients. As decay progresses, the organic matter and associated activities of the microbes facilitate the attraction of invertebrate and vertebrate saprophages that directly consume the necromass and the microbial communities. (c) All of these biotic components of the necrobiome interact in ways that give rise to pathways of microbial and elemental dispersal away from the decaying necromass into adjacent soil or water media, as well as to the surrounding ecosystem at both localized and broad spatial scales. (d) The necrobiome and its functions operate within a complex network of interactions that are constrained by its terrestrial or aquatic context, the regional species pool, and gradients of abiotic factors. Critically, all these aspects of the necrobiome are interlinked, and the relative importance of each component of the necrobiome, and their function, will depend on the intrinsic qualities of decaying necromass and the extrinsic controlling environmental factors (e.g., temperature, moisture, latitude).

organisms (e.g., animals, fungi, protists, and other micro-eukaryotes). We focus our discussion here on the initial and intact forms of necromass exceeding 8 mm^3 in size, for which there is a richer source of literature supporting a more detailed assessment of the necrobiome. We acknowledge that all necromass ultimately becomes smaller than this size and that the decomposition of microorganisms, such as fungal necromass, is ecologically important (Fernandez and Kennedy 2018). For instance, fungi and protists produce macroscopic structures supporting unique necrobiome communities, such as giant kelp (*Macrocystis pyrifera* [Linnaeus]; Inglis 1989, Thunes et al. 2000). The importance of bacteria and fungi to decomposition goes beyond diversity, with reports of soil microbial biomass being an order of magnitude greater than the biomass of other soil organisms and two orders of magnitude greater than aboveground animal biomass (Fierer et al. 2009). This large amount of microbial biomass has the potential to influence ecosystem processes as it dies and becomes microbial necromass (Throckmorton et al. 2012). In fact, this microbial necromass, in combination with microbial metabolites, likely drives a significant

proportion of soil organic matter formation (Kallenbach et al. 2015, Brabcová et al. 2016, Fernandez et al. 2016). Soil fungal mycelia production alone contributes to major functional processes in terrestrial ecosystems, with production (and associated death and decomposition) reported to range from 100–300 kg·ha^{-1}· yr^{-1} (Ekblad et al. 2013). The necrobiome of dead fungal mycelium has been reported to be quite diverse (Ekblad et al. 2013, Brabcová et al. 2016), providing additional evidence that decomposition networks of microorganisms operate at every biological scale and contribute to complex patterns of biodiversity and associated functions in all ecosystems. However, there is much less understood of the species and processes of decomposition of fine particulate necromass and microorganisms (however, see Alldredge and Silver 1988) across ecosystems, a fruitful area of future research and review.

Based on size and composition, plant material can be divided into herbaceous (e.g., leaves) and woody forms. Animal necromass produced by vertebrates can be distinguished from invertebrate based on both size and internal or external skeletal structures. Dung, however, is
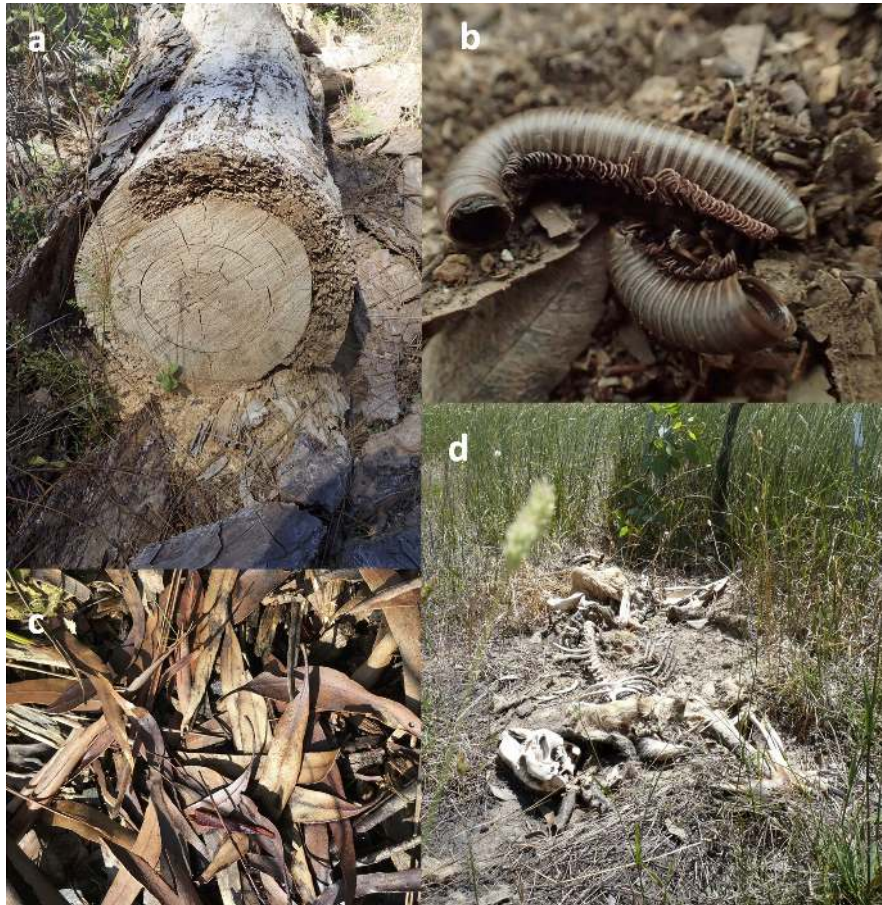
Fig. 2.　Examples of necromass types occurring in ecosystems showing differences in size and heterogeneity. (a) Log cross section showing different rates of decay at edges vs. center, (b) millipede carcass exoskeleton remains, (c) leaf litter, and (d) vertebrate carcass showing skeletal remains. Despite the contrasting physical appearance of necromass types, the broad structure of the necrobiome at each necromass type can be conceptualized in a similar way.

an intermediate and highly transformed form of necromass characterized by fragmented and partially digested plant and/or animal material mixed with host gut-dwelling microbes. Herbivorous invertebrates (Reynolds and Hunter 2004) and vertebrates (Frank and Evans 1997) are known to generate large amounts of dung that play a critical role in nutrient cycling and redistribution in terrestrial and aquatic ecosystems (Wotton and Malmqvist 2001, Carline et al. 2005, Menendez et al. 2016). For the sake of space and focus, we do not elaborate on the dynamics of dung or frass; however, we encourage those interested in this topic to review the literature on the ecology and evolution of dung beetles (Hanski and Cambefort 1991) and the additional importance of feces in terrestrial (Van der Wal et al. 2004) and aquatic (Alldredge and Silver 1988, Wotton and Malmqvist 2001, Joyce et al. 2007) ecosystems. Below, we discuss in more detail the differences in the structure and composition of different forms of plant and animal necromass.

To our knowledge, no efforts have been made to compare the relative production or communities associated with the decomposition of plant and animal necromass in any ecosystem. Several comparisons of biomass in forested systems, however, provide some insight into the question of how much detritus is present in a habitat at any given time. Odum (1970), for example, determined in a Puerto Rican rainforest that plants and animals made up about 58% and 0.03% of the total biomass (including soil organic matter), respectively. Leaves accounted for only about 5% of aboveground plant biomass, with the rest consisted of wood and bark. Fittkau and Klinge (1973) reported animals made up only about 0.02% of the total living biomass in an Amazonian rainforest, with <10% of that component being of vertebrate origin. In most freshwater stream ecosystems leaf litter decomposition is a key process that influences energy and nutrient flow, biodiversity, and links terrestrial and marine ecosystems through a downstream continuum (Vannote et al. 1980, Webster and Benfield 1986, Wallace et al. 1997, Gessner et al. 2010). Detritus in a variety of organic matter forms is thought to represent the dominant energy pathway in most lakes (Rich and Wetzel 1978, Mann

1988) and other lentic surface waters such as wetlands (Brinson et al. 1981), coastal ecosystems (Duggins et al. 1989), and oceans (Parsons and Strickland 1962, Alldredge and Silver 1988). The differences in standing necromass between plants and animals are probably even larger than these estimates of biomass given that animal remains typically decompose much more quickly than plants, even in some aquatic habitats (Parmenter and Lamarra 1991), making carrion a "hidden" source of energy, nutrients and biodiversity.

In many cases, animal necromass will be produced more quickly given the shorter life spans of most animals compared with many plants, especially when comparing invertebrate necromass production with the woody components of plants. However, many plants shed biomass seasonally as leaves and root exudates, thus producing necromass at higher rates than the woody components that make up a large portion of the standing stock biomass. Furthermore, the total production of animal necromass per year could be expected to far exceed the standing animal necromass at any given time due to a combination of short life spans, continuous reproduction, and rapid decay rates such as those for zooplankton (e.g., Tang et al. 2014). By contrast, the production of plant necromass produced per year can be expected to be a small fraction of the standing plant necromass in many ecosystems, and this is especially true for forests where decomposition is slow and woody debris accumulates over time (Luyssaert et al. 2008). The relative importance of these differences in standing stock, production and rate of decay of plant and animal necromass is an area of inquiry that could provide broad ecological understanding of different forms or routes of energy flow and nutrient cycling in ecosystem function.

Focusing on vertebrate animals, Odum (1970) estimated that they accounted for only about 5% of total animal biomass with the remaining 95% consisting of invertebrates (see Tables 7 and 22 in Odum [1970]). Additionally, a meta-analysis by Fierer et al. (2009) determined approximately 50% of animal biomass is belowground. The fact that invertebrates are typically much shorter lived than vertebrates, usually develop to maturity more quickly, and often have multiple generations per year suggests the annual production of necromass by invertebrates far exceeds that produced by vertebrates. Indeed, Seastedt and Tate (1981) estimated the standing arthropod necromass on the forest floor of two oak–hickory forests to be up to double the estimated living arthropod biomass for the same forests. In other habitats, such as aquatic systems, standing stock biomass can be estimated for populations and communities (Waters 1966, 1969, Benke et al. 1988), but some studies also produce estimates of production, often as secondary production of macroinvertebrates (Benke et al. 1988, Huryn and Wallace 2000).

Knowledge of animal biomass in aquatic systems can be derived from measures of secondary production of invertebrates (Hynes 1970, Waters 1977, Benke et al. 1988, Huryn and Wallace 2000). Secondary production includes the elaboration of heterotrophic population biomass and assumes a yield to higher trophic levels that ultimately becomes part of the necromass pool in a given ecosystem. The method employs estimates of individual organismal body mass, often using length–mass regressions (Benke et al. 1999), and densities of those organisms and how they quantitatively change over time. One such method for calculating secondary production (i.e., removal summation) assumes all biomass produced eventually dies and is equivalent to estimated production for that cohort of organisms over a given time and under steady-state conditions (Boysen-Jensen 1919, Waters 1977, Benke and Huryn 2006). Thus, secondary production estimates of invertebrates may provide quantitative insight into the contribution of animal necromass and its turnover to ecosystem energetics, much like it has been done for measuring the importance of leaf necromass on aquatic invertebrate communities (Cummins et al. 1973, Wallace et al. 1999). Measuring living invertebrate biomass over time, however, does not allow for estimating other forms of necromass, such as dung or frass.

The importance of necrobiomes in the decomposition of entire communities of organisms could be pivotal in expanding our understanding of biodiversity contributions to global carbon and nutrient cycling, as has been discussed by Moore et al. (2004). As an example, a fascinating study reported that the quality of grasshopper necromass (affected by fear of predation) mediated subsequent leaf litter decomposition in old field ecosystems, with estimated significant ecosystem-level consequences (Hawlena et al. 2012). Discovering how animal and plant necromass decomposition communities interact with each other to drive nutrient and carbon cycling could lead to paradigm shifts in ecosystem science.

Intrinsic Variability of Necromass Types

Major forms of necromass (e.g., carrion, dung, leaves, and wood) can be distinguished from one another in three important ways: (1) resource size, (2) nutrient availability, and (3) digestibility. First, the unit volumes of different forms of necromass vary by 5–11 orders of magnitude (Fig. 3). While the largest forms of necromass produced globally are the woody stems and collective dead organic matter shedding of large trees, vertebrate carrion is the largest form in many nonforested ecosystems (e.g., bison in grasslands, whales in oceans; Towne 2000, Smith and Baco 2003). Resource size has important implications for the decomposition process, with larger resources decomposing more slowly and involving a greater diversity of species than smaller resources. Small arthropod carcasses, for example, typically disappear within several minutes to hours, being quickly discovered and consumed by ants, wasps, or other scavengers (Fellers and Fellers 1982, Young 1984,
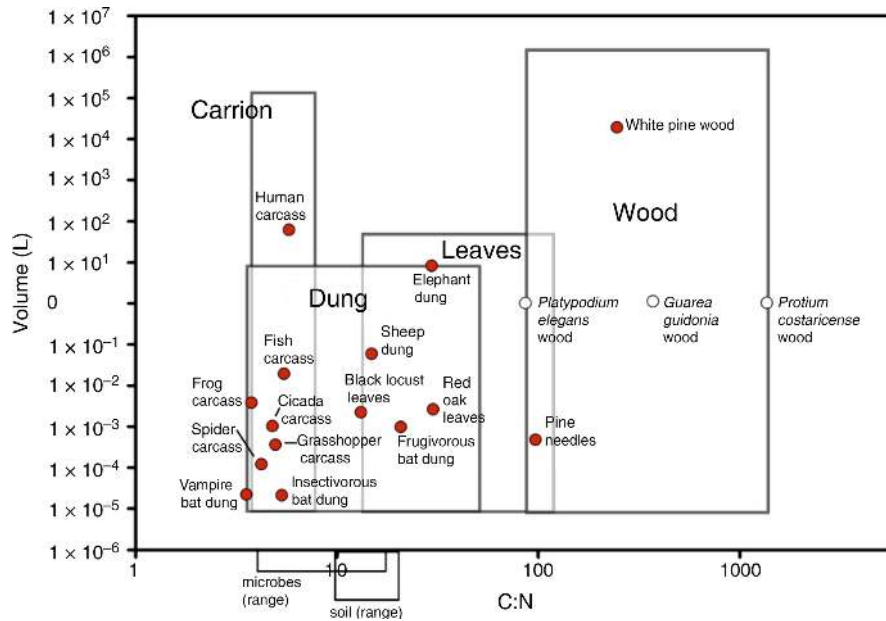
FIG. 3.   Some examples of the range of necromass sizes (L) and nutritional quality (C:N) for carrion, dung, leaf, and wood substrates. Red points represent examples where there is volume data available in the literature, whereas white points are examples for which there is no volume data available. Data used for this figure were deposited the Dryad Digital Repository (see *Data Availability*).

Retana et al. 1991). By contrast, the decomposition of larger carcasses typically involves a much wider variety of species and succession of decomposer communities (Jones et al. 2015, Turner et al. 2017). Large resources also have less surface area relative to volume than small resources and this limits initial accessibility by some decomposers and thus in some cases large vertebrates (e.g., elephants) decompose initially through microbial decomposition (Coe 1978). Fragmentation and penetration of necromass are both mediated by the animal community, and thus are important processes with respect to the acceleration of decomposition.

Second, different forms of necromass vary in nutritional quality. The carbon:nitrogen (C:N) ratio is commonly used to indicate the nutritional quality of organic material. The C:N ratio varies greatly among the various types of necromass, being lowest for carrion and highest for wood (Fig. 3). The C:N ratio also varies widely among necromass types due largely to interspecific variability. For example, it was reported up to 16-fold differences in C:N ratios existed among 59 species of tropical wood species (Martin et al. 2014). Intra-specific variability can also be important. For example, Madritch et al. (2007) reported two- to threefold differences in C:N ratios of caterpillar frass depending on the nutritional quality of their host plants. It has also been suggested that dung beetles are limited by assimilable C and not N (Holter and Scholtz 2007).

The third dimension is digestibility (not shown in Fig. 3). For plants, digestibility is largely determined by the structure of cell walls. Due to the recalcitrance of lignocellulose (i.e., a complex of lignin, cellulose, and hemicellulose) in plant cell walls, plant matter is much more resistant to decomposition than most animal soft tissues. For example, these recalcitrant compounds dominate plant tissues, respectively accounting for 20–35%, 40–45% and 20–40% of dry wood weight (Wilson and White 1986) and are highly variable among leaf litter types that contribute to stream ecosystem function (Webster and Benfield 1986, Woodward et al. 2012). Whereas a wide range of organisms can digest animal tissues, the digestion of lignin and cellulose is almost entirely limited to fungi and prokaryotes that have evolved the enzymes required to break down these compounds. This dependence on microbes to reduce autotrophically derived detritus has given rise to a number of important symbioses between wood and leaf-feeding insects and fungi (see section on symbioses in the necrobiome). Secondary plant compounds and other extractives also reduce the digestibility of dead plant matter and can have toxic effects on decomposers (Käärik 1974, Verhoeven and Liefveld 1997). Among carrion consumers, there is also specialization on recalcitrant body parts. For example, the bearded vulture eats only the bones of vertebrates (Margalida et al. 2009), whereas some tineid moths eat only the horns and hooves of ungulates (Braack 1987). Such specialization, however, involves digestive enzymes and stomach acids, and not symbioses.

Another important difference between the necromass production from plants and animals concerns the gradual process by which many perennial plants, especially woody plants, die. In forest trees, for example, young branches produced at the top cast shade on older

branches below, reducing their ability to capture sunlight and contribute to the growth of the tree. These overshadowed branches eventually die and fall to the ground, ultimately resulting in the long limbless trunks characteristic of many mature forest trees: a very long-term shedding of detritus over the lifetime of the tree. Similarly, growth in tree diameter is accompanied by the senescence and death of the oldest, innermost rings (Fig. 2a). Not only are these tissues not living, they often become colonized by diverse assemblages of decomposers many decades before the rest of the tree fully dies and falls to the forest floor (Elton 1966). This necromass accumulation co-occurs for years to decades with living tissue, providing a unique aspect of the necrobiome concept. Wounds through the bark layer (e.g., caused by extreme weather events, toppled neighboring trees, injuries from animal activity, etc.) expose the underlying phloem and wood for colonization and mark the beginning of the decay process in living trees. Although trees possess a variety of defensive mechanisms to limit the extent to which wounded areas are colonized by microbes and insects (e.g., flooding the site with water or sap, secondary plant compounds, etc.), organisms responsible for decay often become established at these sites. The first to colonize are the more ruderal microbial taxa, such as non-basiodiomycetes and bacteria, whereas wood-rotting fungi arrive later (Boddy 2001). The proportion of dead tissue in otherwise living trees increases with tree age and the largest and oldest trees, or "veteran trees," are full of dead limbs, rot holes, and are believed to be particularly important to supporting necrobiome biodiversity (Speight 1989, Stokland et al. 2012). The decomposition of tree tissue has been shown to be a substantial source of methane (Covey et al. 2012), suggesting broader effects on global biogeochemical cycling rates and atmospheric chemistry that require future investigation.

