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Necrobiome Framework for Bridging Decomposition Ecology of Autotrophically- and Heterotrophically-Derived Organic Matter

Running Title: The Necrobiome in Decomposition Ecology

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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 and global nutrient recycling and energy flow.

Key words: biodiversity; carrion; detritus; decomposition; ecosystem; litter; community assembly; interactions; 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 (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.

81   Dead organic matter of any type is defined as detritus (Petersen et al, 1918; Odum et al, 1963)

82   but has been primarily perceived in the literature as organic matter resulting from plant death,

83   with some, but few, instances of dead animal organic matter (or carrion) referred to as detritus

84   (e.g., Swift et al 1979, Moore et al 2004). In the current literature, the majority of references to

85   detritus describe decomposing plant biomass, reinforcing a separation with other widely

86   ubiquitous forms of biomass with relatively higher turnover, such as carrion and dung/feces.

87   With this understanding we propose to facilitate broader recognition of the commonalities and

88   differences of dead organic matter of any type, defined in this paper as necromass, a term

89   previously used in the literature (e.g., Coûteaux et al. 2005, Lomstein et al. 2012), but

90   understood to be synonymous with the holistic definition of detritus as summarized by Moore et

91   al. (2004).

92

93   Necromass takes a wide range of shapes, sizes and quality (Swift et al. 1979, Carter et al. 2007).

94   It forms the basis of many foodwebs and consequently has significant bottom-up importance for

95   ecosystem function (Gessner et al. 2010). It also forms the focal point for interactions and

96   behaviors among decomposer species comprising complex communities influencing ecosystems

97   across temporal and spatial scales (Yang et al. 2010); and in freshwater habitats, decomposition

98   is considered a fundamental ecosystem process that contributes to watershed biodiversity

99   (Woodward et al. 2012). Despite the importance of decomposer communities there exists no

100 standard framework to conceptualize their complex and dynamic interactions across both plant

101 and animal necromass. This lack of a framework is significant because it limits a comprehensive

102 understanding of the community ecology of decomposition and has implications for defining and

103   testing paradigms related to nutrient recycling, gene flow, population dynamics, and other

104   ecosystem processes at the frontier of ecological research.

105

106   There has been a recent expansion of knowledge about both micro- and macro-scale processes

107   structuring decomposer communities and contributing to the species interactions (e.g., Burkepile

108   et al. 2006, Gessner et al. 2010, Wilson and Wolkovich 2011, Metcalf et al. 2016); however,

109   much is still unknown. To date, ecological theory describing decomposition processes has

110   included succession theory (Payne et al. 1968, Michaud et al. 2015), meta-population theory

111   (Hanski 1987), and aggregation and coexistence theory (Ives 1991). Carrion and dung, in

112   particular, have been useful systems to test and develop these theories and mechanistic

113   hypotheses having relevance to many other areas of ecology (see Box 1). However, a new

114   synthesis is required to integrate existing knowledge with the new discoveries occurring in the

115   animal and plant decomposition disciplines. We propose an expansion of a recent framework to

116   facilitate this synthesis in a way that encompasses all forms, functions, and ecological dynamics

117   of organic matter decomposition – the necrobiome (Figure 1).

118

119   The necrobiome was originally defined as "…the community of species (both prokaryotic and

120   eukaryotic) associated with decomposing remains of heterotrophic biomass, including animal

121   carrion and human corpses" (sensu Benbow et al. 2013). While the original development of this

122   term was focused on vertebrate carrion, we argue it can be expanded to include any form of

123   necromass (e.g., leaves, wood, dung). We also suggest the necrobiome framework is relevant to

124   both plant (i.e., autotrophically-derived) and animal (i.e., heterotrophically-derived) necromass

125   decomposition by highlighting the fundamental similarities and differences in the processes that

126   define decomposition. In this paper, we take a conciliatory approach to more fully develop the

127   necrobiome framework as a unifying construct for guiding research in decomposition, regardless

128   of how the life form was derived (Figure 2). All life is terminal and the remaining nutrients and

129   energy are ultimately recycled within and across ecosystems (Polis et al. 1997). Some aspects of

130   this ecological process are universal across all forms of necromass, such as disintegration,

131   dispersal, and microbial activity. In contrast, other aspects, such as community dynamics and

132   decomposition rates, and specific decomposer taxa, are distinct across the different forms of

133   necromass. The major similarities and differences in necrobiome structure and function have yet

134   to be synthesized in detail but are influenced by the overall composition and quality of the

135   specific necromass, and the associated decomposer species that have evolved to exploit the

136   resource.

137

138   In this review, we provide an overview of the similarities and differences among decomposer

139   communities associated with plant and animal necromass. We suggest plant and animal

140   necromass research findings illustrate a broader generality to the processes structuring

141   decomposer communities across a range of substrates that, cumulatively, have large-scale

142   ecosystem level effects. We synthesize the key similarities and differences among these

143   decomposer communities and place them into a broadened conceptual model of the necrobiome.

144   We then provide details of the biotic structure of the necrobiome, the different ecological

145   functions each part performs, and the key interactions occurring among the decomposer

146   organisms. Further, we explore how the necrobiome provides a useful way to conceptualize how

147   decomposition delivers nutrients, energy, genomes, and communities across space and time with

148   ultimate responses in ecosystem biodiversity and function. By presenting a new synthesis of

149   decomposer communities that continues the approach developed by Moore et al. (2004), we aim

150   to provide an integrative perspective to the key concepts used by researchers that are separated

151   into plant or animal decomposition disciplines. Rather than continuing to consider each

152   necromass type in isolation, we stress the importance of synthesizing this knowledge to develop

153   a holistic understanding of nutrient cycling and food web dynamics across scales.

