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NECROBIOME FRAMEWORK FOR BRIDGING Decomposition ecology of autotrophically and heterotrophically derived organic Matter

Mark Eric Benbow ^(D), Philip S. Barton, Michael D. Ulyshen, James C. Beasley, Travis L. DeVault, Michael S. Strickland, Jeffery K. Tomberlin, Heather R. Jordan, and Jennifer L. Pechal

Study Description

Life arises from death through species that decompose dead biomass or necromass. This paper provides a synthesis of the species responsible for dead plant and animal decomposition and describes a conceptual perspective—the "necrobiome"—that defines the diverse and complex communities that interact to recycle necromass. The concept brings unification to the previously disparate fields of plant and animal decomposition by discussing the universal processes occurring across *all* forms of necromass. It highlights the factors that make each form of dead biomass different in a way that defines how unique necrobiomes drive decomposition and ultimately shape ecosystem structure and function.

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Photo I. Dead and fallen trees are autotrophically derived necromass that can persist for decades. Dead trees act as a food resource and habitat for a succession of prokaryotic and eukaryotic species that slowly recycle the biomass and nutrients in ecosystems around the world. Leaf detritus decomposes much more quickly than large wood debris by another suite of decomposer species of the necrobiome. (Photo by M.E. Benbow)



Photo 2. Necromass of dead and fallen trees also serves as food and habitat at the interface of terrestrial and aquatic ecosystems, sometimes providing these resources to both habitat types. At the end of a long Michigan winter, most fallen leaf detritus has been recycled by both terrestrial and aquatic saprotrophic species, providing carbon and nutrient subsidies downstream into the watershed continuum. (Photo by M.E. Benbow)



Photo 3. Tree necromass sometimes uncovers the subterranean world of the necrobiome, where necromass of microbial species (e.g., bacteria, fungi, protists, and micro-eukaryotes) is recycled and contributes to rhizosphere ecology and the critical soil carbon budgets among global biomes. (Photo by M.E. Benbow)



Photo 4. Necromass also comes in the form of carrion, or the carcasses of terrestrial and aquatic organisms that represent heterotrophically derived biomass in ecosystems. This eastern gray kangaroo carcass serves as a food and habitat resource for a predictable sequence of necrophagous prokaryotic and eukaryotic species of the necrobiome, with blow flies (Diptera: Calliphoridae) often considered the pioneer animal scavengers that compete with vertebrates for the decomposing resource. As the carcass decomposes, it changes the underlying soil chemistry and contributes microbial species that change both the community structure and function of the soil. (Photo by P.S. Barton)

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Photo 5. Many necrobiome species provide additional ecosystem functions and services. Blow flies and other necrophagous insects can emerge in huge numbers from animal carcasses, and are known to serve as pollinators in many ecosystems around the world, like for this yarrow; however, their net importance has only recently been investigated. (Photo by Bob Armstrong)



Photo 6. Some carrion (and autotrophically derived biomass, e.g., seaweed) necromass crosses terrestrial and aquatic biomes, as in the case of anadromous salmon (A) that serve as an important food source for vertebrate scavengers (e.g., bears). Necromass "leftovers" also becomes a food and habitat resource for invertebrate scavengers like blow flies (B). (Photos by M.E. Benbow)



Photo 7. After live or dead plant or animal biomass is consumed and digested, a portion is processed and excreted and becomes new necromass in the form of dung (or frass). Dung can then serve as a food and habitat resource for another unique suite of evolved and specialized saprotrophic species, such as these dung beetles on manure. (Photo by R.W. Merritt)



Photo 8. The different turnover rates of various forms of necromass (e.g., leaf litter, dung, or wood) can be striking and important to the spatially and temporally mediated impacts of nutrient and carbon subsidies to both necrobiome communities and the wider food web in an ecosystem. (Photo by M.E. Benbow)



Photo 9. The interactions among organisms of the necrobiome are sometimes difficult to measure. In this case, dead salmon are decomposing along a riparian corridor of Alaska, with microbes and blow flies functioning as primary consumers. But these consumers are adjacent to bear dung impregnated with blow fly larvae that had once fed on salmon necromass. This dung, in turn, is also adjacent to wood necromass of an unknown age and source, and with an unknown necrobiome. The habitat and ecosystem level spatio-temporal effects of necrobiome processing of decomposing biomass is varied, dynamic, and complex. (Photo by M.E. Benbow)



Photo 10. Aspects of the complexity of necrobiome interactions, and the cascading effects through ecosystems, can be represented by those forms of necromass that indirectly serve as a food resource. Aquatic caddisfly larvae graze on the microbial communities that form on decomposing salmon in a way that mediates their growth, development, and ultimately secondary production. This process occurs across different sized carcasses, with research reporting that whale carcasses provide energy and nutrients to a diverse necrobiome community for decades in deep benthic ecosystems. (Photo by M.E. Benbow)



Photo II. An often overlooked and underappreciated form of necromass is that of surplus gametes produced during mass spawning events (e.g., corals and other invertebrates), like that of spent salmon. This necromass serves as a source of food and nutrients for microbes, invertebrates, and vertebrates as they decompose in large quantities in watershed ecosystems. Unhatched or unfertilized eggs of other species also represent this form of understudied necromass. (Photo by M.E. Benbow)



Photo 12. Necrobiome interactions among species span both intra- and inter-specific relationships among microbes, invertebrates, and vertebrates and can be mediated by seasonal fluctuations in both biotic and abiotic factors. For example, warmer temperatures favor invertebrate and microbial activity, providing these organisms with a competitive advantage over vertebrates for carcass resources (Figure 4). However, in colder environments and during winter, vertebrates such as coyotes dominate consumption of carcasses, which serve as an important source of nutrients for a diversity of obligate and facultative vertebrate scavengers. (Photo by K.Turner and J.C. Beasley)

These photographs illustrate the article "Necrobiome Framework for Bridging Decomposition Ecology of Autotrophically- and Heterotrophically-Derived Organic Matter" by Mark Eric Benbow, Philip S. Barton, Michael D. Ulyshen, James C. Beasley, Travis L. DeVault, Michael S. Strickland, Jeffery K. Tomberlin, Heather R. Jordan, and Jennifer L. Pechal published in *Ecological Monographs*. https:// doi.org/10.1002/ecm.1331