THE NECROBIOME

Necrobiome structure

The necrobiome defines a relatively concentrated set of organisms where many have evolved to detect, use and ultimately congregate with decaying organic matter either as a food or habitat resource (Benbow et al. 2013). We describe in more detail the microbial, invertebrate, and vertebrate components of the decomposer community, as well as important symbioses, interactions with soil, and abiotic factors that govern the composition and dynamics of the necrobiome (Fig. 1).

Microbial communities of the necrobiome

Structurally, the necrobiome consists of the prokaryotic and eukaryotic microbial communities (microbiome) that are internal (endonecrotic) and external (epinecrotic) components of host necromass. While given different names, these microbial communities have been reported in both living plants (Bulgarelli et al. 2013) and animals (Dillon and Dillon 2004). These microbial communities function as symbionts, commensals, pathogens, and parasites during life, and the taxa become the pioneer community of plant detritus or carrion immediately after, or prior to, death in both terrestrial (Frankland 1966, Latter and Cragg 1967) and aquatic ecosystems (Preiswerk et al. 2018). The microbial community succession of carrion is rapid after death without the biotic constraints of host immunology and physiological function (Pechal et al. 2014b, Metcalf et al. 2016), which determines the taxonomic and functional changes of the microbiota of the necrobiome through decomposition (Latter and Cragg 1967, Baldy et al. 1995, Crippen et al. 2015).

In aquatic leaf litter decomposition studies in streams, microbial community structural and functional succession is related to the leaf litter species and quality (Witkamp 1966, Gessner and Chauvet 1994), similar to other forms of necromass like crayfish (*Procambarus versutus* [Hagan]) molted exoskeletons (Aumen 1980), particulate aggregates (Grossart and Simon 1998), lake zooplankton (Tang et al. 2010), and oceanic phytoplankton (Fukami et al. 1985) and zooplankton (Tang et al. 2006) that harbor complex microbial dynamics that change with water chemistry, depth, and system circulation (Karl et al. 1988). While difficult to study, whale and other cetacean carcasses that sink to the oceanic abyss attract a high diversity of vertebrate and invertebrate scavengers (Allison et al. 1991, Jones et al. 1998, Smith and Baco 2003) and also change the microbial ecology of the local habitat in a way that is dominated by chemoautotrophic communities (Bennett et al. 1994) in a network of species interactions (Smith et al. 1998). The microbial community changes associated with the death and deep sea decomposition of whale carcasses has not, to our knowledge, been studied, but may follow successional trajectories similar to those reported for other aquatic organisms (Preiswerk et al. 2018).

Microbial succession facilitates the proliferation of existing saprophytic taxa of the once living host through the secretion of enzymes and other compounds used to convert the newly available organic matter for assimilation. The microbial ecology of decomposing necromass is likely substantially different between plant and animal forms in terrestrial and aquatic ecosystems; however, there have been no comparative studies to directly evaluate microbial succession differences of plant and animal decomposition in either terrestrial or aquatic habitats. When one descriptively compares microbial succession of plant detritus to carrion, there are interesting, and potentially functionally important, differences. For instance, the taxon richness and diversity of microbial communities were shown to increase over decomposition for beech leaves, with predominant phyla not including the Firmicutes (Purahong et al. 2016); whereas for carrion, Firmicutes often make up a significant proportion of the communities and become dominant late in

decomposition when taxon richness and diversity are lowest (Pechal et al. 2014b). Interestingly, the microbial communities of decomposing fungal mycelia in soil show more similar characteristics to carrion than to leaf litter on soil, with Proteobacteria being most dominant early and being replaced by Firmicutes later in decomposition (Brabcová et al. 2016). The microbes are inherently a part of the living organism and part of the initial communities present for decomposition are highly variable depending on the host species, health, habitat, and ecological interactions (Oh et al. 2014, Pechal et al. 2014b, Junker and Keller 2015, Metcalf et al. 2016, Pechal and Benbow 2016). Using a planktonic crustacean (*Daphnia magna*), Preiswerk et al. (2018) followed microbial communities of the living host through initial death and subsequent decomposition, reporting that the communities were highly dynamic and revealed opportunistic microbes that could exploit the host even before death. Thus, the community assembly dynamics of necromass is likely dependent on host condition and interactions with the abiotic environment and other organisms, populations, and communities.

The soil environment and the microbial communities it harbors are intimately associated with the decomposition of plant and animal necromass. When considering plant necromass, decomposition has often been thought to be a product of three hierarchically organized, interacting factors: climate, substrate quality, and the biota (Swift et al. 1979). Of these factors, climate has been assumed to be the driving force behind rates of decomposition at broad spatial scales, whereas litter quality, and to a more minor degree, the biota, play a more important role at finer spatial scales. However, such assumptions have recently been called into question (Bradford et al. 2016). For instance, the decomposition rate of woody debris is largely independent of climate and may actually be driven by its proximity to woody debris previously colonized by wood-decay fungi (Bradford et al. 2014). This interpretation suggests that spatial proximity of decomposer organisms may be a major driver of decomposition across a landscape (Ettema and Wardle 2002).

The microbial communities in the soil and associated with the rhizosphere that decompose leaf litter also play a more pronounced role. One such phenomenon is the occurrence of "home-field advantage" (HFA), whereby decomposer communities sharing a common history with a particular resource often decompose that resource at a greater than expected rate (Gholz et al. 2000). Such a phenomenon has been found when examining the interaction between climate and microbial communities (Strickland et al. 2015, Averill et al. 2016). Although HFA has been observed across a variety of different soil decomposer communities (Ayres et al. 2009, Strickland et al. 2009a), it has been found absent in others (St John et al. 2011, Bachega et al. 2016). One explanation for this divergence is HFA only accounts for adaptation to a particular organic matter resource and does not account

for the fact that some decomposer microbial communities simply decompose an array of necromass types more rapidly due to greater functional breadth (Keiser et al. 2014). That is, some microbial decomposer communities have a greater "ability" to decompose a wide range of litter substrates than do others because they have been historically exposed to chemically complex litter species. Understanding how these two metrics of microbial function drive patterns of necromass decomposition across a landscape, and how they relate to microbial community characteristics, may prove informative to predictions of decomposition rates associated with shifts in plant species or changes in necromass quality (Keiser et al. 2013, Austin et al. 2014, Martiny et al. 2017). Additionally, this HFA and "ability" framework suggests that the function of soil microbial communities is not just a product of the current input of necromass but that it may also be influenced by past inputs as well.

Adding to the complex interactions between soil microbial communities, climate, and necromass quality is the inclusion of the broader soil community in our understanding of decomposition. Soil arthropods are well known for their ability to fragment litter increasing the surface area available for microbial colonization and thereby increasing litter quality as it passes through the invertebrates' gut (Seastedt 1984). Yet there is a growing awareness that trophic interactions within the soil community may also drive the rate and efficiency of decomposition (Buchkowski 2016). For example, increased soil nitrogen can lead to greater wood decaying fungal biomass and extracellular enzyme activity in the absence of a fungivore, but the presence of a fungivore may moderate fungal biomass and wood decay rates (Crowther et al. 2015). More complex trophic cascades have also been observed, such as the removal of predatory microarthropods, which led to an increase in microbivorous nematodes and a subsequent increase in microbial biomass (Santos et al. 1981). Such examples indicate that top-down drivers may play an important role in mediating decomposition (Buchkowski 2016, Hawlena and Zaguri 2016) across a variety of necromass types. The relative strengths of top-down compared to bottom-up constraints on necromass decomposition may vary depending on interacting abiotic factors and climate change (Crowther et al. 2015).

Invertebrates of the necrobiome

Invertebrates play a key role in decomposition. For vertebrate carrion, numerous studies have examined the role of arthropods associated with decomposition (Early and Goff 1986, Anderson 2000, Bharti and Singh 2003, Matuszewski et al. 2011, Michaud et al. 2015), and identified a relatively predictable community succession of this group (Payne 1965), which is often used in forensics (Byrd and Castner 2009). Early work on arthropod communities associated with carrion identified key taxa and their roles in decomposition (Fuller 1934, Bornemissza

1957). Later work on this topic examined arthropod communities associated with decomposing swine in a range of contrasting circumstances, including being buried (Payne et al. 1968), on the soil surface (Payne 1965), or submerged in water (Payne and King 1972). A key outcome of this work was the recognition of the important role arthropods play in returning nutrients to the surrounding ecosystem. Preventing arthropod colonization can result in a significant reduction in the rate of biomass removal from animal carcasses (Payne 1965) and can change the community succession of both microbes and necrophagous insects (Pechal et al. 2013, 2014a). Additional studies have addressed other theoretical aspects of arthropod community responses to carrion resource pulses (Bilby et al. 1996, Yang 2004) or mass mortality events (Fey et al. 2015).

Research has also explored species interactions among carrion arthropods ranging from competition (Goodbrod and Goff 1990), niche partitioning (Denno and Cothran 1975), predator–prey interactions (Brundage et al. 2014), and trophic cascades responsible for variability in succession trajectories (Pechal et al. 2014a). The understanding of carrion arthropods has been facilitated by knowledge of the multiple and distinct functional roles of different taxa at carcasses (Braack 1987). For example, flies (e.g., Diptera: Calliphoridae, Sarcophagidae) are the primary arthropods responsible for consuming soft tissues of vertebrate carrion and thus are traditionally recognized as saprophages (Merritt and De Jong 2015). Certain beetles (Coleoptera) including some rove beetle species (Staphylinidae; Matuszewski et al. 2008), carrion beetles (Silphidae; Trumbo 1990, Trumbo et al. 2016), and skin/hide beetles (Dermestidae, Trogidae; Kulshrestha and Satpathy 2001, Barton et al. 2017) are also saprophagous. Other important functional groups include parasitoid flies (e.g., Diptera: Tachinidae) or wasps (e.g., Hymenoptera: Braconidae; Cammack et al. 2010) and predatory beetles (e.g., Coleoptera: Staphylinidae) and ants (Hymenoptera: Formicidae; Flores et al. 2014, Barton and Evans 2017). Often overlooked arthropods found at vertebrate carrion are those species located in the soil (Bornemissza 1957) or in aquatic environments (Tomberlin and Adler 1998, Merritt and Wallace 2010). In many instances, these arthropods rely on the resource directly as habitat or as a nutritional resource (e.g., tissue in a stream or lake, or in the case of soil, fungi, or liquids seeping into the soil). Research exploring soil or aquatic associations is limited compared with studies in above ground terrestrial environments. The ecology and evolution of dung beetles has been described and tested in detail and demonstrates close evolutionary ties of some invertebrates and necromass (Hanski and Cambefort 1991, Nichols et al. 2008).

Extremely diverse assemblages of invertebrates are associated with decomposing plant material. Approximately 20–30% of all forest insect species, for example, are directly or indirectly dependent on dying or dead wood (Stokland et al. 2012). Included among these are a wide range of phloem or wood feeders (e.g., termites, beetles, wood wasps, etc.), fungus feeders (e.g., beetles, flies, true bugs, etc.), and a variety of predators (Stokland et al. 2012). There is very little overlap known between the invertebrate assemblages involved in the decomposition of animal and plant necromass, as well as between different forms of plant matter (e.g., leaf litter vs. wood; Ferro et al. 2012).

Among macroinvertebrates, earthworms and termites have by far the strongest direct accelerative effects on plant biomass decomposition (Lavelle et al. 1997, Bignell and Eggleton 2000). The importance of earthworms as decomposers was illustrated by the dramatic loss of leaf litter depth following their introduction into formerly earthworm-free (due to glaciation) forests (Addison 2009). Termites are the major consumers of plant debris in soil throughout the tropics and subtropics, perhaps even exceeding fungi in importance in some areas (Liu et al. 2015, Ulyshen 2016), with the different species feeding preferentially on wood, leaf litter, humus, or soil (Donovan et al. 2001). Invertebrates consuming decaying plant material rely heavily upon microbes, which provide a variety of benefits including digesting and softening the material, neutralizing allelopathic substances, and improving nutritional quality in terrestrial and aquatic habitats (Cummins et al. 1973, Swift and Boddy 1984, Webster and Benfield 1986). Microbial biomass is itself quite nutritious relative to most forms of dead plant matter and contributes greatly to the diets of litter- or wood-feeding invertebrates, many of which are essentially fungivorous (Tanahashi et al. 2009, Mishima et al. 2016). Predators are a large proportion of the invertebrate members of the necrobiome (e.g., over one-third of saproxylic beetle species in Germany [Wende et al. 2017]) and exert strong controls on necrophagous populations.

Vertebrates of the necrobiome

No vertebrates, to our knowledge, are known to be specialist consumers of decomposing plant material but many species interact in important ways within the necrobiome of plant necromass. Many birds (e.g., woodpeckers) and mammals (e.g., aardvarks, armadillos, anteaters, echidnas, bears), for instance, are specialist or opportunistic predators of wood-feeding insects such as beetle larvae or termites. The fragmentation of plant matter caused by foraging vertebrates is assumed to have strong indirect effects on decay rates (Ulyshen 2016) but this remains untested. By contrast, vertebrates are known to be major consumers of carrion and are thus direct participants in the decomposition process in addition to any indirect effects they may have as fragmenters (DeVault et al. 2003).

Vertebrates consuming carrion are commonly classified into two categories: obligate scavengers rely entirely on carrion to meet their food requirements, whereas facultative scavengers are active predators or foragers, as well as scavengers (DeVault et al. 2003). In marine systems, there are some deep-water fish that might also be categorized

as obligate scavengers (Smith and Baco 2003). The only obligate vertebrate scavengers in terrestrial systems are Old World and New World vultures (families Accipitridae and Cathartidae, respectively). Vultures have evolved several adaptations that allow for dependence on carrion, which is often an ephemeral and unpredictable food source. First and foremost, obligate scavengers (i.e., vultures) have large wing spans and other physiological mechanisms that allow them to move quickly and efficiently to search vast areas for carrion (Ruxton and Houston 2004, Shivik 2006). Vultures also have well-developed vision, and in some cases olfactory capabilities (e.g., turkey vulture, *Cathartes aura*), which allow them to find carcasses over large distances (Houston 1979, DeVault et al. 2003). Due to microbial decomposition, carrion can contain high levels of toxic compounds and thus vultures have evolved physiological adaptations in their gut that allow them to consume large volumes of these toxins (Houston and Cooper 1975, Roggenbuck et al. 2014). As a group, vultures are relatively large-bodied birds and can withstand several days without food (Ruxton and Houston 2004). The amount of biomass processed by vultures and other vertebrate scavengers varies across ecosystems (Pereira et al. 2014), but historically has been greatly underestimated (DeVault et al. 2003, Wilson and Wolkovich 2011). In one example, an estimated 70% of large ungulates in the Serengeti die from causes other than predation and become available to scavengers. Thus, collectively Serengeti vultures likely consume more biomass than all carnivorous mammals combined (Houston 1979), suggesting a large scale importance of carrion necromass in ecosystem structure and function.

Due to their reliance on carrion, populations of obligate scavengers are inextricably linked to the availability and distribution of carrion on the landscape (Kelly et al. 2007). For some facultative scavengers the availability of carrion can influence local abundance, species distributions, or growth rates, especially in ecosystems with limited food resources (Fuglei et al. 2003, Wilmers et al. 2003, Drazen et al. 2012). For example, local Arctic fox (*Alopex lagopus*) populations in Norway decreased markedly following a decline in reindeer (*Rangifer tarandus platyrhynchus*) carcasses (Fuglei et al. 2003). In Yellowstone National Park, USA, populations of facultative scavengers have benefited from the reintroduction of grey wolves (*Canis lupus*), which provide a more stable subsidy of ungulate carrion (Wilmers et al. 2003). Such effects have also been reported in aquatic ecosystems, where the abundance and distribution of deep-water fish may be modulated by carrion availability (Drazen et al. 2012).

Carrion use by vertebrate scavengers is mediated by a complex suite of biotic and abiotic factors (DeVault et al. 2003, Selva et al. 2005, Moleón et al. 2015, Turner et al. 2017). As a result, use of carrion can also vary extensively within a vertebrate species. From a temporal perspective, variability in food availability and quality can be a key factor and can be a product of intra- and inter-kingdom competition (Allen et al. 2014, Beasley et al. 2015). These forms of competition demonstrate some of the ways that very different taxonomic components of the necrobiome interact to affect decomposition. For example, the activity of invertebrates and microbes is influenced by temperature, and that means that invertebrates and microbes are more active during warmer weather and will more rapidly decompose or render carcasses toxic or unpalatable for vertebrates (Janzen 1977, Burkepile et al. 2006). Consequently, vertebrate scavengers are typically most successful when temperatures are cooler and decomposition is slowed (DeVault et al. 2004a, Selva et al. 2005, Parmenter and MacMahon 2009). However, in some areas, the presence of an abundant and efficient vertebrate scavenger species can shift the balance toward vertebrates, even in warm weather (Houston 1986, DeVault et al. 2011). Competition for carrion resources also differs across habitat types (Beasley et al. 2015, Turner et al. 2017), although such differences likely reflect the composition of local vertebrate communities (DeVault et al. 2004a) and microclimates (Parmenter and MacMahon 2009).

Collectively, obligate and facultative scavengers provide a number of critical ecosystem services through the removal of animal necromass from landscapes (Moleón et al. 2014, DeVault et al. 2016). Intact scavenging communities (especially the presence of vultures) may reduce risks of disease transmission among mammals due to rapid removal of carcasses from ecosystems (Jennelle et al. 2009, Ogada et al. 2012, Hill et al. 2018). There is a clear role of vertebrates in the decomposition of carrion and placing them in the broader necrobiome framework highlights their links with other taxonomic groups (i.e., insects and microbes) and important environmental moderators of decomposition and overall ecosystem structure and function.

Symbioses of the necrobiome

Although symbioses between invertebrates and microbes are common within necrobiomes, the nature of these interactions differs greatly between decomposers associated with autotrophically or heterotrophically derived biomass. Due to the strength of lignocellulose, dead wood is among the most recalcitrant forms of plant matter and is also characterized by some of the highest C:N ratios of any organic material (Fig. 3). Although endogenous cellulases are known from some termites (Blattodea) and may play a particularly important role in the metabolism of Termitidae, which lack the protists of "lower termites" (Lo et al. 2011), wood-feeding insects are mostly unable to digest lignocellulose without the enzymes produced by various endo- or ecto-symbiotic microorganisms. Endo-symbionts include a wide range of gut-dwelling bacteria, archaea, and eukarya (e.g., yeasts and protists) that have been the subjects of intense study in both termites (O'Brien and Slaytor 1982, Brune 2014) and various beetle species (Reid et al. 2011, Urbina et al. 2013).