154

155   **AUTOTROPHICALLY- AND HETEROTROPHICALLY-DERIVED BIOMASS:**

156   **STANDING STOCKS, PRODUCTION AND TURNOVER**

157

158   Autotrophically-derived necromass refers to the dead biomass produced from organisms that use

159   energy from sunlight as energy (e.g., plants and algae) or chemical reactions (various

160   prokaryotes) to produce organic compounds. Heterotrophically-derived necromass, by contrast,

161   refers to the dead biomass produced from organisms that obtain organic material through the

162   consumption of other organisms (e.g., animals, fungi, protists and other micro-eukaryotes). We

163   focus our discussion here on the initial and intact forms of necromass exceeding 8 mm^3 in size

164   for which there is a richer source of literature supporting a more detailed assessment of the

165   necrobiome. We acknowledge that all necromass ultimately becomes smaller than this size, and

166   that the decomposition of microorganisms, such as fungal necromass, is ecologically important

167   (Fernandez and Kennedy 2018). For instance, fungi and protists produce macroscopic structures

168   supporting unique necrobiome communities, such as giant kelp (Macrocystis pyrifera

169   [Linnaeus]) (Inglis 1989, Thunes et al. 2000). The importance of bacteria and fungi to

170   decomposition goes beyond diversity, with reports of soil microbial biomass being an order of

171   magnitude greater than the biomass of other soil organisms, and two orders of magnitude greater

172 than aboveground animal biomass (Fierer et al. 2009). This large amount of microbial biomass

173 has the potential to influence ecosystem processes as it dies and becomes microbial necromass

174 (Throckmorton et al. 2012). In fact, this microbial necromass, in combination with microbial

175 metabolites, likely drives a significant proportion of soil organic matter formation (Kallenbach et

176 al. 2015, Brabcová et al. 2016, Fernandez et al. 2016). Soil fungal mycelia production alone

177 contributes to major functional processes in terrestrial ecosystems, with production (and

178 associated death and decomposition) reported to range from $100 – 300$ kg ha^{-1} yr^{-1} (Ekblad et al.

179 2013). The necrobiome of dead fungal mycelium has been reported to be quite diverse (Ekblad et

180 al. 2013, Brabcová et al. 2016), providing additional evidence that decomposition networks of

181 microorganisms operate at every biological scale and contribute to complex patterns of

182 biodiversity and associated functions in all ecosystems. However, there is much less understood

183 of the species and processes of decomposition of fine particulate necromass and microorganisms

184 (however, see Alldredge and Silver 1988) across ecosystems, a fruitful area of future research

185 and review.

186

187 Based on size and composition, plant material can be divided into herbaceous (e.g., leaves) and

188 woody forms. Animal necromass produced by vertebrates can be distinguished from invertebrate

189 based on both size and internal or external skeletal structures. Dung, however, is an intermediate

190 and highly transformed form of necromass characterized by fragmented and partially digested

191 plant and/or animal material mixed with host gut-dwelling microbes. Herbivorous invertebrates

192 (Reynolds and Hunter 2004) and vertebrates (Frank and Evans 1997) are known to generate large

193 amounts of dung that play a critical role in nutrient cycling and redistribution in terrestrial and

194 aquatic ecosystems (Wotton and Malmqvist 2001, Carline et al. 2005, Menendez et al. 2016).

195 For the sake of space and focus, we do not elaborate on the dynamics of dung or frass; however,

196 we encourage those interested in this topic to review the literature on the ecology and evolution

197 of dung beetles (Hanski and Cambefort 1991) and the additional importance of feces in terrestrial

198 (Van der Wal et al 2004) and aquatic (Alldredge and Silver 1988, Wotton and Malmqvist 2001,

199 Joyce et al 2007) ecosystems. Below, we discuss in more detail the differences in the structure

200 and composition of different forms of plant and animal necromass.

201

202 To our knowledge, no efforts have been made to compare the relative production or communities

203 associated with the decomposition of plant and animal necromass in any ecosystem. Several

204 comparisons of biomass in forested systems, however, provide some insight into the question of

205 how much detritus is present in a habitat at any given time. Odum (1970), for example,

206 determined in a Puerto Rican rainforest that plants and animals made up about 58% and 0.03%

207 of the total biomass (including soil organic matter), respectively. Leaves accounted for only

208 about 5% of above-ground plant biomass, with the rest consisting of wood and bark. Fittkau and

209 Klinge (1973) reported animals made up only about 0.02% of the total living biomass in an

210 Amazonian rainforest, with < 10% of that component being of vertebrate origin. In most

211 freshwater stream ecosystems leaf litter decomposition is a key process that influences energy

212 and nutrient flow, biodiversity and links terrestrial and marine ecosystems through a downstream

213 continuum (Vannote et al. 1980, Webster and Benfield 1986, Wallace et al 1997, Gessner et al.

214 2010). Detritus in a variety of organic matter forms is thought to represent the dominate energy

215 pathway in most lakes (Rich and Wetzel 1978, Mann 1988) and other lentic surface waters such

216 as wetlands (Brinson et al 1981), coastal ecosystems (Duggins et al. 1989) and oceans (Parsons

217 and Strickland 1962, Alldredge and Silver 1988). The differences in standing necromass

218   between plants and animals are probably even larger than these estimates of biomass given that

219   animal remains typically decompose much more quickly than plants, even in some aquatic

220   habitats (Parmenter and Lamarra 1991).

221

222   In many cases animal necromass will be produced more quickly given the shorter life spans of

223   most animals compared with many plants, especially when comparing invertebrate necromass

224   production with the woody components of plants. However, many plants shed biomass

225   seasonally as leaves and root exudates, thus producing necromass at higher rates than the woody

226   components that make up a large portion of the standing stock biomass. Furthermore, the total

227   production of animal necromass per year could be expected to far exceed the standing animal

228   necromass at any given time due to a combination of short life spans, continuous reproduction

229   and rapid decay rates such as those for zooplankton (e.g., Tang et al 2014 and references

230   therein). By contrast, the production of plant necromass produced per year can be expected to be

231   a small fraction of the standing plant necromass in many ecosystems, and this is especially true

232   for forests where decomposition is slow and woody debris accumulates over time (Luyssaert et

233   al. 2008). The relative importance of these differences in standing stock, production and rate of

234   decay of plant and animal necromass is an area of inquiry that could provide broad ecological

235   understanding of different forms or routes of energy flow and nutrient cycling in ecosystem

236   function.