CONCEPTS & SYNTHESIS

In addition to digestion, another important function performed by prokaryotes within the guts or salivary glands of many wood-feeding arthropods is nitrogen fixation, which often provides much of the nitrogen required by these organisms to complete development (Ulyshen 2015). Ecto-symbioses are common between insects and fungi associated with decomposing wood. Ambrosia beetles, for example, cultivate and consume symbiotic fungi within galleries these insects create in dead wood. These insect–fungi associations have repeatedly evolved within scolytine and platypodine Curculionidae and also exist in other beetle families, such as Lymexylidae and Erotylidae (Farrell et al. 2001, Toki et al. 2012). The bodies of these insects possess special storage structures, called mycangia, within which their fungal symbionts are transported. Mycangia also exist in wood-feeding insects that are not technically ambrosia beetles. For example, female stag beetles (Lucanidae) possess mycangia near the ends of their abdomens that contain xylose-fermenting yeasts, which are presumably added to oviposition sites to benefit larval development (Tanahashi et al. 2010). Some of the most effective forms of symbioses between insects and fungi are exhibited by leaf-cutting ants and macrotermitine termites, both of which cultivate fungal gardens within their nests to perform the digestion of plant material (Nobre et al. 2011). Macrotermitines are thought to be among the most efficient wood-consuming insects due to their symbioses with the fungi *Termitomyces* (Basidiomycetes: Lyophyllaceae), which both allows them to process wood more quickly and increases assimilation efficiency (Schuurman 2005, Brune and Ohkuma 2011). Other functions provided by endo- and ecto-symbionts of arthropods associated with decomposing plant material include detoxification of plant secondary compounds (Dowd 1992), defensive mutualism (Chouvenc et al. 2013), and protection from pathogens (Peterson and Scharf 2016).

Whereas symbioses within plant-based necrobiomes largely stem from the recalcitrance and nutrient deficiency of dead plant matter, those within animal-based necrobiomes appear to have arisen largely in response to intense competition with other organisms as well as threats from pathogens. Necrobiome community interactions may follow a gradient of resource quality where the most labile forms of necromass facilitate competition and the most recalcitrant forms support symbioses (Janzen 1977). Microbial competition has been demonstrated to have strong negative effects on the reproductive success of some carrion-feeding insects (Rozen et al. 2008). Although carrion-feeding insects produce a variety of antimicrobial peptides and lysozymes to minimize competition from bacteria (Jordan et al. 2015), they also harbor, within their guts, diverse and unique microbial assemblages (Kaltenpoth and Steiger 2014). The exact functions provided by these microbes remain poorly understood but reducing competition from free-living carrion microbes and other carrion-feeding animals, detoxification, and providing protection from pathogens

are several potential benefits (Kaltenpoth and Steiger 2014, Trumbo et al. 2016). Adult burying beetles, for instance, are known to transmit gut bacteria to their offspring both directly through regurgitation and anal secretions applied during carcass preparation (Wang and Rozen 2017). Although the secretions produced by burying beetles have antimicrobial properties, free-living microbes appear to be reduced in favor of microbes found in the guts of these insects (Duarte et al. 2018). Rather than reducing competition from other microbes, the antimicrobial secretions produced by *Nicrophorus* may serve primarily to help conceal carcasses from competitor scavengers by suppressing the bacterial production of olfactory cues (Trumbo et al. 2016). While research in both plant and animal necromass decomposition has shown many examples of symbioses and cross-domain interactions, including the well-known symbioses of ruminant digestion of plant necromass (Hungate 1966), there are likely many more to be discovered.

Abiotic factors and the habitat template

Decomposition and the necrobiome constituents are constrained by abiotic factors defined by the surrounding habitat or ecosystem. Terrestrial, aquatic, and human-modified habitats each differ in their communities and climate, and this affects the rate and progression of decomposition and the species diversity that uses necromass (Beasley et al. 2012). Future studies should consider how changes in abiotic factors described below, in addition to extreme weather events, ocean acidification, and rising annual global temperatures could alter detritus availability, necrobiome dynamics, and ultimately decomposition processes in ecosystems.

Although many decomposition studies have occurred on land, the majority of Earth's surface is composed of aquatic habitat. Aquatic habitats include freshwater (e.g., streams, ponds, lakes, wetlands), marine (e.g., ocean), and brackish (e.g., estuaries) environments. The inherent physiochemical properties unique to these aquatic habitat types can substantially alter decomposition through direct or indirect abiotic interactions that constrain necrophagous physiology or mechanical ability to breakdown organic matter. Further, depending on where a resource is located within the water column, abiotic factors such as temperature, oxygen availability, carbon dioxide levels, ion concentrations, turbidity, pressure, salinity, pH, and flow dynamics will impact the rate and taphonomic changes of decomposition and determine the biodiversity of consumers that may use the decomposing organic material (Hattenschwiler et al. 2005, Wallace 2015). For example, swine carcasses placed in the deep sea fail to undergo bloat during the decomposition process at these depths because of the increased pressure within the environment (Anderson and Bell 2016). Woody debris and leaf litter in aquatic habitats, primarily in streams, have additional factors to consider that impact the abiotic conditions and ultimately the decomposition process. These include, but are not

limited to, where the wood is located within the stream (e.g., submersion, buried in the substrate, suspended); the morphology of the streambed (e.g., sand or silt, rock size); and hydrology (e.g., season flooding and/or spate events; Scherer 2004, Ruiz-Villanueva et al. 2016).

Terrestrial habitats can be separated into broad biomes: tundra, boreal forest, temperate forest, desert, grassland, and tropical rain forest, with the abiotic factors of temperature, humidity, wind, solar radiation, and exposure substantially altering decomposition (Benbow et al. 2015a). These abiotic factors can further interact with landscape configuration and vegetation within each ecosystem type (García-Palacios et al. 2013). Soil conditions specific to a habitat can alter decomposition dynamics of plants and animals due to direct and indirect associations with soil nutrients, pH, salinity, pollution or other contaminants, temperature, and moisture content (Refsnider and Janzen 2010). Further, landscape features, such as land use and cover, connectivity, and complexity can mediate consumer attraction and use of necromass resources. For example, habitats with increased biodiversity, such as tropical rainforests, have an increased species pool that can utilize a resource during decomposition when compared to habitats with slightly decreased complexity, such as an African tropical woodland (Cornaby 1974, Braack 1987).

The final category of ecosystems, which may not be as apparent as the previous two groups, is anthropogenic-associated ecosystems. These habitats are comprised of human built (e.g., residential structures) or modified areas (e.g., disturbed or change habitats) that impact the decomposition of organic material and biodiversity of the necrobiome. Specifically, modification of ecosystems often leads to habitat loss and fragmentation resulting from human development (e.g., urbanization, deforestation, and monoculture farming). Habitat fragmentation typically elicits negative impacts on biodiversity (MacArthur and Wilson 1967). A recent meta-review, however, revealed approximately three-quarters of studies showed some measures of positive response by communities affected by habitat fragmentation (Fahrig 2017). Overall, the impact of human-modification to decomposition and decomposer communities is underexplored and poorly understood.

Necrobiome Ecological Functions

A key feature of our expanded necrobiome concept is the broad structural and functional template it provides for better understanding the range of similarities and differences in decomposer communities found associated with plant and animal detritus. Volatile organic compound (VOC) emissions result from tissue decomposition and microbial metabolism and are an important mechanism for the attraction of exogenous macro-saprotrophs, such as blow flies, bark beetles, and nematodes (see Table 1), from the contiguous substrate (e.g., soil) and the surrounding local habitat and ecosystem (Ma et al. 2012, Ulyshen 2016). The types of VOCs produced are

determined by necromass composition, quality, and rate of decay; and they are known to affect the recruitment of exogenous macro-saprotrophs (i.e., invertebrate decomposers), in time frames ranging from minutes to years after death (Mądra et al. 2015, Ulyshen 2016). In leaf litter decomposition, microbial communities are known to markedly contribute to the production of associated VOC profiles (Gray et al. 2010). Ultimately, decomposition is achieved by species that directly consume necromass or produce the enzymes that catabolize compounds and degrade dead tissues. However, members of the necrobiome also affect decomposition through physical alterations to the necromass, as well as intra- and interspecific species interactions that generate complex interdependencies among organisms. Among the latter, interactions between invertebrates and microbes are particularly important. We describe below major functions performed by community members of the necrobiome that both directly and indirectly affect decomposition and compare and contrast functions occurring at plant and animal necromass.

Digestion

Many organisms can perform the primary function of digestion with respect to relatively labile animal tissues. The primary digesters at animal necromass are specialist carrion flies (Payne 1965), although there can be minor contributions from other insect groups, such as beetles or ants (Barton and Evans 2017). Vertebrates should also be considered digesters as they will consume entire carcasses before invertebrates are able to proliferate and participate in this function (DeVault et al. 2003). For plant necromass, wood-feeding invertebrate symbionts and saprophytic fungi and microbial communities in the stomachs of ruminant mammals (Hungate 1966) are capable of completely degrading the lignocellulose of plant cell walls to perform a digestion function (Swift et al. 1979). Digestion by saprophytic fungi and microbes is performed via the production of extra-cellular enzymes in ruminants (Refsnider and Janzen 2010) and is an external process rather than internal as for insects and vertebrates.

Fragmentation/penetration

Physical alterations brought about by animals that act to fragment or tunnel into dead material can strongly affect decomposition. The activities of carrion-feeding vertebrate scavengers and vertebrates foraging for insects in dead wood act to fragment large necromass resources. Fragments decompose more quickly than intact pieces due to increased surface area and coverage of microbial biofilms, as well as improved aeration (e.g., Boddy 1983). Penetration of the outer protective layers of dead animals and plants (e.g., skin or bark) is another important physical alteration brought about by animal activity, which facilitates colonization by microbes and other organisms (Connell and Slatyer 1977, Mann et al. 1990).

TABLE 1. Decomposer components and characteristics of heterotrophically and autotrophically derived necromass decomposition with representative studies for each component.

Component/characteristic	Heterotrophically derived biomass (invertebrate and vertebrate animals)	Autotrophically derived biomass (plant leaves and wood and algal detritus)
Communities		
Endonecrotic microbial communities	Can et al. (2014), Hyde et al. (2015), Javan et al. (2016)	Arnold et al. (2000), Wei et al. (2009), Song et al. (2017)
Epinecrotic microbial communities	Burkepile et al. (2006), Pechal et al. (2013, 2014b), Metcalf et al. (2016)	Swift and Boddy (1984), Arnold et al. (2000), Persson et al. (2009), Vořísková and Baldrian (2013)
Macroinvertebrate-saprotrophs	blow flies (e.g., Diptera: Calliphoridae, Sarcophagidae) and Beetles (e.g., Coleoptera: Staphylinidae and Silphidae): Fuller (1934), Chapman and Sankey (1955), Bornemissza (1957), Payne (1965), Greenberg (1971a, b), Lewis and Benbow (2011)	Wood-boring and detrital insects (e.g., Coleoptera: Curculionidae): Hickin (1963), Wallace et al. (1997), Haila and Niemelä (1999), Lieutier et al. (2004), Hattenschwiler et al. (2005)
Vertebrate-saprotrophs	DeVault et al. (2003), Selva et al. (2005), Wilson and Wolkovich (2011), Turner et al. (2017)	Nelson et al. (1999), Rode et al. (2003), Rothman et al. (2006)
Soil/habitat communities	Lauber et al. (2014), Carter et al. (2015), Finley et al. (2016)	Singh and Gupta (1977), Zak et al. (2003), Hawlena et al. (2012)
Taxa and element translocation and dispersal		
Spatial scale context		
Localized (0.1–100 m)	Payne (1965), Moreau et al. (2015)	Lussenhop (1992), Strickland et al. (2009a)
Diffuse (100–1,000 m)	Houston (1974), Holland et al. (2017)	Polis and Hurd (1996), Jiménez et al. (2017)
Temporal scale context		
Ecologically short (minutes to days)	DeVault et al. (2004b), Farwig et al. (2014), Smith et al. (2017)	leaching rates (Nykvist 1959a, b, 1963, Cummins et al. 1973, Kuiters and Sarink 1986)
Ecologically long (weeks to years)	Danell et al. (2002), Barton et al. (2016)	Swift et al. (1979), Handa et al. (2014)
Geological (decades to centuries)	Macdonald (1992), Sun et al. (2000), Dedouit et al. (2010), Kvavadze and Kakhiani (2010), Müller et al. (2011), Boeskorov et al. (2014)	Van de Geel (1978), Middeldorp (1986), Barthelmes et al. (2006), Kvavadze and Kakhiani (2010), Ronkainen et al. (2013)

Notes: Microbial communities include prokaryotes and microscopic protists, fungi, and eukaryotes. Temporal scales range from ecologically relevant scales related to the life history traits of decomposer species to plant and animal biomass protected from decomposer species over geological time scales of decades or centuries (e.g., peat bog mummies).

In animal necromass, this activity is performed by larger scavenging animals (e.g., crows, vultures, and hyenas) that pick at parts of a carcass and enable entry by insects and microbes. In decomposing logs, insects that create holes through bark and tunnel into the heartwood (Leach et al. 1937) play a particularly important role in facilitating the establishment of rot fungi. Some vertebrates, such as aardvarks (*Orycteropus afer*) in Africa or echidnas (*Tachyglossus aculeatus*) in Australia, also play a role in the fragmentation of logs when searching for ant or termite nests. Although there are many insect species that perform a fragmentation or penetration functional role in terrestrial habitats, there are fewer major groups of xylophagous macroinvertebrates in freshwater systems (Anderson et al. 1978), contributing to the slow rates of wood decomposition in these habitats. Certain molluscs perform this function in marine environments and can cause a great deal of damage to wooden boats and pilings (Nair and Saraswathy 1971). Another consequence of fragmentation can be changes in microbial community composition. The production of fine woody particulate material by many wood-boring insects is thought to favor bacterial communities (Swift and Boddy 1984, Van der Wal et al. 2007), including free-living N-fixers (Ausmus 1977).

Nutrient and microbe transport and dispersal

Organisms within the necrobiome play a role in moving nutrients away from decaying necromass through both passive and biological means (Fig. 1). The microbes and elements of decaying organic matter can move by direct translocation of microbial cells or along elemental concentration gradients within the biomass and into, onto, and within contiguous substrata. This transfer is perhaps best visualized by the process of purging, whereby fluids and gases from a decaying animal escape into soil or the atmosphere. Nutrients and particles also are dispersed by mobile micro- (e.g., fungi, protists) or macro-saprotrophs (e.g., flies) that act as vectors of the organic matter, microbes, and elements. The dispersal of these materials can occur in multiple

ways: (1) trophic transfer where the microorganisms and elements are ingested but not assimilated, and then egested after saprotroph movement away from the necromass source; (2) trophic transfer where the microorganisms and elements are ingested and assimilated, and released after saprotroph movement and then death either through predation or decomposition; (3) external attachment to the saprotroph by physical or chemical means during movement; and (4) by being aerosolized or passively dispersed by winds, rainfall, water currents, or thermal energy (e.g., convection). Additional discussion is given below of how members of the necrobiome interact in networks to transport and disperse microbes and nutrients.

Detoxification

Non-structural secondary compounds are often present in heartwood and are known to be toxic to many microbial decomposers and insects (Käärik 1974). The abundance of these compounds can vary by as much as 50-fold among angiosperms and 20-fold among gymnosperms (Cornwell et al. 2009), and the variance is thought to be largely responsible for the differences in decay resistance observed among different wood species (Bultman and Southwell 1976). The protective effects of these and other extractives diminish over time (Bultman and Southwell 1976); however, bacteria, and fungi both play a part in neutralizing these potentially toxic compounds (Burnes et al. 2000, Dorado et al. 2000). Further, microbial symbionts of some insects associated with detritus provide detoxification function of plant secondary compounds (Dowd 1992). As far as we are aware, there are no analogous intrinsic toxins present associated with microbial communities of animal necromass that retard microbial or insect activity. However, a burying beetle, *Nicrophorus vespilloides* (Silphidae; Arce et al. 2012), produces antimicrobial secretions that compete with microbes on carrion. Overall, the detoxification pathways in plants suggest this function is primarily the activity of microbial components of the plant necrobiome. However, there are likely undiscovered analogous activities in animal necromass decomposition.

Predation

Predators are conspicuous and important members of the necrobiome. It is not uncommon for predators to be among the most species-rich guilds in dead wood (Hammond et al. 2001, Wende et al. 2017), as well as at carcasses (Barton and Evans 2017). Moreover, opportunistic predation by non-predatory invertebrates is commonplace in decomposing wood. Termites are known to feed on dead insect larvae and other invertebrate carcasses encountered while foraging in wood (Thorne and Kimsey 1983), which includes cannibalizing dead or injured nestmates (Wilson 1971). Many wood-boring beetle larvae are also known to prey on

other larvae encountered in dead wood (Soper and Olson 1963) and this probably relieves the limitations imposed by the low nutritional quality of wood.

For carrion, cannibalism among fly larvae may be an adaptation to intense competition rather than a nutritional requirement (e.g., the hairy maggot blow fly *Chyrsomya rufifacies* Macquart 1842; Baumgartner 1993). Most predatory beetles and ants at carcasses tend to be generalists and take advantage of the concentrated and abundant insects associated with carrion (Barton and Evans 2017). Some species of predatory insect may also opportunistically scavenge on carcass tissue, possibly due to the similar stoichiometric composition and easy switching between resources. The function of predators (and parasitoids, not discussed here) in decomposition is largely restricted to moderating the abundance of other decomposer organisms, and in most cases probably does not alter the rate or pattern of decomposition to any notable degree. Predatory ants, however, have been shown to dominate the insect community and retard rates of mass loss of both wood (Warren and Bradford 2012) and animal carcasses (Barton and Evans 2017). Indeed, Houston (1985) argued that ant communities in South America prolong carcass availability to vertebrates by feeding on dipteran larvae that otherwise would quickly consume the carcasses. Further, it is known that some invertebrate predators approach carrion specifically to prey on other organisms and not necessarily the necromass (Payne 1965).

Necrobiome Interactions and Networks

In addition to discussing the taxonomic and functional organization of the necrobiome, we expand the necrobiome concept to also consider the complex biotic and abiotic mechanisms of species and element (e.g., nutrients, carbon) translocation and dispersal from the decaying necromass into adjacent substrates, the local habitat, and ultimately into the larger ecosystem, as originally presented by Polis and Strong (1996). We argue that the decaying biomass holds a community of microbial species that often follow elemental movement into and throughout the environment, thus providing a way to track the dispersal of species, their genomes, metabolic diversity, and function after host death and through decomposition. While understudied, the dispersal of genetic and metabolic information into the surrounding environments (Preiswerk et al. 2018) is arguably a potentially transformative way to view decomposition as an ecosystem process through multiple disciplines and areas of scientific inquiry.