237

238   Focusing on vertebrate animals, Odum (1970) estimated that they accounted for only about 5%

239   of total animal biomass, with the remaining 95% consisting of invertebrates [see Tables 7 and 22

240   in Odum (1970)]. Additionally, a meta-analysis by Fierer et al. (2009) determined approximately

241 50% of animal biomass is belowground. The fact that invertebrates are typically much shorter

242 lived than vertebrates, usually develop to maturity more quickly, and often have multiple

243 generations per year suggests the annual production of necromass by invertebrates far exceeds

244 that produced by vertebrates. Indeed, Seastedt and Tate (1981) estimated the standing arthropod

245 necromass on the forest floor of two oak-hickory forests to be up to double the estimated living

246 arthropod biomass for the same forests. In other habitats, such as aquatic systems, standing stock

247 biomass can be estimated for populations and communities (Waters 1966, 1969, Benke et al

248 1988), but some studies also produce estimates of production, often as secondary production of

249 macroinvertebrates (Benke et al. 1988, Huryn and Wallace 2000).

250

251 Knowledge of animal biomass in aquatic systems can be derived from measures of secondary

252 production of invertebrates (Hynes 1970, Waters 1977, Benke et al. 1988, Huryn and Wallace

253 2000). Secondary production includes the elaboration of heterotrophic population biomass and

254 assumes a yield to higher trophic levels that ultimately becomes part of the necromass pool in a

255 given ecosystem. The method employs estimates of individual organismal body mass, often

256 using length-mass regressions (Benke et al 1999), and densities of those organisms and how they

257 quantitatively change over time. One such method for calculating secondary production (i.e.,

258 removal-summation) assumes all biomass produced eventually dies and is equivalent to

259 estimated production for that cohort of organisms over a given time and under steady-state

260 conditions (Boysen-Jensen 1919, Waters 1977, Benke and Huryn 2006). Thus, secondary

261 production estimates of invertebrates may provide quantitative insight into the contribution of

262 animal necromass and its turnover to ecosystem energetics, much like it has been done for

263 measuring the importance of leaf necromass on aquatic invertebrate communities (Cummins et al

264 1973, Wallace et al 1999). Measuring living invertebrate biomass over time, however, does not

265 allow for estimating other forms of necromass, such as dung or frass.

266

267 The importance of necrobiomes in the decomposition of entire communities of organisms could

268 be pivotal in expanding our understanding of biodiversity contributions to global carbon and

269 nutrient cycling, as has been discussed by Moore et al (2004). As an example, a fascinating study

270 reported that the quality of grasshopper necromass (affected by fear of predation) mediated

271 subsequent leaf litter decomposition in old field ecosystems, with estimated significant

272 ecosystem level consequences (Hawlena et al. 2012). Discovering how animal and plant

273 necromass decomposition communities interact with each other to drive nutrient and carbon

274 cycling could lead to paradigm shifts in ecosystem science.

275

276 **INTRINSIC VARIABILITY OF NECROMASS TYPES**

277

278 Major forms of necromass (e.g., carrion, dung, leaves and wood) can be distinguished from one

279 another in three important ways: (i) resource size, (ii) nutrient availability, and (iii) digestibility.

280 First, the unit volumes of different forms of necromass vary by 5 to 11 orders of magnitude

281 (Figure 3). While the largest forms of necromass produced globally are the woody stems and

282 collective dead organic matter shedding of large trees, vertebrate carrion is the largest form in

283 many non-forested ecosystems (e.g., bison in grasslands, whales in oceans) (Towne 2000, Smith

284 and Baco 2003). Resource size has important implications for the decomposition process, with

285 larger resources decomposing more slowly and involving a greater diversity of species than

286 smaller resources. Small arthropod carcasses, for example, typically disappear within several

287   minutes to hours, being quickly discovered and consumed by ants, wasps or other scavengers

288   (Fellers and Fellers 1982, Young 1984, Retana et al. 1991). By contrast, the decomposition of

289   larger carcasses typically involves a much wider variety of species and succession of

290   decomposer communities (Jones et al. 2015, Turner et al. 2017). Large resources also have less

291   surface area relative to volume than small resources and this limits initial accessibility by some

292   decomposers and thus in some cases large vertebrates (e.g., elephants) decompose initially

293   through microbial decomposition (Coe 1978). Fragmentation and penetration of necromass are

294   both mediated by the animal community, and thus are important processes with respect to the

295   acceleration of decomposition (see below).

296

297   Second, different forms of necromass vary in nutritional quality. The carbon:nitrogen (C:N) ratio

298   is commonly used to indicate the nutritional quality of organic material. The C:N ratio varies

299   greatly among the various types of necromass, being lowest for carrion and highest for wood

300   (Figure 3). The C:N ratio also varies widely among necromass types due largely to inter-specific

301   variability. For example, it was reported up to 16-fold differences in C:N ratios existed among 59

302   species of tropical wood species (Martin et al. 2014). Intra-specific variability can also be

303   important. For example, Madritch et al. (2007) reported 2-3-fold differences in C:N ratios of

304   caterpillar frass depending on the nutritional quality of their host plants. It has also been

305   suggested that dung beetles are limited by assimilable C and not N (Holter and Scholtz 2007).

306

307   The third dimension is digestibility (not shown in Figure 3). For plants, digestibility is largely

308   determined by the structure of cell walls. Due to the recalcitrance of lignocellulose (i.e., a

309   complex of lignin, cellulose, and hemicellulose) in plant cell walls, plant matter is much more

310   resistant to decomposition than most animal soft tissues. For example, these recalcitrant

311   compounds dominate plant tissues, respectively accounting for 20-35%, 40-45% and 20-40% of

312   dry wood weight (Wilson and White 1986) and are highly variable among leaf litter types that

313   contribute to stream ecosystem function (Webster and Benfield 1986, Woodward et al. 2012).

314   Whereas a wide range of organisms can digest animal tissues, the digestion of lignin and

315   cellulose is almost entirely limited to fungi and prokaryotes that have evolved the enzymes

316   required to break down these compounds. This dependence on microbes to reduce

317   autotrophically-derived detritus has given rise to a number of important symbioses between

318   wood and leaf-feeding insects and fungi (see section on symbioses in the necrobiome).

319   Secondary plant compounds and other extractives also reduce the digestibility of dead plant

320   matter and can have toxic effects on decomposers (Käärik 1974, Verhoeven and Liefveld 1997).

321   Among carrion consumers, there is also specialization on recalcitrant body parts. For example,

322   the bearded vulture eats only the bones of vertebrates (Margalida et al. 2009), whereas some

323   tineid moths eat only the horns and hooves of ungulates (Braack 1987). Such specialization,

324   however, involves digestive enzymes and stomach acids, and not symbioses.