Many invertebrates act as vectors of microbial digesters from one resource to another. This transfer by insects can disperse gut symbionts as well as those that passively carry microbes on their bodies (Persson et al. 2009, Strid et al. 2014). Fungus-farming termites perform the reverse role, where dead plant particles are transported back to nests containing ecto-symbiotic

fungal gardens (Wood and Thomas 1989). Blow flies and house flies are known to carry and transmit pathogenic bacteria to and from decomposing organic matter (Greenberg and Bornsetein 1964, Greenberg et al. 1970, Greenberg 1973, Macovei and Zurek 2006, Nayduch 2017). A recent study by Weatherbee et al. (2017) showed that carrion-associated microbial taxa consumed by blow fly larvae are transferred into the gut of the larvae. Although it is not definitively known whether microbes are passed transstadially to adults in all species (Singh et al. 2015), evidence from adult flies suggests a high likelihood that some bacteria ingested from carrion are assimilated by larvae, persist into the adults, and then are dispersed into the landscape (Weatherbee et al. 2017).

In addition to vectoring microbes, many insects also carry other invertebrates from one ephemeral or isolated resource patch to another. Phoresy is common among invertebrates associated with dung and carrion (Krantz 1998), fungal fruiting structures (Fain and Ide 1976), and dead wood. Examples of saproxylic insects from which phoretic passengers have been recorded include bark beetles, click beetles, cerambycid beetles, passalid beetles, and parasitic wasps (Haack and Wilkinson 1986). As pointed out by Moser and Roton (1971), virtually all relatively large insects capable of long distance dispersal serve as hosts for one or more phoretic species. Many host species carry not just a single phoretic species but a whole community of passengers. For example, at least 18 species of mites are known to be phoretic on the bark beetle *Dendroctonus frontalis* (Coleoptera: Curculionidae) in the southeastern United States (Moser 1976). Although phoresy is often viewed as a form of commensalism where the phoretic species benefits and the host is unaffected, this is not always the case with reports of both negative (Lindquist 1969, Hodgkin et al. 2010) and positive impacts (Purrington and Drake 2008) on the host.

Interactions between decomposer organisms belonging to different kingdoms (or domains) are quite common and warrant separate attention. Recent evidence indicates that microscopic species interacting with higher organisms are playing a far greater role in regulating succession patterns (Ezenwa et al. 2012). Interkingdom interactions between plants and microbes are prevalent, and these interactions may also transect invertebrate communities. A specific example is with *Sphagnum* mosses. These plant assemblages dominate peatland bog ecosystems and form a unique and extreme habitat for microbes. This moss genus is well known for its preservative properties and slow rate of decomposition, occupies one-third of land on the planet, and stores more carbon than any other single genus of plant (Turetsky 2003). Highly acidic conditions along with low concentrations of nutrients, together with specialized leaf structures with high water content, lead to very specialized microbial colonization that is unique to *Sphagnum* species (Opelt et al. 2007). Furthermore, *Sphagnum* moss species

produce secondary metabolites, such as phenolics, terpenoids, and tannins, and accumulate carbohydrates, that influence microbial colonization and subsequently microbially mediated decomposition. These plant specific factors may facilitate peat accumulation through lowering of redox potential that leads to decreased microbial decomposition rates (Belyea 1996). Methanotropic bacteria within the bogs themselves are well documented with *Burkholderia* and *Serratia* to be among the most dominant bacteria colonizing *Sphagnum* plants (Juottonen et al. 2005). Very few fungi colonize the actual plants, as these hosts are known for their antifungal and antibacterial activity (Opelt et al. 2007). A recent study showed that bacterial isolates from two *Sphagnum* species had antagonistic activities against fungi, while also performing nitrogen fixation and lowering host plant ethylene levels (Knorr et al. 2015). Despite these documented antimicrobial properties, a relatively large number of fungal taxa have been identified on *S. fuscum* (Thormann et al. 2001). Thus, the overall functioning of peat bog ecosystems is heavily influenced by interkingdom interactions occurring among plants, bacteria, and fungi, as well as their associated chemicals associated with high volumes of necromass.

Microbes have evolved complex strategies for outcompeting one another for resources available within carrion. Although in the early stages of discovery, it is clear microbes associated with carrion play important roles in regulation of arthropod attraction, colonization, and utilization of the remains. Furthermore, recent evidence indicates within kingdom interactions (e.g., blow fly predator vs. blow fly prey) are partially governed by their associated microbiome in carrion (Crippen et al. 2015, Weatherbee et al. 2017) and other necromass decomposition networks (Purahong et al. 2016, Deveau et al. 2018). Some compounds serve as a mechanism of communication and group responses, better known as quorum sensing (Nealson and Hastings 1979), while others serve to disrupt communication. In both cases, these processes give a competitive advantage to the producer of these compounds by reducing competition with other microbes within the environment. For example, indole, a by-product of tryptophan degradation, is a key molecule used by *Escherichia coli* (gut microbe of many vertebrate species) as a quorum-sensing molecule (Kim and Park 2015) and is a bacterial taxon commonly associated with vertebrate carrion (Metcalf et al. 2016). In contrast, dimethyl disulphide (DMDS) is detected during the later stages of vertebrate decomposition (Forbes and Perrault 2014) and is a quorum-quenching molecule for many Gram-negative species. In both instances, these compounds regulate blow fly attraction (Ma et al. 2012, Tomberlin et al. 2012b). In addition to being an attractant, the response of blow flies to these compounds tends to be sex and physical state (e.g., gravid vs. nongravid) specific (Brundage et al. 2017).

The roles of microbial and invertebrate activity during animal necromass decomposition also scales to

vertebrates and can affect vertebrate scavenger interactions (DeVault et al. 2003, Beasley et al. 2015). For instance, temperature is known to impact invertebrate and microbial activity (Vass 2001, Zhou and Byard 2011), and was later found to affect the percentage of consumption of small-mammal carcasses by vertebrate scavengers (DeVault et al. 2004a). Although the mechanism of this interaction has not been tested, microbial and invertebrate communities are known to affect the rate of decomposition (Simmons et al. 2010) and quality of the carcass (Payne et al. 1968, Pechal et al. 2013, 2014a), which likely influences the quality and quantity of these resources available to vertebrate scavengers. The reciprocal effect can be inferred from high vertebrate scavenging rates (DeVault et al. 2011) that eliminate these resources via consumption of fresh carcasses as they become available and therefore reducing persistence in the landscape (Jones et al. 2015). Additionally, there is some evidence that microbes of carcasses and vertebrate scavengers may have coevolved, as hyenas frequently feed on ungulate carcasses that have died from anthrax without showing disease characteristics (Villiers Pienaar 1969, Gasaway et al. 1991). There is precedent for evolved adaptations in avian scavengers for competing with carrion microbial communities (Houston 1974, Houston and Cooper 1975). These cross-kingdom scavenger interactions are important to ecosystems but are often overlooked aspects of the ecology of animal decomposition (Wilson and Wolkovich 2011); however, they constitute linkages that make up food webs, indirect predator–prey effects, and necrobiome community networks.

The biotic structure and interactions among necrobiome taxa inherently give rise to network structure that can be used to define the complex and dynamic nature of organic matter decomposition. Food webs are biotic networks of interacting organisms, energy, and nutrient flow and define communities and metacommunities. The complexity of food web networks has been studied in several systems (Polis and Strong 1996, Eklöf et al. 2013, Wende et al. 2017), and has been proposed as a useful tool for developing a systems approach to understanding ecosystems (Dunne et al. 2002). The necrobiome framework offers an opportunity to quantify a subset of overall ecosystem food web networks and test novel hypotheses related to the strength of direct and indirect interactions among species and trophic levels. Furthermore, the necrobiome approach affords the opportunity to test hypotheses and further theory with evolutionary importance of the decomposer communities, much like that argued for understanding the broader importance of scavenging in food web research (DeVault et al. 2003, Wilson and Wolkovich 2011). The complexity and stability of plant and animal necromass networks likely arises, in part, from the indirect (non-physical) interactions that involve evolved sensing, physiology and behavior associated with finding and consuming decomposing resources (Tomberlin et al. 2011) and direct interactions of the necrobiome.

SPATIAL AND TEMPORAL DIMENSIONS OF THE NECROBIOME

Dead wood and animal carcasses vary in size, spatial density, and temporal input and turnover, adding another layer to necrobiome dynamics. Succession and related theory (Box 1) is well documented for decomposer communities associated with plant and animal necromass (Refsnider and Janzen 2010). Yet, scaling up these localized processes and integrating them into the higher-level spatial and temporal dynamics occurring among multiple decomposer communities at ecosystem scales is a significant challenge. Indeed, very few studies have yet to document the large-scale dynamics of single sources of detritus (e.g., forest stand blow downs) beyond ontogeny-based death events of anadromous fishes (e.g., Pacific salmon, *Oncorhynchus* spp.), despite recent work demonstrating that large animal mass mortality events are increasing in both magnitude and frequency globally (Fey et al. 2015). Empirical studies of large-scale carrion effects include the mass emergence of cicadas (*Magicicada* spp.) in North American forests (Yang 2004), the annual spawning runs of salmon (e.g., *Oncorhynchus* spp.; Hocking and Reynolds 2011), and the mass drowning of wildebeest in the Mara River in Kenya (Subalusky et al. 2017). These studies have shown how substantial quantities of carrion can alter forest soil microbial communities (Yang 2004), change the biomass and composition of riparian plant communities (Hocking and Reynolds 2011), and subsidize 50% of the diet of fish communities (Subalusky et al. 2017). Such instances provide evidence of carrion and associated necrobiomes changing nutrient cycling in a way that alters ecosystem functioning. Examples of plant necromass altering ecosystems are more common, with litter fall and decomposition having critical role in the cycling of 100 megatonnes of carbon annually (Gessner et al. 2010). Plant litter is ubiquitous in vegetated ecosystems, and associated decomposer communities are similarly widespread (Refsnider and Janzen 2010). Similar to the spatially discrete dead trees and coarse woody debris, there are fewer instances of analogous, highly recalcitrant, structures of animal carcasses (e.g., whale bones) that provide focal points for the assemblages of distinct necrobiome communities over long (e.g., years to decades) temporal scales. However, the impact of such spatially and temporally unpredictable events on bottom-up or top-down processes are still not fully understood.

Across a landscape are many dead logs and carcasses of different sizes and decay stages, with each stage having a different necrobiome defined by its attendant species and their interactions. This variability emphasizes the *among*-necromass dynamics of multiple necrobiomes. Succession is well documented (see Box 1) and tells us that any single necrobiome exists only for a certain window of time (Table 1), which might range from hours to days for carcasses in warm conditions (Payne 1965, Barton and Evans 2017) or months to years for some large fallen trees (Weedon et al. 2009) or mummified animal necromass in habitats such as dry deserts or peat bogs

(Brothwell et al. 2002, Chapman 2015). Decomposer organisms searching for their next resource to continue their life cycle are therefore not only looking for another log or carcass, but also a specific decay stage, thus further emphasizing the rapid temporal turnover of the necrobiome *within* a necromass source. For specialist decomposers in the necrobiome, their existence is entirely dependent on resource continuity through time, with continuity also dependent on spatial proximity due to dispersal limitation. Thus, the implications of high-level *among*-necromass necrobiome dynamics become apparent across multiple scales in ways that include (1) the reproductive success and survival of individuals, and their subsequent dispersal and contribution to population genetics (Stokland et al. 2012); (2) competition among species, coexistence, and community diversity and heterogeneity; (3) the consumption and metabolic breakdown of necromass via microbes and saprophytes; and (4) dispersal of necromass energy, genomes, and elements through the environment as new living biomass.

There are gaps in our knowledge of ecosystem-scale responses to plant and animal necromass, and many fundamental questions remain. A framework that joins patch-scale phenomena with ecosystem-scale consequences is therefore needed to fully appreciate the cross-scale dynamics of the necrobiome. We synthesize in Fig. 4 previous work that has attempted to conceptualize
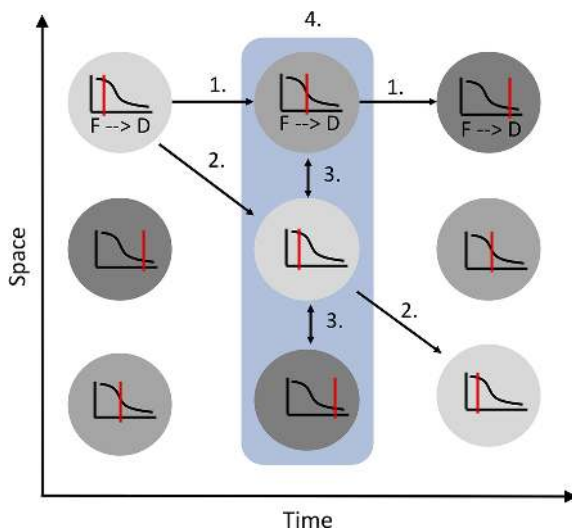
Fig. 4. The spatial and temporal dimensions of the necrobiome among multiple necromass patches introduce an additional level of dynamics important to understanding ecosystem-scale processes. (1) Each item of necromass decomposes from fresh (F) to dry (D), and the attendant necrobiome changes in diversity and composition through time. (2) This creates time windows for colonization and dispersal by specialist decomposers and their predators as they search for the next similar decay stage. (3) Multiple necromass resources occur at any one time and generate a range of decay states with different necrobiomes. (4) This creates a shifting spatial mosaic of necrobiome patches over time, each with unique levels of diversity, composition, and types of interactions and processes.

among-carcass dynamics (Barton et al. 2013a, Benbow et al. 2015b), but which also applies conceptually to leaf litter, dead trees, and course woody debris. We suggest that the spatial and temporal dimensions of the dynamic necrobiome are best conceptualized hierarchically, with community dynamics occurring spatially and temporally *within* necromass sources as well as spatially and temporally *among* multiple sources of necromass (Fig. 4).

BUILDING THEORY IN DECOMPOSITION ECOLOGY

The necrobiome framework illustrates the links and interactions among decomposer organisms associated with defined substrates, and the key interactions with each other and the environment over a range of spatial and temporal scales. For example, microbes and necrophagous insects interact on individual carcasses and come into direct contact with one another (Crippen et al. 2015). Similarly, phoretic mites interact directly with their insect hosts and carcasses, which provides focal points for their movement via necrophilous insects across landscapes (Perotti and Braig 2009). Yet these examples of direct contact that occur over relatively small spatial and temporal scales can have implications at much larger scales by altering metacommunity structure and the rate and pathway of nutrient and genome movement through ecosystems. The necrobiome allows for clearer conceptualization of the links between groups of species and their environmental context, and we believe this can help to develop empirical tests of ecological theory related to decomposition. For example, for many forms of necromass, especially large and recalcitrant forms, the decomposition process is characterized by a succession of species (see Box 1). Succession is, in part, guided by colonization history and priority effects as early colonizers can have facilitative or inhibitory effects on later colonizers (Connell and Slatyer 1977). In addition to direct interactions among decomposers coexisting at the same time and place, the indirect priority effects among species across time are known to be of great importance to the development of these communities as well as to their collective effects on decomposition. In Sweden, for example, Weslien et al. (2011) showed that colonization of Norway spruce (*Picea abies* L. Karst.) by two beetle species within one year of cutting influenced the occurrence of another beetle species a decade later in a way that was mediated through a species of wood-decaying fungi.

The examination of species traits can also benefit from the necrobiome concept by understanding what traits mediate key functions or processes. Greater general understanding of species assemblage and food web responses to decomposition is necessary to improve the transferability of findings across geographic regions with different sets of species, which is a source of variation among applied research, such as forensics, using these ecological concepts (Tomberlin et al. 2012a). For example, dispersal is a key trait that determines species ability

to search and colonize different forms of necromass (Tomberlin et al. 2011) but has not been widely examined among carrion-associated arthropods (Barton et al. 2013b). Additionally, the feeding traits of species are closely related to specialization and arrival dynamics (Barton and Evans 2017), can be associated with tissue quality (Ulyshen 2016), and drive competition and interactions among insects and microbial species (Burkepile et al. 2006). These complex interactions form ecological networks upon which ecosystem functions rest. There is a need for a unified ecological theory building upon the previous knowledge from plant and animal necromass across ecosystems to more comprehensively understand decomposition ecology.

IMPLICATIONS AND CONCLUSIONS

The proposed necrobiome framework provides a general template to conceptualize the structure and function of decomposer communities. A set of questions naturally arises from the necrobiome framework and its spatial and temporal dimensions. For example, what is the functional outcome for decomposition by adding or subtracting different biotic components of the necrobiome? What is the effect of altered interactions in the presence or absence of these biotic components and are the responses consistent among necromass types? Landscape consequences extend from these localized questions, such as, how does altered necrobiome structure and function lead to altered rates and pathways of genomic, element, and nutrient movement through ecosystems? Manipulative experiments have shown that excluding insects from carrion (Payne 1965, Pechal et al. 2014a) and plant matter (Heneghan et al. 1998, Wall et al. 2008, Ulyshen 2014, Stoklosa et al. 2015) resulted in changes to necromass loss rates. But what about experiments that change various functional components, or enhance fragmentation by insects, or manipulate the internal or external microbial communities, such as excluding detoxifying bacteria? Necromass varies along important gradients of nutrient quality, size, and digestibility, and decomposition progresses as a function of the attendant necrobiome and surrounding abiotic template. Clarity in our understanding of these controlling parameters means that future research on decomposition can soon be standardized across resource types. Future experimental studies that control for these parameters can then focus on manipulating key functional groups or interactions within the necrobiome to reveal the consequences for decomposition, food webs, and ecosystem services.

The necrobiome concept and the further development of decomposition theory have implications to disciplines ranging from ecosystem restoration to forensics. In restoration ecology, new comparative work could examine the effects of manipulation of plant and animal necromass to return key processes critical to decomposition and nutrient cycling and broader ecosystem-scale functioning. Using the necrobiome framework, functional

and biotic components can be identified that enhance or slow nutrient cycling, change community network stability, generate ecosystem heterogeneity, or add biodiversity per se. In the field of forensics, insects are the primary source of evidence used by practitioners for death cases requiring legal action. Although the dynamics of forensically important insects are rooted in ecological theory (e.g., community assembly, succession, priority effects, metacommunities, perturbation impacts, biodiversity, and patch dynamics; Benbow et al. 2015a), there must be an expansion of this basic knowledge and potential use to other constituents of the necrobiome (e.g., microbes). The necrobiome concept provides a strong conceptual basis to further both theoretical and empirical endeavors.

LITERATURE CITED

Addison, J. A. 2009. Distribution and impacts of invasive earthworms in Canadian forest ecosystems. Biological Invasions 11:59–79.