325

326   Another important difference between the necromass production from plants and animals

327   concerns the gradual process by which many perennial plants, especially woody plants, die. In

328   forest trees, for example, young branches produced at the top cast shade on older branches

329   below, reducing their ability to capture sunlight and contribute to the growth of the tree. These

330   overshadowed branches eventually die and fall to the ground, ultimately resulting in the long

331   limbless trunks characteristic of many mature forest trees: a very long-term shedding of detritus

332   over the lifetime of the tree. Similarly, growth in tree diameter is accompanied by the senescence

333   and death of the oldest, innermost rings (Figure 2a). Not only are these tissues not living, they

334   often become colonized by diverse assemblages of decomposers many decades before the rest of

335   the tree fully dies and falls to the forest floor (Elton 1966). This necromass accumulation co-

336   occurs for years to decades with living tissue, providing a unique aspect of the necrobiome

337   concept. Wounds through the bark layer (e.g., caused by extreme weather events, toppled

338   neighboring trees, injuries from animal activity, etc.) expose the underlying phloem and wood

339   for colonization and mark the beginning of the decay process in living trees. Although trees

340   possess a variety of defensive mechanisms to limit the extent to which wounded areas are

341   colonized by microbes and insects (e.g., flooding the site with water or sap, secondary plant

342   compounds, etc.), organisms responsible for decay often become established at these sites. The

343   first to colonize are the more ruderal microbial taxa, such as non-basiodiomycetes and bacteria,

344   whereas wood-rotting fungi arrive later (Boddy 2001). The proportion of dead tissue in otherwise

345   living trees increases with tree age and the largest and oldest trees, or "veteran trees", are full of

346   dead limbs, rot holes and are believed to be particularly important to supporting necrobiome

347   biodiversity (Speight 1989, Stokland et al. 2012). The decomposition of tree tissue has been

348   shown to be a substantial source of methane (Covey et al. 2012), suggesting broader effects on

349   global biogeochemical cycling rates and atmospheric chemistry that require future investigation.

350

351   **THE NECROBIOME**

352

353   **Necrobiome Structure**

354

355   The necrobiome defines a relatively concentrated set of organisms where many have evolved to

356   detect, use and ultimately congregate with decaying organic matter either as a food or habitat

357   resource (Benbow et al. 2013). Below, we describe in more detail the microbial, invertebrate,

358   and vertebrate components of the decomposer community, as well as important symbioses,

359   interactions with soil, and abiotic factors that govern the composition and dynamics of the

360   necrobiome (Figure 1).

361

362   **Microbial Communities of the Necrobiome**

363

364   Structurally, the necrobiome consists of the prokaryotic and eukaryotic microbial communities

365   (microbiome) that are internal (endonecrotic) and external (epinecrotic) components of host

366   necromass. While given different names, these microbial communities have been reported in

367   both living plants (Bulgarelli et al. 2013) and animals (Dillon and Dillon 2004). These microbial

368   communities function as symbionts, commensals, pathogens and parasites during life, and the

369   taxa become the pioneer community of plant detritus or carrion immediately after, or prior to,

370   death in both terrestrial (Frankland 1966, Latter and Cragg 1967) and aquatic ecosystems

371   (Preiswerk et al. 2018). The community succession of carrion is rapid after death without the

372   biotic constraints of host immunology and physiological function (Pechal et al. 2014b, Metcalf et

373   al. 2016), which determines the taxonomic and functional changes of the microbiota of the

374   necrobiome through decomposition (Latter and Cragg 1965, Baldy et al 1995, Crippen et al.

375   2015).

376

377   In aquatic leaf litter decomposition studies in streams, microbial community structural and

378   functional succession is related to the leaf litter species and quality (Witkamp 1966, Gessner and

379   Chauvet 1994), similar to other forms of necromass like crayfish (Procambarus versutus

380   [Hagan]) molted exoskeletons (Aumen 1980); particulate aggregates (Grossart and Simon 1988)

381   lake zooplankton (Yang et al. 2009); and oceanic phytoplankton (Fukami et al. 1985) and

382   zooplankton (Tang et al. 2006) that harbor complex microbial dynamics that change with water

383   chemistry, depth and system circulation (Karl et al. 1988). While difficult to study, whale and

384   other cetacean carcasses that sink to the oceanic abyss attract a high diversity of vertebrate and

385   invertebrate scavengers (Allison et al. 1991, Jones et al. 1998, Smith and Baco 2003) and also

386   change the microbial ecology of the local habitat in a way that is dominated by

387   chemoautotrophic communities (Bennett et al. 1994) in a network of species interactions (Smith

388   et al. 1998). The microbial community changes associated with the death and deep sea

389   decomposition of whale carcasses has not, to our knowledge, been studied, but may follow

390   successional trajectories similar to those reported for other aquatic organisms (Preiswerk et al.

391   2018).

392

393   Microbial succession facilitates the proliferation of existing saprophytic taxa of the once living

394   host through the secretion of enzymes and other compounds used to convert the newly available

395   organic matter for assimilation. The microbial ecology of decomposing necromass is likely

396   substantially different between plant and animal forms in terrestrial and aquatic ecosystems;

397   however, there have been no comparative studies to directly evaluate microbial succession

398   differences of plant and animal decomposition in either terrestrial or aquatic habitats. When one

399   descriptively compares microbial succession of plant detritus to carrion there are interesting, and

400 potentially functionally important, differences. For instance, the taxon richness and diversity of

401 microbial communities were shown to increase over decomposition for beech leaves, with

402 predominate phyla not including the Firmicutes (Purahong et al. 2016); whereas for carrion,

403 Firmicutes often make up a significant proportion of the communities and become dominant late

404 in decomposition when taxon richness and diversity are lowest (Pechal et al. 2014b).

405 Interestingly, the microbial communities of decomposing fungal mycelia in soil show more

406 similar characteristics to carrion than leaf litter on soil, with Proteobacteria being most dominant

407 early and being replaced by Firmicutes later in decomposition (Brabcová et al. 2016). The

408 microbes inherently a part of the living organism and part of the initial communities present for

409 decomposition are highly variable depending on the host species, health, habitat and ecological

410 interactions (Oh et al. 2014, Pechal et al. 2014b, Junker and Keller 2015, Metcalf et al. 2016,

411 Pechal and Benbow 2016). Using a planktonic crustacean (Daphnia magna), Preiswerk et al.

412 (2018) followed microbial communities of the living host through initial death and subsequent

413 decomposition, reporting that the communities were highly dynamic and revealed opportunistic

414 microbes that could exploit the host even before death. Thus, the community assembly dynamics

415 of necromass is likely dependent on host condition and interactions with the abiotic environment

416 and other organisms, populations and communities.