Alldredge, A. L., and M. W. Silver. 1988. Characteristics, dynamics and significance of marine snow. Progress in Oceanography 20:41–82.

Allen, M. L., L. M. Elbroch, C. C. Wilmers, and H. U. Wittmer. 2014. Trophic facilitation or limitation? Comparative effects of pumas and black bears on the scavenger community. PLoS ONE 9:e102257.

Allison, P. A., C. R. Smith, H. Kukert, J. W. Deming, and B. A. Bennett. 1991. Deep-water taphonomy of vertebrate carcasses: a whale skeleton in the bathyal Santa Catalina Basin. Paleobiology 17:78–89.

Anderson, G. S. 2000. Insect succession on carrion and its relationship to determining time since death. Pages 143–176 in J. H. Byrd and J. L. Castner, editors. Forensic entomology: the utility of arthropods in legal investigations. CRC Press, Boca Raton, Florida, USA.

Anderson, G. S., and L. S. Bell. 2016. Impact of marine submergence and season on faunal colonization and decomposition of pig carcasses in the Salish Sea. PLoS ONE 11:e0149107.

Anderson, N. H., J. R. Sedell, L. M. Roberts, and F. J. Triska. 1978. The role of aquatic invertebrates in processing of wood debris in coniferous forest streams. American Midland Naturalist 100:64–82.

Arce, A., P. Johnston, P. Smiseth, and D. Rozen. 2012. Mechanisms and fitness effects of antibacterial defences in a carrion beetle. Journal of Evolutionary Biology 25:930–937.

CONCEPTS & SYNTHESIS

Arnold, A. E., Z. Maynard, G. S. Gilbert, P. D. Coley, and T. A. Kursar. 2000. Are tropical fungal endophytes hyperdiverse? Ecology Letters 3:267–274.

Aumen, N. G. 1980. Microbial succession on a chitinous substrate in a woodland stream. Microbial Ecology 6:317–327.

Ausmus, B. S. 1977. Regulation of wood decomposition rates by arthropod and annelid populations. Ecological Bulletins (Stockholm) 25:180–192.

Austin, A. T., L. Vivanco, A. Gonzalez-Arzac, and L. I. Perez. 2014. There's no place like home? An exploration of the mechanisms behind plant litter–decomposer affinity in terrestrial ecosystems. New Phytologist 204:307–314.

Averill, C., B. G. Waring, and C. V. Hawkes. 2016. Historical precipitation predictably alters the shape and magnitude of microbial functional response to soil moisture. Global Change Biology 22:1957–1964.

Ayres, E., H. Steltzer, B. L. Simmons, R. T. Simpson, J. M. Steinweg, M. D. Wallenstein, N. Mellor, W. J. Parton, J. C. Moore, and D. H. Wall. 2009. Home-field advantage accelerates leaf litter decomposition in forests. Soil Biology and Biochemistry 41:606–610.

Bachega, L. R., J. P. Bouillet, M. D. C. Piccolo, L. Saint-Andre, J. M. Bouvet, Y. Nouvellon, J. L. D. Goncalves, A. Robin, and J. P. Laclau. 2016. Decomposition of *Eucalyptus grandis* and *Acacia mangium* leaves and fine roots in tropical conditions did not meet the Home Field Advantage hypothesis. Forest Ecology and Management 359:33–43.

Baldy, V., M. O. Gessner, and E. Chauvet. 1995. Bacteria, fungi and the breakdown of leaf litter in a large river. Oikos 74:93–102.

Barthelmes, A., A. Prager, and H. Joosten. 2006. Palaeoecological analysis of *Alnus* wood peats with special attention to non-pollen palynomorphs. Review of Palaeobotany and Palynology 141:33–51.

Barton, P. S. 2015. The role of carrion in ecosystems. Page 512 *in* M. E. Benbow, J. K. Tomberlin, and A. M. Tarone, editors. Carrion ecology, evolution, and their applications. CRC Press, Boca Raton, Florida, USA.

Barton, P. S., and M. J. Evans. 2017. Insect biodiversity meets ecosystem function: differential effects of habitat and insects on carrion mass loss. Ecological Entomology 42:364–374.

Barton, P. S., S. A. Cunningham, D. B. Lindenmayer, and A. D. Manning. 2013a. The role of carrion in maintaining biodiversity and ecological processes in terrestrial ecosystems. Oecologia 171:761–772.

Barton, P. S., S. A. Cunningham, B. C. T. Macdonald, S. McIntyre, D. B. Lindenmayer, and A. D. Manning. 2013b. Species traits predict assemblage dynamics at ephemeral resource patches created by carrion. PLoS ONE 8:e53961.

Barton, P. S., S. McIntyre, M. J. Evans, J. K. Bump, S. A. Cunningham, and A. D. Manning. 2016. Substantial long-term effects of carcass addition on soil and plants in a grassy eucalypt woodland. Ecosphere 7:e01537.

Barton, P. S., M. J. Evans, J. L. Pechal, and M. E. Benbow. 2017. Necrophilous insect dynamics at small vertebrate carrion in a temperate eucalypt woodland. Journal of Medical Entomology 54:964–973.

Baumgartner, D. L. 1993. Review of *Chrysomya rufifacies* (Diptera: Calliphoridae). Journal of Medical Entomology 30:338–352.

Beasley, J. C., Z. Olson, and T. DeVault. 2012. Carrion cycling in food webs: comparisons among terrestrial and marine ecosystems. Oikos 121:1021–1026.

Beasley, J. C., Z. H. Olson, and T. L. DeVault. 2015. Ecological role of vertebrate scavengers. Pages 107–127 *in* M. E. Benbow, J. K. Tomberlin, and A. M. Tarone, editors. Carrion ecology, evolution, and their applications. CRC Press, Boca Raton, Florida, USA.

Belyea, L. R. 1996. Separating the effects of litter quality and microenvironment on decomposition rates in a patterned peatland. Oikos 77:529–539.

Benbow, M. E., A. J. Lewis, J. K. Tomberlin, and J. L. Pechal. 2013. Seasonal necrophagous insect community assembly during vertebrate carrion decomposition. Journal of Medical Entomology 50:440–450.

Benbow, M. E., J. K. Tomberlin, and A. M. Tarone. 2015a. Carrion ecology, evolution, and their applications. CRC Press, Boca Raton, Florida, USA.

Benbow, M. E., J. L. Pechal, and R. M. Mohr. 2015b. Community and landscape ecology of carrion. Pages 151–185 *in* M. E. Benbow, J. K. Tomberlin, and A. M. Tarone, editors. Carrion ecology, evolution, and their applications. CRC Press, Boca Raton, Florida, USA.

Benbow, M. E., J. K. Tomberlin, and A. M. Tarone. 2015c. Introduction to carrion ecology, evolution, and their applications. Pages 3–12 *in* M. E. Benbow, J. K. Tomberlin, and A. M. Tarone, editors. Carrion ecology, evolution, and their applications. CRC Press, Boca Raton, Florida, USA.

Benke, A. C., and A. D. Huryn. 2006. Secondary production of macroinvertebrates. Pages 691–710 *in* F. R. Hauer and G. A. Lamberti, editors. Methods in stream ecology. Academic Press, New York, New York, USA.

Benke, A. C., C. A. S. Hall, C. P. Hawkins, R. H. Lowe-McConnell, J. A. Stanford, K. Suberkropp, and J. V. Ward. 1988. Bioenergetic considerations in the analysis of stream ecosystems. Journal of the North American Benthological Society 7:480–502.

Benke, A. C., A. D. Huryn, L. A. Smock, and J. B. Wallace. 1999. Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. Journal of the North American Benthological Society 18:308–343.

Bennett, B. A., C. R. Smith, B. Glaser, and H. L. Maybaum. 1994. Faunal community structure of a chemoautotrophic assemblage on whale bones in the deep northeast Pacific Ocean. Marine Ecology Progress Series 108:205–223.

Bharti, M., and D. Singh. 2003. Insect faunal succession on decaying rabbit carcasses in Punjab, India. Journal of Forensic Sciences 48:1–11.

Bignell, D. E., and P. Eggleton. 2000. Termites in ecosystems. Pages 363–387 *in* T. Abe, D. Bignell, and M. Higashi, editors. Termites: evolution, sociality, symbioses, ecology. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Bilby, R. E., B. R. Fransen, and P. A. Bisson. 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. Canadian Journal of Fisheries and Aquatic Sciences 53:164–173.

Boddy, L. 1983. Carbon dioxide release from decomposing wood: effect of water content and temperature. Soil Biology and Biochemistry 15:501–510.

Boddy, L. 2001. Fungal community ecology and wood decomposition processes in angiosperms: from standing tree to complete decay of coarse woody debris. Ecological Bulletins 49:43–56.

Boeskorov, G. G., O. R. Potapova, E. N. Mashchenko, A. V. Protopopov, T. V. Kuznetsova, L. Agenbroad, and A. N. Tikhonov. 2014. Preliminary analyses of the frozen mummies of mammoth (*Mammuthus primigenius*), bison (*Bison priscus*) and horse (*Equus* sp.) from the Yana-Indigirka Lowland, Yakutia, Russia. Integrative Zoology 9:471–480.

Bornemissza, G. F. 1957. An analysis of arthropod succession in carrion and the effect of its decomposition on the soil fauna. Australian Journal of Zoology 5:1–12.

Boysen-Jensen, P. 1919. Valuation of the Limfjord. I. Studies on the fish-food in the Limfjord 1909-1917, its quantity variation and annual production. Reports of the Danish Biological Station 26:3–44.

Braack, L. E. O. 1987. Community dynamics of carrion-attendant arthropods in tropical African woodland. Oecologia 72:402–409.

Brabcová, V., M. Nováková, A. Davidová, and P. Baldrian. 2016. Dead fungal mycelium in forest soil represents a decomposition hotspot and a habitat for a specific microbial community. New Phytologist 210:1369–1381.

Bradford, M. A., R. J. Warren, P. Baldrian, T. W. Crowther, D. S. Maynard, E. E. Oldfield, W. R. Wieder, S. A. Wood, and J. R. King. 2014. Climate fails to predict wood decomposition at regional scales. Nature Climate Change 4:625–630.

Bradford, M. A., B. Berg, D. S. Maynard, W. R. Wieder, and S. A. Wood. 2016. Understanding the dominant controls on litter decomposition. Journal of Ecology 104:229–238.

Brinson, M. M., A. E. Lugo, and S. Brown. 1981. Primary productivity, decomposition and consumer activity in freshwater wetlands. Annual Review of Ecology and Systematics 12:123–161.

Brothwell, D., H. Gill-Robinson, and W. Haglund. 2002. Taphonomic and forensic aspects of bog bodies. Pages 119–131 in W. D. Haglund and M. H. Sorg, editors. Advances in forensic taphonomy. Method, theory and archaeological perspectives. CRC Press, Boca Raton, Florida, USA.

Brundage, A. L., M. E. Benbow, and J. K. Tomberlin. 2014. Priority effects on the life-history traits of two carrion blow fly (Diptera, Calliphoridae) species. Ecological Entomology 39:539–547.

Brundage, A. L., T. L. Crippen, B. Singh, M. E. Benbow, W. Liu, A. M. Tarone, T. K. Wood, and J. K. Tomberlin. 2017. Interkingdom cues by bacteria associated with conspecific and heterospecific eggs of Cochliomyia macellaria and Chrysomya rufifacies (Diptera: Calliphoridae) potentially govern succession on carrion. Annals of the Entomological Society of America 110:73–82.

Brune, A. 2014. Symbiotic digestion of lignocellulose in termite guts. Nature Reviews Microbiology 12:168–180.

Brune, A., and M. Ohkuma. 2011. Role of the termite gut microbiota in symbiotic digestion. Pages 439–475 in D. E. Bignell, Y. Roisin, and N. Lo, editors. Biology of termites: a modern synthesis. Springer, New York, New York, USA.

Buchkowski, R. W. 2016. Top-down consumptive and trait-mediated control do affect soil food webs: it's time for a new model. Soil Biology and Biochemistry 102:29–32.

Bulgarelli, D., K. Schlaeppi, S. Spaepen, E. V. L. van Themaat, and P. Schulze-Lefert. 2013. Structure and functions of the bacterial microbiota of plants. Annual Review of Plant Biology 64:807–838.

Bultman, J. D., and C. R. Southwell. 1976. Natural resistance of tropical American woods to terrestrial wood-destroying organisms. Biotropica 8:71–95.

Bump, J. K., R. O. Peterson, and J. A. Vucetich. 2009a. Wolves modulate soil nutrient heterogeneity and foliar nitrogen by configuring the distribution of ungulate carcasses. Ecology 90:3159–3167.

Bump, J. K., C. R. Webster, J. A. Vucetich, R. O. Peterson, J. M. Shields, and M. D. Powers. 2009b. Ungulate carcasses perforate ecological filters and create biogeochemical hotspots in forest herbaceous layers allowing trees a competitive advantage. Ecosystems 12:996–1007.

Burkepile, D. E., J. D. Parker, C. B. Woodson, H. J. Mills, J. Kubanek, P. A. Sobecky, and M. E. Hay. 2006. Chemically mediated competition between microbes and animals: microbes as consumers in food webs. Ecology 87:2821–2831.

Burnes, T. A., R. A. Blanchette, and R. L. Farrell. 2000. Bacterial biodegradation of extractives and patterns of bordered pit membrane attack in pine wood. Applied and Environmental Microbiology 66:5201–5205.

Byrd, J., and J. Castner, editors. 2009. Forensic entomology: the utility of arthropods in legal investigations. CRC Press, Boca Raton, Florida, USA.

Cammack, J. A., P. H. Adler, J. K. Tomberlin, Y. Arai, and W. C. Bridges, Jr. 2010. Influence of parasitism and soil compaction on pupation of the green bottle fly, Lucilia sericata. Entomologia Experimentalis Et Applicata 136:134–141.

Can, I., G. T. Javan, A. E. Pozhitkov, and P. A. Noble. 2014. Distinctive thanatomicrobiome signatures found in the blood and internal organs of humans. Journal of Microbiological Methods 106:1–7.

Carline, K. A., H. E. Jones, and R. D. Bardgett. 2005. Large herbivores affect the stoichiometry of nutrients in a regenerating woodland ecosystem. Oikos 110:453–460.

Carter, D. O., D. Yellowlees, and M. Tibbett. 2007. Cadaver decomposition in terrestrial ecosystems. Naturwissenschaften 94:12–24.

Carter, D. O., J. L. Metcalf, A. Bibat, and R. Knight. 2015. Seasonal variation of postmortem microbial communities. Forensic Science, Medicine, and Pathology 11:202–207.

Cebrian, J. 1999. Patterns in the fate of production in plant communities. American Naturalist 154:449–468.

Chapman, H. 2015. The landscape archaeology of bog bodies. Journal of Wetland Archaeology 15:109–121.

Chapman, R., and J. Sankey. 1955. The larger invertebrate fauna of three rabbit carcasses. Journal of Animal Ecology 24:395–402.

Chouvenc, T., C. A. Efstathion, M. L. Elliott, and N.-Y. Su. 2013. Extended disease resistance emerging from the faecal nest of a subterranean termite. Proceedings of the Royal Society B 280:20131885.

Coe, M. 1978. The decomposition of elephant carcasses in the Tsavo (East) National Park, Kenya. Journal of Arid Environments 1:71–86.

Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalist 111:1119–1144.

Cornaby, B. W. 1974. Carrion reduction by animals in contrasting tropical habitats. Biotropica 6:51–63.

Cornwell, W. K., J. H. C. Cornelissen, S. D. Allison, J. Bauhus, P. Eggleton, C. M. Preston, F. A. Scarff, J. T. Weedon, C. Wirth, and A. E. Zanne. 2009. Plant traits and wood fates across the globe: rotted, burned, or consumed? Global Change Biology 15:2431–2449.

Coûteaux, M.-M., L. Sarmiento, D. Hervé, and D. Acevedo. 2005. Determination of water-soluble and total extractable polyphenolics in biomass, necromass and decomposing plant material using near-infrared reflectance spectroscopy (NIRS). Soil Biology and Biochemistry 37:795–799.

Covey, K. R., S. A. Wood, R. J. Warren, X. Lee, and M. A. Bradford. 2012. Elevated methane concentrations in trees of an upland forest. Geophysical Research Letters 39:L15705.

Crippen, T. L., M. E. Benbow, and J. L. Pechal. 2015. Microbial interactions during carrion decomposition. Pages 31–63 in M. E. Benbow, J. K. Tomberlin, and A. M. Tarone, editors. Carrion ecology, evolution, and their applications. CRC Press, Boca Raton, Florida, USA.

Crowther, T. W., S. M. Thomas, D. S. Maynard, P. Baldrian, K. Covey, S. D. Frey, L. T. A. van Diepen, and M. A. Bradford. 2015. Biotic interactions mediate soil microbial feedbacks to climate change. Proceedings of the National Academy of Sciences USA 112:7033–7038.

CONCEPTS & SYNTHESIS

Cummins, K. W., R. C. Petersen, F. O. Howard, J. C. Wuycheck, and V. I. Holt. 1973. The utilization of leaf litter by stream detritivores. Ecology 54:336–345.

Danell, K., D. Berteaux, and K. A. Brathen. 2002. Effect of muskox carcasses on nitrogen concentration in tundra vegetation. Arctic 55:389–392.

Dedouit, F., A. Géraut, V. Baranov, B. Ludes, D. Rougé, N. Telmon, and E. Crubézy. 2010. Virtual and macroscopical studies of mummies—Differences or complementarity? Report of a natural frozen Siberian mummy. Forensic Science International 200:e7–e13.

Denno, R. F., and W. R. Cothran. 1975. Niche relationships of a guild of necrophagous flies. Annals of the Entomological Society of America 68:741–753.

DeVault, T. L., O. E. Jr Rhodes, and J. A. Shivik. 2003. Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. Oikos 102:225–234.

DeVault, T. L., J. Brisbin, I. Lehr, J. Rhodes, and E. Olin. 2004a. Factors influencing the acquisition of rodent carrion by vertebrate scavengers and decomposers. Canadian Journal of Zoology 82:502–509.

DeVault, T. L., B. D. Reinhart, I. L. Jr Brisbin, and O. E. Rhodes, Jr. 2004b. Home ranges of sympatric black and turkey vultures in South Carolina. Condor 106:706–711.

DeVault, T. L., Z. H. Olson, J. C. Beasley, and O. E. Rhodes. 2011. Mesopredators dominate competition for carrion in an agricultural landscape. Basic and Applied Ecology 12:268–274.

DeVault, T. L., J. C. Beasley, Z. H. Olson, M. Moleón, M. Carrete, A. Margalida, and J. A. Sánchez-Zapata. 2016. Ecosystem services provided by avian scavengers. Pages 235–270 in Ç. H. Sekercioglu, D. G. Wenny, and C. J. Whelan, editors. Ecosystem services provided by birds. The University of Chicago Press, Chicago, Illinois, USA.

Deveau, A., G. Bonito, J. Uehling, M. Paoletti, M. Becker, S. Bindschedler, S. Hacquard, V. Hervé, J. Labbé, and O. Lastovetsky. 2018. Bacterial-fungal interactions: ecology, mechanisms and challenges. FEMS Microbiology Reviews 42:335–352.

Dillon, R. J., and V. M. Dillon. 2004. The gut bacteria of insects: nonpathogenic interactions. Annual Review of Entomology 49:71–92.

Donovan, S. E., P. Eggleton, and D. E. Bignell. 2001. Gut content analysis and a new feeding group classification of termites. Ecological Entomology 26:356–366.

Dorado, J., F. W. Claassen, G. Lenon, T. A. van Beek, J. B. P. A. Wijnberg, and R. Sierra-Alvarez. 2000. Degradation and detoxification of softwood extractives by sapstain fungi. Bioresource Technology 71:13–20.

Dowd, P. F. 1992. Insect fungal symbionts: a promising source of detoxifying enzymes. Journal of Industrial Microbiology 9:149–161.

Drazen, J. C., D. M. Bailey, H. A. Ruhl, and K. L. Jr Smith. 2012. The role of carrion supply in the abundance of deepwater fish off California. PLoS ONE 7:e49332.

Duarte, A., M. Welch, C. Swannack, J. Wagner, and R. M. Kilner. 2018. Strategies for managing rival bacterial communities: lessons learned from burying beetles. Journal of Animal Ecology 87:424–427.

Duggins, D., C. Simenstad, and J. Estes. 1989. Magnification of secondary production by kelp detritus in coastal marine ecosystems. Science 245:170–173.

Dunne, J. A., R. J. Williams, and N. D. Martinez. 2002. Network structure and biodiversity loss in food webs: robustness increases with connectance. Ecology Letters 5:558–567.

Early, M., and M. L. Goff. 1986. Arthropod succession patterns in exposed carrion on the island of O'ahu, Hawaiian Islands, USA. Journal of Medical Entomology 23:520–531.

Ekblad, A., H. Wallander, D. Godbold, C. Cruz, D. Johnson, P. Baldrian, R. Björk, D. Epron, B. Kieliszewska-Rokicka, and R. Kjøller. 2013. The production and turnover of extramatrical mycelium of ectomycorrhizal fungi in forest soils: role in carbon cycling. Plant and Soil 366:1–27.

Eklöf, A., U. Jacob, J. Kopp, J. Bosch, R. Castro-Urgal, N. P. Chacoff, B. Dalsgaard, C. Sassi, M. Galetti, and P. R. Guimarães. 2013. The dimensionality of ecological networks. Ecology Letters 16:577–583.

Elton, C. S. 1966. The pattern of animal communities. Methuen and Company, London, UK.

Ettema, C. H., and D. A. Wardle. 2002. Spatial soil ecology. Trends in Ecology and Evolution 17:177–183.

Ezenwa, V. O., N. M. Gerardo, D. W. Inouye, M. Medina, and J. B. Xavier. 2012. Animal behavior and the microbiome. Science 338:198–199.

Fahrig, L. 2017. Ecological responses to habitat fragmentation per se. Annual Review of Ecology, Evolution, and Systematics 48:1–23.

Fain, A., and G. S. Ide. 1976. Ellipsopus ornatus, a new genus and species of Acaridae (Acari) phoretic on the beetle Bolitotherus cornutus (Panzer, 1794). Entomological News 87:233–236.

Farrell, B. D., A. S. Sequeira, B. C. O'Meara, B. B. Normark, J. H. Chung, and B. H. Jordal. 2001. The evolution of agriculture in beetles (Curculionidae: Scolytinae and Platypodinae). Evolution 55:2011–2027.

Farwig, N., R. Brandl, S. Siemann, F. Wiener, and J. Mueller. 2014. Decomposition rate of carrion is dependent on composition not abundance of the assemblages of insect scavengers. Oecologia 175:1291–1300.

Fellers, G. M., and J. H. Fellers. 1982. Scavenging rates of invertebrates in an eastern deciduous forest. American Midland Naturalist 107:389–392.

Fernandez, C. W., and P. G. Kennedy. 2018. Melanization of mycorrhizal fungal necromass structures microbial decomposer communities. Journal of Ecology 106:468–479.

Fernandez, C. W., J. A. Langley, S. Chapman, M. L. McCormack, and R. T. Koide. 2016. The decomposition of ectomycorrhizal fungal necromass. Soil Biology and Biochemistry 93:38–49.

Ferro, M. L., M. L. Gimmel, K. E. Harms, and C. E. Carlton. 2012. Comparison of the Coleoptera communities in leaf litter and rotten wood in Great Smoky Mountains National Park, USA. Insecta Mundi 259:1–58.

Fey, S. B., A. M. Siepielski, S. Nusslé, K. Cervantes-Yoshida, J. L. Hwan, E. R. Huber, M. J. Fey, A. Catenazzi, and S. M. Carlson. 2015. Recent shifts in the occurrence, cause, and magnitude of animal mass mortality events. Proceedings of the National Academy of Sciences USA 112:1083–1088.

Fiene, J. G., G. A. Sword, S. L. Vanlaerhoven, and A. M. Tarone. 2014. The role of spatial aggregation in forensic entomology. Journal of Medical Entomology 51:1–9.

Fierer, N., M. Strickland, D. Liptzin, M. Bradford, and C. Cleveland. 2009. Global patterns in belowground communities. Ecology Letters 103:1238–1249.

Finley, S. J., J. L. Pechal, M. E. Benbow, B. K. Robertson, and G. T. Javan. 2016. Microbial signatures of cadaver gravesoil during decomposition. Microbial Ecology 71:1–6.

Finn, J. A. 2001. Ephemeral resource patches as model systems for diversity-function experiments. Oikos 92:363–366.

Fittkau, E. J., and H. Klinge. 1973. On biomass and trophic structure of the central Amazonian rain forest ecosystem. Biotropica 5:2–14.

Flores, M., M. Longnecker, and J. K. Tomberlin. 2014. Effects of temperature and tissue type on *Chrysomya rufifacies* (Diptera: Calliphoridae) (Macquart) development. Forensic Science International 245:24–29.

Forbes, S. A. 1887. The lake as a microcosm. Reprinted in Bulletin of the Illinois State Natural History Survey (1925) 15:537–550.

Forbes, S. L., and K. A. Perrault. 2014. Decomposition odour profiling in the air and soil surrounding vertebrate carrion. PLoS ONE 9:e95107.

Frank, D. A., and R. D. Evans. 1997. Effects of native grazers on grassland N cycling in Yellowstone National Park. Ecology 78:2238–2248.

Frankland, J. C. 1966. Succession of fungi on decaying petioles of *Pteridium aquilinum*. Journal of Ecology 54:41–63.

Fuglei, E., N. A. Øritsland, and P. Prestrud. 2003. Local variation in arctic fox abundance on Svalbard, Norway. Polar Biology 26:93–98.

Fukami, K., U. Simidu, and N. Taga. 1985. Microbial decomposition of phyto-and zooplankton in seawater. II. Changes in the bacterial community. Marine Ecology Progress Series 21:7–13.

Fuller, M. E. 1934. The insect inhabitants of carrion: a study in animal ecology. CSIR Bulletin 82:5–62.

García-Palacios, P., F. T. Maestre, J. Kattge, and D. H. Wall. 2013. Climate and litter quality differently modulate the effects of soil fauna on litter decomposition across biomes. Ecology Letters 16:1045–1053.

Gasaway, W., K. Mossestad, and P. Standers. 1991. Food acquisition by spotted hyaenas in Etosha National Park, Namibia: predation versus scavenging. African Journal of Ecology 29:64–75.

Gessner, M. O., and E. Chauvet. 1994. Importance of stream microfungi in controlling breakdown rates of leaf litter. Ecology 75:1807–1817.

Gessner, M. O., C. M. Swan, C. K. Dang, B. G. McKie, R. D. Bardgett, D. H. Wall, and S. Hattenschwiler. 2010. Diversity meets decomposition. Trends in Ecology and Evolution 25:372–380.

Gholz, H. L., D. A. Wedin, S. M. Smitherman, M. E. Harmon, and W. J. Parton. 2000. Long-term dynamics of pine and hardwood litter in contrasting environments: toward a global model of decomposition. Global Change Biology 6:751–765.

Goodbrod, J. R., and M. L. Goff. 1990. Effects of larval population-density on rates of development and interactions between two species of *Chrysomya* (Diptera, Calliphoridae) in laboratory culture. Journal of Medical Entomology 27:338–343.

Gravel, D., F. Guichard, M. Loreau, and N. Mouquet. 2010. Source and sink dynamics in meta-ecosystems. Ecology 91:2172–2184.

Gray, C. M., R. K. Monson, and N. Fierer. 2010. Emissions of volatile organic compounds during the decomposition of plant litter. Journal of Geophysical Research 115:G03015.

Greenberg, B. 1971*a*. Flies and disease, volume 1, ecology, classification and biotic associations. Princeton University Press, Princeton, New Jersey, USA.

Greenberg, B. 1971*b*. Flies and disease, volume 2, biology and disease transmission. Princeton University Press, Princeton, New Jersey, USA.

Greenberg, B. 1973. Biology and disease transmission. Princeton University Press, Princeton, New Jersey, USA.

Greenberg, B., and A. A. Bornsetein. 1964. Fly dispersion from a rural Mexican slaughterhouse. American Journal of Tropical Medicine and Hygiene 13:881–886.

Greenberg, B., J. A. Kowalski, and M. J. Klowden. 1970. Factors affecting the transmission of salmonella by flies: natural resistance to colonization and bacterial interference. Infection and Immunity 2:800–809.

Grossart, H.-P., and M. Simon. 1998. Bacterial colonization and microbial decomposition of limnetic organic aggregates (lake snow). Aquatic Microbial Ecology 15:127–140.

Haack, R. A., and R. C. Wilkinson. 1986. Phoresy by *Dendrochernes pseudoscorpions* on Cerambyicdae (Coleoptera) and Aulacidae (Hymenoptera) in Florida. American Midland Naturalist 117:369–373.

Haila, Y., and J. Niemelä. 1999. Leaf litter and the small-scale distribution of carabid beetles (Coleoptera, Carabidae) in the boreal forest. Ecography 22:424–435.

Hammond, H. E. J., D. W. Langor, and J. R. Spence. 2001. Early colonization of *Populus* wood by saproxylic beetles (Coleoptera). Canadian Journal of Forest Research 31:1175–1183.

Handa, I. T., et al. 2014. Consequences of biodiversity loss for litter decomposition across biomes. Nature 509:218–221.

Hanski, I. 1987. Carrion fly community dynamics: patchiness, seasonality and coexistence. Ecological Entomology 12:257–266.

Hanski, I., and Y. Cambefort, editors. 1991. Dung beetle ecology. Princeton University Press, Princeton, New Jersey, USA.

Hanski, I., and M. Gilpin. 1991. Metapopulation dynamics—brief history and conceptual domain. Biological Journal of the Linnean Society 42:3–16.

Harmon, M. E., et al. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15:133–302.

Hattenschwiler, S., A. V. Tiunov, and S. Scheu. 2005. Biodiversity and litter decomposition in terrestrial ecosystems. Annual Review of Ecology Evolution and Systematics 36:191–218.

Hawlena, D., and M. Zaguri. 2016. Fear and below-ground food-webs. Soil Biology and Biochemistry 102:26–28.

Hawlena, D., M. S. Strickland, M. A. Bradford, and O. J. Schmitz. 2012. Fear of predation slows plant-litter decomposition. Science 336:1434–1438.

Heard, S. B. 1998. Resource patch density and larval aggregation in mushroom-breeding flies. Oikos 81:187–195.

Heneghan, L., D. Coleman, X. Zou, D. Jr Crossley, and B. Haines. 1998. Soil microarthropod community structure and litter decomposition dynamics: a study of tropical and temperate sites. Applied Soil Ecology 9:33–38.

Hickin, N. E. 1963. The insect factor in wood decay. An account of wood-boring insects with particular reference to timber indoors. London, Hutchinson & Co., London, UK.

Hill, J. E., T. L. DeVault, J. C. Beasley, O. E. Rhodes Jr., and J. L. Belant. 2018. Effects of vulture exclusion on carrion consumption by facultative scavengers. Ecology and Evolution 8:2518–2526.

Hobischak, N. R., S. L. VanLaerhoven, and G. S. Anderson. 2006. Successional patterns of diversity in insect fauna on carrion in sun and shade in the Boreal Forest Region of Canada, near Edmonton, Alberta. Canadian Entomologist 138:376–383.

Hocking, M. D., and J. D. Reynolds. 2011. Impacts of salmon on riparian plant diversity. Science 331:1609–1612.

Hodgkin, L. K., M. A. Elgar, and M. R. E. Symonds. 2010. Positive and negative effects of phoretic mites on the reproductive output of an invasive bark beetle. Australian Journal of Zoology 58:198–204.

Holland, A. E., M. E. Byrne, A. L. Bryan, T. L. DeVault, O. E. Rhodes, and J. C. Beasley. 2017. Fine-scale assessment of home ranges and activity patterns for resident black vultures (*Coragyps atratus*) and turkey vultures (*Cathartes aura*). PLoS ONE 12:e0179819.

Holter, P., and C. H. Scholtz. 2007. What do dung beetles eat? Ecological Entomology 32:690–697.

CONCEPTS & SYNTHESIS

Houston, D. 1974. Food searching in griffon vultures. African Journal of Ecology 12:63–77.

Houston, D. C. 1979. The adaptations of scavengers. Pages 236–286 in N. Sinclair and N. Griffiths, editors. Serengeti: dynamics of an ecosystem. The University of Chicago Press, Chicago, Illinois, USA.

Houston, D. C. 1985. Evolutionary ecology of Afrotropical and Neotropical vultures in forests. Ornithological Monographs 36:856–864.

Houston, D. C. 1986. Scavenging efficiency of turkey vultures in tropical forest. Condor 88:318–323.

Houston, D. C., and J. Cooper. 1975. The digestive tract of the whiteback griffon vulture and its role in disease transmission among wild ungulates. Journal of Wildlife Diseases 11:306–313.

Hungate, R. E. 1966. The rumen and its microbes. Academic Press, New York, New York, USA.

Huryn, A. D., and J. B. Wallace. 2000. Life history and production of stream insects. Annual Review of Entomology 45:83–110.

Hyde, E., D. Haarmann, J. Petrosino, A. Lynne, and S. Bucheli. 2015. Initial insights into bacterial succession during human decomposition. International Journal of Legal Medicine 129:661–671.

Hynes, H. B. N. 1970. The ecology of running waters. Liverpool University Press, Liverpool, UK.

Inglis, G. 1989. The colonisation and degradation of stranded Macrocystis pyrifera (L.) C. Ag. by the macrofauna of a New Zealand sandy beach. Journal of Experimental Marine Biology and Ecology 125:203–217.

Ives, A. R. 1991. Aggregation and coexistence in a carrion fly community. Ecological Monographs 61:75–94.

Janzen, D. H. 1977. Why fruits rot, seeds mold, and meat spoils. American Naturalist 111:691–713.

Javan, G. T., S. J. Finley, I. Can, J. E. Wilkinson, J. D. Hanson, and A. M. Tarone. 2016. Human thanatomicrobiome succession and time since death. Scientific Reports 6:29598.

Jennelle, C. S., M. D. Samuel, C. A. Nolden, and E. A. Berkley. 2009. Deer carcass decomposition and potential scavenger exposure to chronic wasting disease. Journal of Wildlife Management 73:655–662.

Jiménez, M. A., R. Beltran, A. Traveset, M. L. Calleja, A. Delgado-Huertas, and N. Marbà. 2017. Aeolian transport of seagrass (Posidonia oceanica) beach-cast to terrestrial systems. Estuarine, Coastal and Shelf Science 196:31–44.

Jones, E. G., M. A. Collins, P. M. Bagley, S. Addison, and I. G. Priede. 1998. The fate of cetacean carcasses in the deep sea: observations on consumption rates and succession of scavenging species in the abyssal north-east Atlantic Ocean. Proceedings of the Royal Society B 265:1119–1127.

Jones, S. C., E. D. Strauss, and K. E. Holekamp. 2015. Ecology of African carrion. Pages 461–491 in M. E. Benbow, J. K. Tomberlin, and A. M. Tarone, editors. Carrion ecology. Evolution and their applications. CRC Press, Boca Raton, Florida, USA.

Jordan, H. R., J. K. Tomberlin, T. K. Wood, and M. E. Benbow. 2015. Interkingdom ecological interactions of carrion decomposition. Pages 433–460 in M. E. Benbow, J. K. Tomberlin, and A. M. Tarone, editors. Carrion ecology. Evolution and their applications. CRC Press, Boca Raton, Florida, USA.

Joyce, P., L. L. Warren, and R. S. Wotton. 2007. Faecal pellets in streams: their binding, breakdown and utilization. Freshwater Biology 52:1868–1880.

Junker, R. R., and A. Keller. 2015. Microhabitat heterogeneity across leaves and flower organs promotes bacterial diversity. FEMS Microbiology Ecology 91:fiv097.

Juottonen, H., P. E. Galand, E. Tuittila, J. Laine, H. Fritze, and K. Yrjaelae. 2005. Methanogen communities and bacteria along an ecohydrological gradient in a northern raised bog complex. Environmental Microbiology 7:1547–1557.

Käärik, A. A. 1974. Decomposition of wood. Pages 129–174 in C. H. Dickinson and G. J. F. Pugh, editors. Biology of plant litter decomposition. Volume 1. Academic Press, London, UK.

Kallenbach, C. M., A. S. Grandy, S. D. Frey, and A. F. Diefendorf. 2015. Microbial physiology and necromass regulate agricultural soil carbon accumulation. Soil Biology and Biochemistry 91:279–290.

Kaltenpoth, M., and S. Steiger. 2014. Unearthing carrion beetles' microbiome: characterization of bacterial and fungal hindgut communities across the Silphidae. Molecular Ecology 23:1251–1267.

Karl, D. M., G. A. Knauer, and J. H. Martin. 1988. Downward flux of particulate organic matter in the ocean: a particle decomposition paradox. Nature 332:438.

Keiser, A. D., J. D. Knoepp, and M. A. Bradford. 2013. Microbial communities may modify how litter quality affects potential decomposition rates as tree species migrate. Plant and Soil 372:167–176.

Keiser, A. D., D. A. Keiser, M. S. Strickland, and M. A. Bradford. 2014. Disentangling the mechanisms underlying functional differences among decomposer communities. Journal of Ecology 102:603–609.