417

418 The soil environment and the microbial communities it harbors are intimately associated with the

419 decomposition of plant and animal necromass. When considering plant necromass,

420 decomposition has often been thought to be a product of three hierarchically organized,

421 interacting factors: climate, substrate quality, and the biota (Swift et al. 1979). Of these factors,

422 climate has been assumed to be the driving force behind rates of decomposition at broad spatial

423 scales, whereas litter quality, and to a more minor degree, the biota, play a more important role at

424 finer spatial scales. However, such assumptions have recently been called into question

425 (Bradford et al. 2016). For instance, the decomposition rate of woody debris is largely

426 independent of climate and may actually be driven by its proximity to woody debris previously

427 colonized by wood-decay fungi (Bradford et al. 2014). This interpretation suggests that spatial

428 proximity of decomposer organisms may be a major driver of decomposition across a landscape

429 (Ettema and Wardle 2002).

430

431 The microbial communities in the soil and associated with the rhizosphere that decompose leaf

432 litter also play a more pronounced role. One such phenomenon is the occurrence of 'home-field

433 advantage' (HFA), whereby decomposer communities sharing a common history with a

434 particular resource often decompose that resource at a greater than expected rate (Gholz et al.

435 2000). Such a phenomenon has been found when examining the interaction between climate and

436 microbial communities (Strickland et al. 2015, Averill et al. 2016). Although HFA has been

437 observed across a variety of different soil decomposer communities (Ayres et al. 2009,

438 Strickland et al. 2009a), it has been found absent in others (St John et al. 2011, Bachega et al.

439 2016). One explanation for this divergence is HFA only accounts for adaptation to a particular

440 organic matter resource and does not account for the fact that some decomposer microbial

441 communities simply decompose an array of necromass types more rapidly due to greater

442 functional breadth (Keiser et al. 2014). That is, some microbial decomposer communities have a

443 greater "ability" to decompose a wide range of litter substrates than do others because they have

444 been historically exposed to chemically complex litter species. Understanding how these two

445 metrics of microbial function drive patterns of necromass decomposition across a landscape, and

446   how they relate to microbial community characteristics, may prove informative to predictions of

447   decomposition rates associated with shifts in plant species or changes in necromass quality

448   (Keiser et al. 2013, Austin et al. 2014, Martiny et al. 2017). Additionally, this HFA and 'ability'

449   framework suggests that the function of soil microbial communities is not just a product of the

450   current input of necromass but that it may also be influenced by past inputs as well.

451

452   Adding to the complex interactions between soil microbial communities, climate, and necromass

453   quality is the inclusion of the broader soil community in our understanding of decomposition.

454   Soil arthropods are well known for their ability to fragment litter increasing the surface area

455   available for microbial colonization and thereby increasing litter quality as it passes through the

456   invertebrates' gut (Seastedt 1984). Yet there is a growing awareness that trophic interactions

457   within the soil community may also drive the rate and efficiency of decomposition (Buchkowski

458   2016). For example, increased soil nitrogen can lead to greater wood decaying fungal biomass

459   and extracellular enzyme activity in the absence of a fungivore, but the presence of a fungivore

460   may moderate fungal biomass and wood decay rates (Crowther et al. 2015). More complex

461   trophic cascades have also been observed, such as the removal of predatory microarthropods

462   which led to an increase in microbivorous nematodes and a subsequent increase in microbial

463   biomass (Santos et al. 1981). Such examples indicate that top-down drivers may play an

464   important role in mediating decomposition (Buchkowski 2016, Hawlena and Zaguri 2016) across

465   a variety of necromass types. The relative strengths of top-down compared to bottom-up

466   constraints on necromass decomposition may vary depending on interacting abiotic factors and

467   climate change (Crowther et al. 2015).

468

469   **Invertebrates of the Necrobiome**

470

471   Invertebrates play a key role in decomposition. For vertebrate carrion, numerous studies have

472   examined the role of arthropods associated with decomposition (Early and Goff 1986, Anderson

473   2000, Bharti and Singh 2003, Matuszewski et al. 2011, Michaud et al. 2015), and identified a

474   relatively predictable community succession of this group (Payne 1965), which is often used in

475   forensics (Byrd and Castner 2009). Early work on arthropod communities associated with

476   carrion identified key taxa and their roles in decomposition (Fuller 1934, Bornemissza 1957).

477   Later work on this topic examined arthropod communities associated with decomposing swine in

478   a range of contrasting circumstances, including being buried (Payne et al. 1968), on the soil

479   surface (Payne 1965) or submerged in water (Payne and King 1972). A key outcome of this work

480   was the recognition of the important role arthropods play in returning nutrients to the

481   surrounding ecosystem. Preventing arthropod colonization can result in a significant reduction in

482   the rate of biomass removal from animal carcasses (Payne 1965) and can change the community

483   succession of both microbes and necrophagous insects (Pechal et al. 2013, Pechal et al. 2014a).

484   Additional studies have addressed other theoretical aspects of arthropod community responses to

485   carrion resource pulses (Bilby et al. 1996, Yang 2004) or mass mortality events (Fey et al. 2015).