Kelly, N. E., D. W. Sparks, T. L. DeVault, and O. E. Jr Rhodes. 2007. Diet of black and turkey vultures in a forested landscape. Wilson Journal of Ornithology 119:267–270.

Kim, J., and W. Park. 2015. Indole: a signaling molecule or a mere metabolic byproduct that alters bacterial physiology at a high concentration? Journal of Microbiology 53:421–428.

Knorr, K. H., M. A. Horn, and W. Borken. 2015. Significant nonsymbiotic nitrogen fixation in Patagonian ombrotrophic bogs. Global Change Biology 21:2357–2365.

Kouki, J., and I. Hanski. 1995. Population aggregation facilitates coexistence of many competing carrion fly species. Oikos 72:223–227.

Krantz, G. W. 1998. Reflections on the biology, morphology and ecology of the Macrochelidae. Experimental & Applied Acarology 22:125–137.

Kuiters, A., and H. Sarink. 1986. Leaching of phenolic compounds from leaf and needle litter of several deciduous and coniferous trees. Soil Biology and Biochemistry 18:475–480.

Kulshrestha, P., and D. K. Satpathy. 2001. Use of beetles in forensic entomology. Forensic Science International 120:15–17.

Kvavadze, E., and K. Kakhiani. 2010. Palynology of the Paravani burial mound (Early Bronze Age, Georgia). Vegetation History and Archaeobotany 19:469–478.

Latter, P. M., and J. Cragg. 1967. The decomposition of Juncus squarrosus leaves and microbiological changes in the profile of Juncus moor. Journal of Ecology 55:465–482.

Lauber, C. L., J. L. Metcalf, K. Keepers, G. Ackermann, D. O. Carter, and R. Knight. 2014. Vertebrate decomposition is accelerated by soil microbes. Applied and Environmental Microbiology 80:4920–4929.

Lavelle, P., D. Bignell, M. Lepage, V. Wolters, P. Roger, P. Ineson, O. W. Heal, and S. Dhillion. 1997. Soil function in a changing world: the role of invertebrate ecosystem engineers. European Journal of Soil Biology 33:159–193.

Leach, J. G., L. W. Orr, and C. Christensen. 1937. Further studies on the interrelationship of insects and fungi in the deterioration of felled Norway pine logs. Journal of Agricultural Research 55:129–140.

Leroux, S. J., and M. Loreau. 2008. Subsidy hypothesis and strength of trophic cascades across ecosystems. Ecology Letters 11:1147–1156.

Lewis, A. J., and M. E. Benbow. 2011. When entomological evidence crawls away: *Phormia regina en masse* larval dispersal. Journal of Medical Entomology 48:1112–1119.

Lieutier, F., K. R. Day, A. Battisti, J.-C. Gregoire, and H. F. Evans. 2004. Editors. Bark and wood boring insects in living trees in Europe: a synthesis. Springer, Dordrecht, The Netherlands.

Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. Ecology 23:399–418.

Lindquist, E. E. 1969. Review of holarctic tarsonemid mites (Acari: Prostigmata) parasitizing eggs of ipine bark beetles. Memoirs of the Entomological Society of Canada 60:5–111.

Liu, G., et al. 2015. Termites amplify the effects of wood traits on decomposition rates among multiple bamboo and dicot woody species. Journal of Ecology 103:1214–1223.

Lo, N., G. Tokuda, and H. Watanabe. 2011. Evolution and function of endogenous termite cellulases. Pages 51–67 *in* D. E. Bignell, Y. Roisin, and N. Lo, editors. Biology of termites: a modern synthesis. Springer, New York, New York, USA.

Lomstein, B. A., A. T. Langerhuus, S. D'Hondt, B. B. Jørgensen, and A. J. Spivack. 2012. Endospore abundance, microbial growth and necromass turnover in deep sub-seafloor sediment. Nature 484:101.

Lussenhop, J. 1992. Mechanisms of microarthropod-microbial interactions in soil. Advances in Ecological Research 23:1–33.

Luyssaert, S., E.-S. Schulze, A. Börner, A. Knohl, D. Hessenmöller, B. E. Law, P. Ciais, and J. Grace. 2008. Old-growth forests as global carbon sinks. Nature 455:213–215.

Ma, Q., A. Fonseca, W. Liu, A. T. Fields, M. L. Pimsler, A. F. Spindola, A. M. Tarone, T. L. Crippen, J. K. Tomberlin, and T. K. Wood. 2012. *Proteus mirabilis* interkingdom swarming signals attract blow flies. ISME Journal 6:1356–1366.

MacArthur, R. H., and E. O. Wilson. 1967. Theory of island biogeography. Princeton University Press, Princeton, New Jersey, USA..

Macdonald, J. 1992. The decomposition of animal remains in caves. Thesis. Nottingham Polytechnic, Nottingham, UK.

Macovei, L., and L. Zurek. 2006. Ecology of antibiotic resistance genes: characterization of enterococci from houseflies collected in food settings. Applied and Environmental Microbiology 72:4028–4035.

Mądra, A., K. Frątczak, A. Grzywacz, and S. Matuszewski. 2015. Long-term study of pig carrion entomofauna. Forensic Science International 252:1–10.

Madritch, M. D., J. R. Donaldson, and R. L. Lindroth. 2007. Canopy herbivory can mediate the influence of plant genotype on soil processes through frass deposition. Soil Biology and Biochemistry 39:1192–1201.

Mann, K. 1988. Production and use of detritus in various freshwater, estuarine, and coastal marine ecosystems. Limnology and Oceanography 33:910–930.

Mann, R. W., W. M. Bass, and L. Meadows. 1990. Time since death and decomposition of the human body: variables and observations in case and experimental field studies. Journal of Forensic Science 35:103–111.

Margalida, A., J. Bertran, and R. Heredia. 2009. Diet and food preferences of the endangered Bearded Vulture *Gypaetus barbatus*: a basis for their conservation. Ibis 151:235–243.

Martin, A. R., D. L. Erickson, W. J. Kress, and S. C. Thomas. 2014. Wood nitrogen concentrations in tropical trees: phylogenetic patterns and ecological correlates. New Phytologist 204:484–495.

Martiny, J. B. H., A. C. Martiny, C. Weihe, Y. Lu, R. Berlemont, E. L. Brodie, M. L. Goulden, K. K. Treseder, and S. D. Allison. 2017. Microbial legacies alter decomposition in response to simulated global change. ISME Journal 11:490–499.

Matuszewski, S., D. Bajerlein, S. Konwerski, and K. Szpila. 2008. An initial study of insect succession and carrion decomposition in various forest habitats of Central Europe. Forensic Science International 180:61–69.

Matuszewski, S., D. Bajerlein, S. Konwerski, and K. Szpila. 2011. Insect succession and carrion decomposition in selected forests of Central Europe. Part 3: succession of carrion fauna. Forensic Science International 2007:150–163.

Mégnin, P. 1894. La faune des cadavres application de l'entomologie à la médecine légale. Encyclopédie Scientifique des Aide-Mémoire, Paris, France.

Menendez, R., P. Webb, and K. H. Orwin. 2016. Complementarity of dung beetle species with different functional behaviours influence dung-soil carbon cycling. Soil Biology and Biochemistry 92:142–148.

Merritt, R. W., and G. D. De Jong. 2015. Arthropod communities in terrestrial environments. Pages 65–92 *in* M. E. Benbow, J. K. Tomberlin, and A. M. Tarone, editors. Carrion ecology, evolution, and their applications. CRC Press, Boca Raton, Florida, USA.

Merritt, R. W., and J. R. Wallace. 2010. The role of aquatic insects in forensic investigations. Pages 271–320 *in* J. H. Byrd and J. L. Castner, editors. Forensic entomology: the utility of arthropods in legal investigations. CRC Press, Boca Raton, Florida, USA.

Metcalf, J. L., et al. 2016. Microbial community assembly and metabolic function during mammalian corpse decomposition. Science 351:158–162.

Michaud, J. P., K. G. Schoenly, and G. Moreau. 2015. Rewriting ecological succession history: did carrion ecologists get there first? Quarterly Review of Biology 90:45–66.

Middeldorp, A. A. 1986. Functional palaeoecology of the Hahnenmoor raised bog ecosystem—A study of vegetation history, production and decomposition by means of pollen density dating. Review of Palaeobotany and Palynology 49:1–73.

Mishima, T., N. Wada, R. Iwata, H. Anzai, T. Hosoya, and K. Araya. 2016. Super-protective child-rearing by Japanese bess beetles, *Cylindrocaulus patalis*: adults provide their larvae with chewed and predigested wood. Insects 7:18.

Moleón, M., J. A. Sanchez-Zapata, N. Selva, J. A. Donazar, and N. Owen-Smith. 2014. Inter-specific interactions linking predation and scavenging in terrestrial vertebrate assemblages. Biological Reviews 89:1042–1054.

Moleón, M., J. A. Sánchez-Zapata, E. Sebastián-González, and N. Owen-Smith. 2015. Carcass size shapes the structure and functioning of an African scavenging assemblage. Oikos 124:1391–1403.

Moore, J. C., E. L. Berlow, D. C. Coleman, P. C. Ruiter, Q. Dong, A. Hastings, N. C. Johnson, K. S. McCann, K. Melville, and P. J. Morin. 2004. Detritus, trophic dynamics and biodiversity. Ecology Letters 7:584–600.

Moreau, G., J-P. Michaud, and K. G. Schoenly. 2015. Experimental design, inferential statistics, and computer modeling. Pages 205–229 *in* J. K. Tomberlin and M. E. Benbow, editors. Forensic entomology: international dimensions and frontiers. CRC Press, Boca Raton, Florida, USA.

Moser, J. C. 1976. Surveying mites (Acarina) phoretic on the southern pine beetle (Coleoptera: Scolytidae) with sticky traps. Canadian Entomologist 108:809–813.

Moser, J. C., and L. M. Roton. 1971. Mites associated with southern pine bark beetles in Allen Parish, Louisiana. Canadian Entomologist 103:1775–1798.

Müller, K., C. Chadefaux, N. Thomas, and I. Reiche. 2011. Microbial attack of archaeological bones versus high

CONCEPTS & SYNTHESIS

concentrations of heavy metals in the burial environment. A case study of animal bones from a mediaeval copper workshop in Paris. Palaeogeography, Palaeoclimatology, Palaeoecology 310:39–51.

Nair, N. B., and M. Saraswathy. 1971. The biology of wood-boring teredinid molluscs. Advances in Marine Biology 9:335–509.

Nakano, S., H. Miyasaka, and N. Kuhara. 1999. Terrestrial–aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. Ecology 80:2435–2441.

Nayduch, D. 2017. Special collection: filth fly microbe interactions. Annals of the Entomological Society of America 110:2–5.

Nealson, K. H., and J. W. Hastings. 1979. Bacterial bioluminescence: its control and ecological significance. Microbiological Reviews 43:496–518.

Nelson, J., D. Wubah, M. Whitmer, E. Johnson, and D. Stewart. 1999. Wood-eating catfishes of the genus Panaque: gut microflora and cellulolytic enzyme activities. Journal of Fish Biology 54:1069–1082.

Nichols, E., S. Spector, J. Louzada, T. Larsen, S. Amezquita, M. Favila, and T. S. R. Network. 2008. Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. Biological conservation 141:1461–1474.

Nobre, T., C. Rouland-Lefevre, and D. K. Aanen. 2011. Comparative biology of fungus cultivation in termites and ants. Pages 193–210 in D. Bignell, Y. Roisin, and N. Lo, editors. Biology of termites: a modern synthesis. Springer, New York, New York, USA.

Nowlin, W. H., M. J. Gonzalez, M. J. Vanni, M. H. H. Stevens, M. W. Fields, and J. J. Valentei. 2007. Allochthonous subsidy of periodical cicadas affects the dynamics and stability of pond communities. Ecology 88:2174–2186.

Nykvist, N. 1959a. Leaching and decomposition of litter I. Experiments on leaf litter of Fraxinus excelsior. Oikos 10:190–211.

Nykvist, N. 1959b. Leaching and decomposition of litter II. Experiments on needle litter of Pinus silvestris. Oikos 10:212–224.

Nykvist, N. 1963. Leaching and decomposition of water-soluble organic substances from different types of leaf and needle litter. Studia Forestalia Suecica No 3, Stockholm, Sweden.

O'Brien, R. W., and M. Slaytor. 1982. The role of microorganisms in the metabolism of termites. Australian Journal of Biological Sciences 35:239–262.

Odum, E. P. 1969. The strategy of ecosystem development. Science 164:262–270.

Odum, H. T. 1970. Summary: an emerging view of the ecological system at El Verde. Pages I191–I289 in H. T. Odum and R. F. Pigeon, editors. A tropical rain forest: a study of irradiation and ecology at El Verde, Puerto Rico. U.S. Atomic Energy Commission, Oak Ridge, Tennessee, USA.

Odum, E. P., and A. A. de la Cruz. 1963. Detritus as a major component of ecosystems. AIBS Bulletin 13:39–40.

Ogada, D., M. Torchin, M. Kinnaird, and V. Ezenwa. 2012. Effects of vulture declines on facultative scavengers and potential implications for mammalian disease transmission. Conservation Biology 26:453–460.

Oh, J., A. L. Byrd, C. Deming, S. Conlan, N. C. S. Program, H. H. Kong, and J. A. Segre. 2014. Biogeography and individuality shape function in the human skin metagenome. Nature 514:59–64.

Opelt, K., V. Chobot, F. Hadacek, S. Schönmann, L. Eberl, and G. Berg. 2007. Investigations of the structure and function of bacterial communities associated with Sphagnum mosses. Environmental Microbiology 9:2795–2809.

Parmenter, R. R., and V. A. Lamarra. 1991. Nutrient cycling in a freshwater marsh: the decomposition of fish and waterfowl carrion. Limnology and Oceanography 36:976–987.

Parmenter, R., and J. MacMahon. 2009. Carrion decomposition and nutrient cycling in a semiarid shrub-steppe ecosystem. Ecological Monographs 79:637–661.

Parsons, T., and J. Strickland. 1962. Oceanic detritus. Science 136:313–314.

Payne, J. A. 1965. A summer carrion study of the baby pig Sus scrofa Linnaeus. Ecology 46:592–602.

Payne, J. A., and E. W. King. 1972. Insect succession and decomposition of pig carcasses in water. Journal of the Georgia Entomological Society 7:153–162.

Payne, J. A., E. W. King, and G. Beinhart. 1968. Arthropod succession and decomposition of buried pigs. Nature 219:1180–1181.

Pechal, J. L., and M. E. Benbow. 2016. Microbial ecology of the salmon necrobiome: evidence salmon carrion decomposition influences aquatic and terrestrial insect microbiomes. Environmental Microbiology 18:1511–1522.

Pechal, J. L., T. L. Crippen, A. M. Tarone, A. J. Lewis, J. K. Tomberlin, and M. E. Benbow. 2013. Microbial community functional change during vertebrate carrion decomposition. PLoS ONE 8:e79035.

Pechal, J. L., M. E. Benbow, T. L. Crippen, A. M. Tarone, and J. K. Tomberlin. 2014a. Delayed insect access alters carrion decomposition and necrophagous insect community assembly. Ecosphere 5. https://doi.org/10.1890/es1814-00022.00021

Pechal, J. L., T. L. Crippen, M. E. Benbow, A. M. Tarone, S. Dowd, and J. K. Tomberlin. 2014b. The potential use of bacterial community succession in forensics as described by high throughput metagenomic sequencing. International Journal of Legal Medicine 128:193–205.

Pereira, L. M., N. Owen-Smith, and M. Moleon. 2014. Facultative predation and scavenging by mammalian carnivores: seasonal, regional and intra-guild comparisons. Mammal Review 44:44–55.

Perotti, M. A., and H. R. Braig. 2009. Phoretic mites associated with animal and human decomposition. Experimental and Applied Acarology 49:85–124.

Persson, Y., R. Vasaitis, B. Långström, P. Öhrn, K. Ihrmark, and J. Stenlid. 2009. Fungi vectored by the bark beetle Ips typographus following hibernation under the bark of standing trees and in the forest litter. Microbial Ecology 58:651–659.

Petersen, C. G. J. 1918. The Sea Bottom and Its Production of Fish-food, a Survey of the Work Done in Connection with Valuation of the Danish Waters from 1883-1917. C. Ferslew.

Peterson, B. F., and M. E. Scharf. 2016. Lower termite associations with microbes: synergy, protection, and interplay. Frontiers in Microbiology 7:422.

Polis, G. A., and S. D. Hurd. 1995. Extraordinarily high spider densities on islands: flow of energy from the marine to terrestrial food webs and the absence of predation. Proceedings of the National Academy of Sciences USA 92:4382–4386.

Polis, G. A., and S. D. Hurd. 1996. Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. American Naturalist 147:396–423.

Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. American Naturalist 147:813–846.

Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annual Review of Ecology and Systematics 28:289–316.

Preiswerk, D., J.-C. Walser, and D. Ebert. 2018. Temporal dynamics of microbiota before and after host death. ISME Journal 12:2076–2085.

Purahong, W., T. Wubet, G. Lentendu, M. Schloter, M. J. Pecyna, D. Kapturska, M. Hofrichter, D. Krüger, and F. Buscot. 2016. Life in leaf litter: novel insights into community

dynamics of bacteria and fungi during litter decomposition. Molecular Ecology 25:4059–4074.

Purrington, F. F., and C. J. Drake. 2008. Phoretic deutonymphs of *Schwiebea* sp. (Acari: Astigmata: Acaridae) travel in commodious nitid dorsal pits of adult *Lagocheirus araneiformis stroheckeri* Dillon (Coleoptera: Cerambycidae: Lamiinae) in Florida, U.S.A. Entomological News 119:415–419.

Refsnider, J. M., and F. J. Janzen. 2010. Putting eggs in one basket: ecological and evolutionary hypotheses for variation in oviposition-site choice. Annual Review of Ecology, Evolution, and Systematics 41:39–57.

Reid, N. M., S. L. Addison, L. J. Macdonald, and G. Lloyd-Jones. 2011. Biodiversity of active and inactive bacteria in the gut flora of wood-feeding Huhu beetle larvae (*Prionoplus reticularis*). Applied and Environmental Microbiology 77:7000–7006.

Retana, J., X. Cerdà, and X. Espadaler. 1991. Arthropod corpses in a temperate grassland: a limited supply? Ecography 14:63–67.

Reynolds, B. C., and M. D. Hunter. 2004. Nutrient cycling. Pages 387–396 in M. D. Lowman and H. B. Rinker, editors. Forest canopies. Elsevier, New York, New York, USA.

Rich, P. H., and R. G. Wetzel. 1978. Detritus in the lake ecosystem. American Naturalist 112:57–71.

Richards, E. N., and M. L. Goff. 1997. Arthropod succession on exposed carrion in three contrasting tropical habitats on Hawaii Island, Hawaii. Journal of Medical Entomology 34:328–339.

Rode, K. D., C. A. Chapman, L. J. Chapman, and L. R. McDowell. 2003. Mineral resource availability and consumption by colobus in Kibale National Park, Uganda. International Journal of Primatology 24:541–573.

Roggenbuck, M., I. B. Schnell, N. Blom, J. Bælum, M. F. Bertelsen, T. Sicheritz-Pontén, S. J. Sørensen, M. T. P. Gilbert, G. R. Graves, and L. H. Hansen. 2014. The microbiome of new world vultures. Nature Communications 5:5498.

Ronkainen, T., E. L. McClymont, M. Väliranta, and E.-S. Tuittila. 2013. The n-alkane and sterol composition of living fen plants as a potential tool for palaeoecological studies. Organic Geochemistry 59:1–9.

Rothman, J. M., P. J. Van Soest, and A. N. Pell. 2006. Decaying wood is a sodium source for mountain gorillas. Biology Letters 2:321–324.

Rozen, D. E., D. J. P. Engelmoer, and P. T. Smiseth. 2008. Antimicrobial strategies in burying beetles breeding on carrion. Proceedings of the National Academy of Sciences USA 105:17890–17895.

Ruiz-Villanueva, V., H. Piégay, A. A. Gurnell, R. A. Marston, and M. Stoffel. 2016. Recent advances quantifying the large wood dynamics in river basins: new methods and remaining challenges. Reviews of Geophysics 54:611–652.

Ruxton, G. D., and D. C. Houston. 2004. Obligate vertebrate scavengers must be large soaring fliers. Journal of Theoretical Biology 228:431–436.

Santos, P. F., J. Phillips, and W. G. Whitford. 1981. The role of mites and nematodes in early stages of buried litter decomposition in a desert. Ecology 62:664–669.

Scherer, R. 2004. Decomposition and longevity of in-stream woody debris: a review of literature from North America. Pages 127–133 in Forest Land–Fish Conference–Ecosystem Stewardship through Collaboration. Proceedings Forest-Land-Fish Conference II. April 26–28, 2004, Edmonton, Alberta.

Schoenly, K., and W. Reid. 1987. Dynamics of heterotrophic succession in carrion arthropod assemblages: discrete series or a continuum of change? Oecologia 73:192–202.

Schuurman, G. 2005. Decomposition rates and termite assemblage composition in semiarid Africa. Ecology 86:1236–1249.

Seastedt, T. R. 1984. The role of microarthropods in decomposition and mineralization processess. Annual Review of Entomology 29:25–46.

Seastedt, T. R., and C. M. Tate. 1981. Decomposition rates and nutrient contents of arthropod remains in forest litter. Ecology 62:13–19.

Selva, N., B. Jędrzejewska, W. Jędrzejewski, and A. Wajrak. 2005. Factors affecting carcass use by a guild of scavengers in European temperate woodland. Canadian Journal of Zoology 83:1590–1601.

Shivik, J. A. 2006. Are vultures birds, and do snakes have venom, because of macro- and microscavenger conflict? AIBS Bulletin 56:819–823.

Simmons, T., R. E. Adlam, and C. Moffatt. 2010. Debugging decomposition data—comparative taphonomic studies and the influence of insects and carcass size on decomposition rate. Journal of Forensic Sciences 55:8–13.

Singh, J., and S. Gupta. 1977. Plant decomposition and soil respiration in terrestrial ecosystems. Botanical Review 43:449–528.

Singh, B., T. L. Crippen, L. Zheng, A. T. Fields, Z. Yu, Q. Ma, T. K. Wood, S. E. Dowd, M. Flores, and J. K. Tomberlin. 2015. A metagenomic assessment of the bacteria associated with *Lucilia sericata* and *Lucilia cuprina* (Diptera: Calliphoridae). Applied Microbiology and Biotechnology 99:869–883.

Smith, C. R., and A. R. Baco. 2003. Ecology of whale falls at the deep-sea floor. Oceanography and Marine Biology 41:311–354.

Smith, C. R., H. L. Maybaum, A. R. Baco, R. H. Pope, S. D. Carpenter, P. L. Yager, S. A. Macko, and J. W. Deming. 1998. Sediment community structure around a whale skeleton in the deep Northeast Pacific: macrofaunal, microbial and bioturbation effects. Deep Sea Research Part II: Topical Studies in Oceanography 45:335–364.

Smith, J. B., L. J. Laatsch, and J. C. Beasley. 2017. Spatial complexity of carcass location influences vertebrate scavenger efficiency and species composition. Scientific Reports 7:10250.

Song, Z., P. G. Kennedy, F. J. Liew, and J. S. Schilling. 2017. Fungal endophytes as priority colonizers initiating wood decomposition. Functional Ecology 31:407–418.

Soper, R. S., and R. E. Olson. 1963. Survey of biota associated with Monochamus (Coleoptera: Cerambycidae) in Maine. Canadian Entomologist 95:83–95.

Speight, M. C. D. 1989. Saproxylic invertebrates and their conservation. Council of Europe, Strasbourg, France.

St John, M. G., K. H. Orwin, and I. A. Dickie. 2011. No 'home' versus 'away' effects of decomposition found in a grassland-forest reciprocal litter transplant study. Soil Biology & Biochemistry 43:1482–1489.

Stokland, J. N., J. Siitonen, and B. G. Jonsson. 2012. Biodiversity in dead wood. Cambridge University Press, Cambridge, UK.

Stoklosa, A. M., M. D. Ulyshen, Z. Fan, M. Varner, S. Seibold, and J. Müller. 2015. Effects of mesh bag enclosure and termites on fine woody debris decomposition in a subtropical forest. Basic and Applied Ecology 17:463–470.

Strickland, M. S., C. Lauber, N. Fierer, and M. A. Bradford. 2009a. Testing the functional significance of microbial community composition. Ecology 90:441–451.

Strickland, M., A. Keiser, and M. Bradford. 2015. Climate history shapes contemporary leaf litter decomposition. Biogeochemistry 122:165–174.

Strid, Y., M. Schroeder, B. Lindahl, K. Ihrmark, and J. Stenlid. 2014. Bark beetles have a decisive impact on fungal

CONCEPTS & SYNTHESIS

communities in Norway spruce stem sections. Fungal Ecology 7:47–58.

Subalusky, A. L., C. L. Dutton, E. J. Rosi, and D. M. Post. 2017. Annual mass drownings of the Serengeti wildebeest migration influence nutrient cycling and storage in the Mara River. Proceedings of the National Academy of Sciences USA 114:7647–7652.

Summerhayes, V., and C. S. Elton. 1923. Contributions to the Ecology of Spitsbergen and Bear Island. Journal of Ecology 11:214–286.

Sun, L., Z. Xie, and J. Zhao. 2000. A 3,000-year record of penguin populations. Nature 407:858.

Swift, M. J., and L. Boddy. 1984. Animal-microbial interactions in wood decomposition. Pages 89–131 in J. M. Anderson, A. D. M. Rayner, and D. W. H. Walton, editors. Invertebrate-microbial interactions. Cambridge University Press, Cambridge, UK.

Swift, M. J., O. W. Heal, and J. M. Anderson. 1979. Decomposition in terrestrial ecosystems. Studies in ecology. Blackwell Scientific, Oxford, UK.

Tanahashi, M., N. Matsushita, and K. Togashi. 2009. Are stag beetles fungivorous? Journal of Insect Physiology 55:983–988.

Tanahashi, M., K. Kubota, N. Matsushita, and K. Togashi. 2010. Discovery of mycangia and the associated xylose-fermenting yeasts in stag beetles (Coleoptera: Lucanidae). Naturwissenschaften 97:311–317.

Tang, K. W., C. S. Freund, and C. L. Schweitzer. 2006. Occurrence of copepod carcasses in the lower Chesapeake Bay and their decomposition by ambient microbes. Estuarine, Coastal and Shelf Science 68:499–508.

Tang, K. W., V. Turk, and H. P. Grossart. 2010. Linkage between crustacean zooplankton and aquatic bacteria. Aquatic Microbial Ecology 61:261–277.

Tang, K. W., M. I. Gladyshev, O. P. Dubovskaya, G. Kirillin, and H.-P. Grossart. 2014. Zooplankton carcasses and non-predatory mortality in freshwater and inland sea environments. Journal of Plankton Research 36:597–612.

Teal, J. M. 1962. Energy flow in the salt marsh ecosystem of Georgia. Ecology 43:614–624.

Thormann, M. N., R. S. Currah, and S. E. Bayley. 2001. Microfungi isolated from Sphagnum fuscum from a southern boreal bog in Alberta, Canada. Bryologist 104:548–559.

Thorne, B. L., and R. B. Kimsey. 1983. Attraction of neotropical Nasutitermes termites to carrion. Biotropica 15:295–296.

Throckmorton, H. M., J. A. Bird, L. Dane, M. K. Firestone, and W. R. Horwath. 2012. The source of microbial C has little impact on soil organic matter stabilisation in forest ecosystems. Ecology Letters 15:1257–1265.

Thunes, K. H., F. Midtgaard, and I. Gjerde. 2000. Diversity of coleoptera of the bracket fungus Fomitopsis pinicola in a Norwegian spruce forest. Biodiversity and Conservation 9:833–852.

Toki, W., M. Tanahashi, K. Togashi, and T. Fukatsu. 2012. Fungal farming in a non-social beetle. PLoS ONE 7:e41893.

Tomberlin, J. K., and P. H. Adler. 1998. Seasonal colonization and decomposition of rat carrion in water and on land in an open field in South Carolina. Journal of Medical Entomology 35:704–709.

Tomberlin, J. K., R. Mohr, M. E. Benbow, A. M. Tarone, and S. VanLaerhoven. 2011. A roadmap for bridging basic and applied research in forensic entomology. Annual Review of Entomology 56:401–421.

Tomberlin, J. K., J. Byrd, J. R. Wallace, and E. M. Benbow. 2012a. Assessment of decomposition studies indicates need for standardized and repeatable research methods in forensic entomology. Journal of Forensic Research 3:147.

Tomberlin, J. K., et al. 2012b. Interkingdom responses of flies to bacteria mediated by fly physiology and bacterial quorum sensing. Animal Behaviour 84:1449–1456.

Towne, E. G. 2000. Prairie vegetation and soil nutrient responses to ungulate carcasses. Oecologia 122:232–239.

Trumbo, S. T. 1990. Reproductive success, phenology and biogeography of burying beetles (Silphidae, Nicrophorus spp.). American Midland Naturalist 124:1–11.

Trumbo, S. T., D. S. Sikes, and P. K. B. Philbrick. 2016. Parental care and competition with microbes in carrion beetles: a study of ecological adaptation. Animal Behaviour 118:47–54.

Tscharntke, T., et al. 2012. Landscape moderation of biodiversity patterns and processes—eight hypotheses. Biological Reviews 87:661–685.

Turetsky, M. R. 2003. The role of bryophytes in carbon and nitrogen cycling. Bryologist 106:395–409.

Turner, K. L., E. F. Abernethy, M. L. Conner, O. E. Rhodes, and J. C. Beasley. 2017. Abiotic and biotic factors modulate carrion fate and vertebrate scavenging communities. Ecology 98:2413–2424.

Ulyshen, M. D. 2014. Interacting effects of insects and flooding on wood decomposition. PLoS ONE 9:e101867.

Ulyshen, M. D. 2015. Insect-mediated nitrogen dynamics in decomposing wood. Ecological Entomology 40:97–112.

Ulyshen, M. D. 2016. Wood decomposition as influenced by invertebrates. Biological Reviews 91:70–85.

Urbina, H., J. Schuster, and M. Blackwell. 2013. The gut of Guatemalan passalid beetles: a habitat colonized by cellobiose- and xylose-fermenting yeasts. Fungal Ecology 6:339–355.

Van der Wal, R., R. D. Bardgett, K. A. Harrison, and A. Stien. 2004. Vertebrate herbivores and ecosystem control: cascading effects of faeces on tundra ecosystems. Ecography 27:242–252.

Van der Wal, A., W. de Boer, W. Smant, and A. van Veen. 2007. Initial decay of woody fragments in soil is influenced by size, vertical position, nitrogen availability and soil origin. Plant and Soil 301:189–201.

Van Geel, B. 1978. A palaeoecological study of Holocene peat bog sections in Germany and The Netherlands, based on the analysis of pollen, spores and macro- and microscopic remains of fungi, algae, cormophytes and animals. Review of Palaeobotany and Palynology 25:1–120.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. River continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130–137.

Vass, A. A. 2001. Beyond the grave: understanding human decomposition. Microbiology Today 28:190–192.

Verhoeven, J. T. A., and W. M. Liefveld. 1997. The ecological significance of organochemical compounds in Sphagnum. Acta Botanica Neerlandica 46:117–130.

Villiers Pienaar, U. D.. 1969. Predator-prey relationship amongst the larger mammals of the Kruger National Park. Koedoe 12:108–176.

Voříšková, J., and P. Baldrian. 2013. Fungal community on decomposing leaf litter undergoes rapid successional changes. ISME Journal 7:477–486.

Wall, D. H., M. A. Bradford, M. G. S. T. John, J. A. Trofymow, V. Behan-Pelletier, D. E. Bignell, J. M. Dangerfield, W. J. Parton, J. Rusek, and W. Voigt. 2008. Global decomposition experiment shows soil animal impacts on decomposition are climate-dependent. Global Change Biology 14:2661–2677.

Wallace, J. R. 2015. Aquatic vertebrate carrion decomposition. Pages 247–271 in M. E. Benbow, J. K. Tomberlin, and A. M. Tarone, editors. Carrion ecology. Evolution and their applications. CRC Press, Boca Raton, Florida, USA.

Wallace, J. B., S. L. Eggert, J. L. Meyer, and J. R. Webster. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. Science 277:102–104.

Wallace, J. B., S. Eggert, J. L. Meyer, and J. Webster. 1999. Effects of resource limitation on a detrital-based ecosystem. Ecological Monographs 69:409–442.

Wang, Y., and D. E. Rozen. 2017. Gut microbiota colonization and transmission in the burying beetle *Nicrophorus vespilloides* throughout development. Applied and Environmental Microbiology 83:e03250-16.

Warren, R. J., and M. A. Bradford. 2012. Ant colonization and coarse woody debris decomposition in temperate forests. Insectes Sociaux 59:215–221.

Waters, T. F. 1966. Production rate, population density, and drift of a stream invertebrate. Ecology 47:595–604.

Waters, T. F. 1969. The turnover ratio in production ecology of freshwater invertebrates. American Naturalist 103:173–185.

Waters, T. F. 1977. Secondary production in inland waters. Advances in Ecological Research 10:91–164.

Weatherbee, C., J. Pechal, and M. Benbow. 2017. The dynamic maggot mass microbiome. Annals of the Entomological Society of America 110:45–53.

Webster, J., and E. Benfield. 1986. Vascular plant breakdown in freshwater ecosystems. Annual Review of Ecology and Systematics 17:567–594.

Weedon, J. T., W. K. Cornwell, J. H. C. Cornelissen, A. E. Zanne, C. Wirth, and D. A. Coomes. 2009. Global meta-analysis of wood decomposition rates: a role for trait variation among tree species? Ecology Letters 12:45–56.

Wei, H., Q. Xu, L. E. Taylor, J. O. Baker, M. P. Tucker, and S.-Y. Ding. 2009. Natural paradigms of plant cell wall degradation. Current Opinion in Biotechnology 20:330–338.

Wende, B., M. M. Gossner, I. Grass, T. Arnstadt, M. Hofrichter, A. Floren, K. E. Linsenmair, W. W. Weisser, and I. Steffan-Dewenter. 2017. Trophic level, successional age and trait matching determine specialization of deadwood-based interaction networks of saproxylic beetles. Proceedings of the Royal Society B 284:20170198.

Weslien, J., L. B. Djupström, M. Schroeder, and O. Widenfalk. 2011. Long-term priority effects among insects and fungi colonizing decaying wood. Journal of Animal Ecology 80:1155–1162.

Wiens, J. A. 1995. Landscape mosaics and ecological theory. Pages 1–26 *in* L. Hannsson, L. Fahrig, and G. Merriam, editors. Mosaic landscapes and ecological processes. Springer, Dordrecht, The Netherlands.

Wilmers, C. C., R. L. Crabtree, D. W. Smith, K. M. Murphy, and W. M. Getz. 2003. Trophic facilitation by introduced top predators: grey wolf subsidies to scavengers in Yellowstone National Park. Journal of Animal Ecology 72:909–916.

Wilson, E. O. 1971. The insect societies. Harvard University Press, Cambridge, UK.

Wilson, K., and D. J. B. White. 1986. The anatomy of wood: its diversity and variability. Stobart and Son, London, UK.

Wilson, E. E., and E. M. Wolkovich. 2011. Scavenging: how carnivores and carrion structure communities. Trends in Ecology and Evolution 26:129–135.

Witkamp, M. 1966. Decomposition of leaf litter in relation to environment, microflora, and microbial respiration. Ecology 47:194–201.

Wood, T. G., and R. J. Thomas. 1989. The mutualistic association between Macrotermitinae and Termitomyces. Pages 69–92 *in* N. Wilding, N. M. Collins, P. M. Hammond, and J. F. Webber, editors. Insect-fungus interactions. Academic Press, London, UK.

Woodcock, B. A., A. D. Watt, and S. R. Leather. 2002. Aggregation, habitat quality and coexistence: a case study on carrion fly communities in slug cadavers. Journal of Animal Ecology 71:131–140.

Woodward, G., et al. 2012. Continental-scale effects of nutrient pollution on stream ecosystem functioning. Science 336:1438–1440.

Wotton, R. S., and B. Malmqvist. 2001. Feces in aquatic ecosystems. BioScience 51:537–544.

Yang, L. H. 2004. Periodical cicadas as resource pulses in North American forests. Science 306:1565–1567.

Yang, L. H., K. F. Edwards, J. E. Byrnes, J. L. Bastow, A. N. Wright, and K. O. Spence. 2010. A meta-analysis of resource pulse–consumer interactions. Ecological Monographs 80:125–151.

Young, O. P. 1984. Utilization of dead insects on the soil surface in row crop situations. Environmental Entomology 13:1346–1351.

Zak, D. R., W. E. Holmes, D. C. White, A. D. Peacock, and D. Tilman. 2003. Plant diversity, soil microbial communities, and ecosystem function: are there any links? Ecology 84:2042–2050.

Zhou, C., and R. W. Byard. 2011. Factors and processes causing accelerated decomposition in human cadavers–An overview. Journal of Forensic and Legal Medicine 18:6–9.

DATA AVAILABILITY

CONCEPTS & SYNTHESIS