486

487   Research has also explored species interactions among carrion arthropods ranging from

488   competition (Goodbrod and Goff 1990), niche partitioning (Denno and Cothran 1975), predator-

489   prey interactions (Brundage et al. 2014), and trophic cascades responsible for variability in

490   succession trajectories (Pechal et al. 2014a). The understanding of carrion arthropods has been

491   facilitated by knowledge of the multiple and distinct functional roles of different taxa at

492 carcasses (Braack 1987). For example, flies (e.g., Diptera: Calliphoridae, Sarcophagidae) are the

493 primary arthropods responsible for consuming soft tissues of vertebrate carrion and thus are

494 traditionally recognized as saprophages (Merritt and De Jong 2015). Certain beetles (Coleoptera)

495 including some rove beetle species (Staphylinidae) (Matuszewski et al. 2008), carrion beetles

496 (Silphidae) (Trumbo 1990, Trumbo et al. 2016), and skin/hide beetles (Dermestidae, Trogidae)

497 (Kulshrestha and Satpathy 2001, Barton et al. 2017) are also saprophagous. Other important

498 functional groups include parasitoid flies (e.g., Diptera: Tachinidae) or wasps (e.g.,

499 Hymenoptera: Braconidae) (Cammack et al. 2010) and predatory beetles (e.g., Staphylinidae)

500 and ants (Hymenoptera: Formicidae) (Flores et al. 2014, Barton and Evans 2017). Often

501 overlooked arthropods found at vertebrate carrion are those species located in the soil

502 (Bornemissza 1957) or in aquatic environments (Tomberlin and Adler 1998, Merritt and Wallace

503 2010). In many instances, these arthropods rely on the resource directly as habitat or as a

504 nutritional resource (e.g., tissue in a stream or lake, or in the case of soil, fungi or liquids seeping

505 into the soil). Research exploring soil or aquatic associations is limited compared with studies in

506 above ground terrestrial environments. The ecology and evolution of dung beetles has been

507 described and tested in detail and demonstrates close evolutionary ties of some invertebrates and

508 necromass (Hanski and Cambefort 1991, Nichols et al. 2008).

509

510 Extremely diverse assemblages of invertebrates are associated with decomposing plant material.

511 Approximately 20-30% of all forest insect species, for example, are directly or indirectly

512 dependent on dying or dead wood (Stokland et al. 2012). Included among these are a wide range

513 of phloem- or wood-feeders (e.g., termites, beetles, wood-wasps, etc.), fungus-feeders (e.g.,

514 beetles, flies, true bugs, etc.) and a variety of predators (Stokland et al. 2012). There is very little

515 overlap known between the invertebrate assemblages involved in the decomposition of animal

516 and plant necromass, as well as between different forms of plant matter (e.g., leaf litter vs. wood)

517 (Ferro et al. 2012).

518

519 Among macroinvertebrates, earthworms and termites have by far the strongest direct accelerative

520 effects on plant biomass decomposition (Lavelle et al. 1997, Bignell and Eggleton 2000). The

521 importance of earthworms as decomposers was illustrated by the dramatic loss of leaf litter depth

522 following their introduction into formerly earthworm-free (due to glaciation) forests (Addison

523 2009 and references therein. Termites are the major consumers of plant debris in soil throughout

524 the tropics and subtropics, perhaps even exceeding fungi in importance in some areas (Liu et al.

525 2015, Ulyshen 2016), with the different species feeding preferentially on wood, leaf litter, humus

526 or soil (Donovan et al. 2001). Invertebrates consuming decaying plant material rely heavily upon

527 microbes which provide a variety of benefits including digesting and softening the material,

528 neutralizing allelopathic substances and improving nutritional quality in terrestrial and aquatic

529 habitats (Cummins et al. 1973, Swift and Boddy 1984, Webster and Benfield 1986). Microbial

530 biomass is itself quite nutritious relative to most forms of dead plant matter and contributes

531 greatly to the diets of litter- or wood-feeding invertebrates, many of which are essentially

532 fungivorous (Tanahashi et al. 2009, Mishima et al. 2016). Predators are a large proportion of the

533 invertebrate members of the necrobiome [e.g., over a third of saproxylic beetle species in

534 Germany (Wende et al. 2017)] and exert strong controls on necrophagous populations.

535

536 **Vertebrates of the Necrobiome**

537

538 No vertebrates, to our knowledge, are known to be specialist consumers of decomposing plant

539 material but many species interact in important ways within the necrobiome of plant necromass.

540 Many birds (e.g., woodpeckers) and mammals (e.g., aardvarks, armadillos, anteaters, echidnas,

541 bears), for instance, are specialist or opportunistic predators of wood-feeding insects such as

542 beetle larvae or termites. The fragmentation of plant matter caused by foraging vertebrates is

543 assumed to have strong indirect effects on decay rates (Ulyshen 2016) but this remains untested.

544 By contrast, vertebrates are known to be major consumers of carrion and are thus direct

545 participants in the decomposition process in addition to any indirect effects they may have as

546 fragmenters (DeVault et al. 2003).

547

548 Vertebrates consuming carrion are commonly classified into two categories: obligate scavengers

549 rely entirely on carrion to meet their food requirements, whereas facultative scavengers are

550 active predators or foragers, as well as scavengers (DeVault et al. 2003). In marine systems there

551 are some deep-water fish that might also be categorized as obligate scavengers (Smith and Baco

552 2003). The only obligate vertebrate scavengers in terrestrial systems are Old World and New

553 World vultures (families Accipitridae and Cathartidae, respectively). Vultures have evolved

554 several adaptations that allow for dependence on carrion, which is often an ephemeral and

555 unpredictable food source. First and foremost, obligate scavengers (i.e., vultures) have large

556 wing spans and other physiological mechanisms that allow them to move quickly and efficiently

557 to search vast areas for carrion (Ruxton and Houston 2004, Shivik 2006). Vultures also have

558 well-developed vision, and in some cases olfactory capabilities (e.g., turkey vulture, Cathartes

559 aura), which allow them to find carcasses over large distances (Houston 1979, DeVault et al.

560 2003). Due to microbial decomposition, carrion can contain high levels of toxic compounds and

561 thus vultures have evolved physiological adaptations in their gut that allow them to consume

562 large volumes of these toxins (Houston and Cooper 1975, Roggenbuck et al. 2014). As a group,

563 vultures are relatively large-bodied birds and can withstand several days without food (Ruxton

564 and Houston 2004). The amount of biomass processed by vultures and other vertebrate

565 scavengers varies across ecosystems (Pereira et al. 2014), but historically has been greatly

566 underestimated (DeVault et al. 2003, Wilson and Wolkovich 2011). In one example, an

567 estimated 70% of large ungulates in the Serengeti die from causes other than predation and

568 become available to scavengers. Thus, collectively Serengeti vultures likely consume more

569 biomass than all carnivorous mammals combined (Houston 1979), suggesting a large scale

570 importance of carrion necromass in ecosystem structure and function.

571

572 Due to their reliance on carrion, populations of obligate scavengers are inextricably linked to the

573 availability and distribution of carrion on the landscape (Kelly et al. 2007). For some facultative

574 scavengers the availability of carrion can influence local abundance, species distributions, or

575 growth rates, especially in ecosystems with limited food resources (Fuglei et al. 2003, Wilmers

576 et al. 2003, Drazen et al. 2012). For example, local arctic fox (Alopex lagopus) populations in

577 Norway decreased markedly following a decline in reindeer (Rangifer tarandus platyrhynchus)

578 carcasses (Fuglei et al. 2003). In Yellowstone National Park, USA, populations of facultative

579 scavengers have benefited from the reintroduction of grey wolves (Canis lupus), which provide a

580 more stable subsidy of ungulate carrion (Wilmers et al. 2003). Such effects have also been

581 reported in aquatic ecosystems, where the abundance and distribution of deep-water fish may be

582 modulated by carrion availability (Drazen et al. 2012).

583

584   Carrion use by vertebrate scavengers is mediated by a complex suite of biotic and abiotic factors

585   (DeVault et al. 2003, Selva et al. 2005, Moleón et al. 2015, Turner et al. 2017). As a result, use

586   of carrion can also vary extensively within a vertebrate species. From a temporal perspective,

587   variability in food availability and quality can be a key factor and can be a product of intra- and

588   inter-kingdom competition (Allen et al. 2014, Beasley et al. 2015). These forms of competition

589   demonstrate some of the ways that very different taxonomic components of the necrobiome

590   interact to affect decomposition. For example, the activity of invertebrates and microbes is

591   influenced by temperature, and that means that invertebrates and microbes are more active

592   during warmer weather and will more rapidly decompose or render carcasses toxic or

593   unpalatable for vertebrates (Janzen 1977, Burkepile et al. 2006). Consequently, vertebrate

594   scavengers are typically most successful when temperatures are cooler and decomposition is

595   slowed (DeVault et al. 2004a, Selva et al. 2005, Parmenter and MacMahon 2009). However, in

596   some areas the presence of an abundant and efficient vertebrate scavenger species can shift the

597   balance toward vertebrates, even in warm weather (Houston 1986, DeVault et al. 2011).

598   Competition for carrion resources also differs across habitat types (Beasley et al. 2015, Turner et

599   al. 2017), although such differences likely reflect the composition of local vertebrate

600   communities (DeVault et al. 2004a) and microclimates (Parmenter and MacMahon 2009).

601

602   Collectively, obligate and facultative scavengers provide a number of critical ecosystem services

603   through the removal of animal necromass from landscapes (Moleón et al. 2014, DeVault et al.

604   2016). Intact scavenging communities (especially the presence of vultures) may reduce risks of

605   disease transmission among mammals due to rapid removal of carcasses from ecosystems

606 (Jennelle et al. 2009, Ogada et al. 2012, Hill et al. 2018). There is a clear role of vertebrates in

607 the decomposition of carrion and placing them in the broader necrobiome framework highlights

608 their links with other taxonomic groups (i.e. insects and microbes) and important environmental

609 moderators of decomposition and overall ecosystem structure and function.

610

611 **Symbioses of the Necrobiome**

612

613 Although symbioses between invertebrates and microbes are common within necrobiomes, the

614 nature of these interactions differs greatly between decomposers associated with autotrophically-

615 or heterotrophically-derived biomass. Due to the strength of lignocellulose, dead wood is among

616 the most recalcitrant forms of plant matter and is also characterized by some of the highest C:N

617 ratios of any organic material (Figure 3). Although endogenous cellulases are known from some

618 termites (Blattodea) and may play a particularly important role in the metabolism of Termitidae,

619 which lack the protists of "lower termites" (Lo et al. 2011), wood-feeding insects are mostly

620 unable to digest lignocellulose without the enzymes produced by various endo- or ecto-symbiotic

621 microorganisms. Endo-symbionts include a wide range of gut-dwelling bacteria, archaea and

622 eukarya (e.g., yeasts and protists) that have been the subjects of intense study in both termites

623 (O'Brien and Slaytor 1982, Brune 2014) and various beetle species (Reid et al. 2011, Urbina et

624 al. 2013).

625

626 In addition to digestion, another important function performed by prokaryotes within the guts or

627 salivary glands of many wood-feeding arthropods is nitrogen fixation, which often provides

628 much of the nitrogen required by these organisms to complete development (Ulyshen 2015, and

629 references therein). Ecto-symbioses are common between insects and fungi associated with

630 decomposing wood. Ambrosia beetles, for example, cultivate and consume symbiotic fungi

631 within galleries these insects create in dead wood. These insect-fungi associations have

632 repeatedly evolved within scolytine and platypodine Curculionidae and also exist in other beetle

633 families, such as Lymexylidae and Erotylidae (Farrell et al. 2001, Toki et al. 2012). The bodies

634 of these insects possess special storage structures, called mycangia, within which their fungal

635 symbionts are transported. Mycangia also exist in wood-feeding insects that are not technically

636 ambrosia beetles. For example, female stag beetles (Lucanidae) possess mycangia near the ends

637 of their abdomens that contain xylose-fermenting yeasts, which are presumably added to

638 oviposition sites to benefit larval development (Tanahashi et al. 2010). Some of the most

639 effective forms of symbioses between insects and fungi are exhibited by leaf-cutting ants and

640 macrotermitine termites, both of which cultivate fungal gardens within their nests to perform the

641 digestion of plant material (Nobre et al. 2011). Macrotermitines are thought to be among the

642 most efficient wood-consuming insects due to their symbioses with the fungi Termitomyces

643 (Basidiomycetes: Lyophyllaceae) which both allows them to process wood more quickly and

644 increases assimilation efficiency (Schuurman 2005, Brune and Ohkuma 2011). Other functions

645 provided by endo- and ecto-symbionts of arthropods associated with decomposing plant material

646 include detoxification of plant secondary compounds (Dowd 1992), defensive mutualism

647 (Chouvenc et al. 2013), and protection from pathogens (Peterson and Scharf 2016, and

648 references therein).

649

650 Whereas symbioses within plant-based necrobiomes largely stem from the recalcitrance and

651 nutrient deficiency of dead plant matter, those within animal-based necrobiomes appear to have

652 arisen largely in response to intense competition with other organisms as well as threats from

653 pathogens. Necrobiome community interactions may follow a gradient of resource quality where

654 the most labile forms of necromass facilitate competition and the most recalcitrant forms support

655 symbioses (Janzen 1977). Microbial competition has been demonstrated to have strong negative

656 effects on the reproductive success of some carrion-feeding insects (Rozen et al. 2008). Although

657 carrion-feeding insects produce a variety of antimicrobial peptides and lysozymes to minimize

658 competition from bacteria (Jordan et al. 2015), they also harbor, within their guts, diverse and

659 unique microbial assemblages (Kaltenpoth and Steiger 2014). The exact functions provided by

660 these microbes remain poorly understood but reducing competition from free-living carrion

661 microbes and other carrion-feeding animals, detoxification and providing protection from

662 pathogens are several potential benefits (Kaltenpoth and Steiger 2014, Trumbo et al. 2016).

663 Adult burying beetles, for instance, are known to transmit gut bacteria to their offspring both

664 directly through regurgitation and anal secretions applied during carcass preparation (Wang and

665 Rozen 2017). Although the secretions produced by burying beetles have antimicrobial properties,

666 free living microbes appear to be reduced in favor of microbes found in the guts of these insects

667 (Duarte et al. 2018). Rather than reducing competition from other microbes, the antimicrobial

668 secretions produced by Nicrophorus may serve primarily to help conceal carcasses from

669 competitor scavengers by suppressing the bacterial production of olfactory cues (Trumbo et al.

670 2016). While research in both plant and animal necromass decomposition has shown many

671 examples of symbioses and cross-domain interactions, including the well-known symbioses of

672 ruminant digestion of plant necromass (Hungate 1966), there are likely many more to be

673 discovered.

674

675 **Abiotic Factors and the Habitat Template**

676

677 Decomposition and the necrobiome constituents are constrained by abiotic factors defined by the

678 surrounding habitat or ecosystem. Terrestrial, aquatic, and human-modified habitats each differ

679 in their communities and climate, and this affects the rate and progression of decomposition and

680 the species diversity that uses necromass (Beasley et al. 2012). Future studies should consider

681 how changes in abiotic factors described below, in addition to extreme weather events, ocean

682 acidification, and rising annual global temperatures could alter detritus availability, necrobiome

683 dynamics, and ultimately decomposition processes in ecosystems.

684

685 Although many decomposition studies have occurred on land, the majority of Earth's surface is

686 comprised of aquatic habitat. Aquatic habitats include freshwater (e.g., streams, ponds, lakes,

687 wetlands), marine (e.g., ocean) and brackish (e.g., estuaries) environments. The inherent

688 physiochemical properties unique to these aquatic habitat types can substantially alter

689 decomposition through direct or indirect abiotic interactions that constrain necrophagous

690 physiology or mechanical ability to breakdown organic matter. Further, depending on where a

691 resource is located within the water column, abiotic factors such as temperature, oxygen

692 availability, carbon dioxide levels, ion concentrations, turbidity, pressure, salinity, pH, and flow

693 dynamics will impact the rate and taphonomic changes of decomposition and determine the

694 biodiversity of consumers that may use the decomposing organic material (Hattenschwiler et al.

695 2005, Wallace 2015). For example, swine carcasses placed in the deep-sea fail to undergo bloat

696 during the decomposition process at these depths because of the increased pressure within the

697 environment (Anderson and Bell 2016). Woody debris and leaf litter in aquatic habitats,

698 primarily in streams, have additional factors to consider that impact the abiotic conditions and

699 ultimately the decomposition process. These include but are not limited to: where the wood is

700 located within the stream (e.g., submersion, buried in the substrate, suspended); the morphology

701 of the streambed (e.g., sand or silt, rock size); and hydrology (e.g., season flooding and/or spate

702 events) (Scherer 2004, Ruiz- Villanueva et al. 2016).

703

704 Terrestrial habitats can be separated into broad biomes: tundra, boreal forest, temperate forest,

705 desert, grassland, and tropical rain forest, with the abiotic factors of temperature, humidity, wind,

706 solar radiation, and exposure substantially altering decomposition (Benbow et al. 2015a). These

707 abiotic factors can further interact with landscape configuration and vegetation within each

708 ecosystem type (García- Palacios et al. 2013). Soil conditions specific to a habitat can alter

709 decomposition dynamics of plants and animals due to direct and indirect associations with soil

710 nutrients, pH, salinity, pollution or other contaminants, temperature and moisture content

711 (Refsnider and Janzen 2010). Further, landscape features, such as land use and cover,

712 connectivity and complexity can mediate consumer attraction and use of necromass resources.

713 For example, habitats with increased biodiversity, such as tropical rainforests, have an increased

714 species pool that can utilize a resource during decomposition when compared to habitats with

715 slightly decreased complexity, such as an African tropical woodland (Cornaby 1974, Braack

716 1987).

717

718 The final category of ecosystems, which may not be as apparent as the previous two groups, is

719 anthropogenic-associated ecosystems. These habitats are comprised of human built (e.g.,

720 residential structures) or modified areas (e.g., disturbed or change habitats) that impact the

721 decomposition of organic material and biodiversity of the necrobiome. Specifically, modification

722 of ecosystems often leads to habitat loss and fragmentation resulting from human development

723 (e.g., urbanization, deforestation and monoculture farming). Habitat fragmentation typically

724 elicits negative impacts on biodiversity (MacArthur and Wilson 1967). A recent meta-review,

725 however, revealed approximately three-quarters of studies showed some measures of positive

726 response by communities affected by habitat fragmentation (Fahrig 2017). Overall, the impact of

727 human-modification to decomposition and decomposer communities is underexplored and

728 poorly understood.

729

730 **NECROBIOME ECOLOGICAL FUNCTIONS**

731

732 A key feature of our expanded necrobiome concept is the broad structural and functional

733 template it provides for better understanding the range of similarities and differences in

734 decomposer communities found associated with plant and animal detritus. Volatile organic

735 compound (VOC) emissions result from tissue decomposition and microbial metabolism and are

736 an important mechanism for the attraction of exogenous macro-saprotrophs, such as blow flies,

737 bark beetles, and nematodes (see Table 1), from the contiguous substrate (e.g., soil) and the

738 surrounding local habitat and ecosystem (Ma et al. 2012, Ulyshen 2016). The types of VOCs

739 produced are determined by necromass composition, quality, and rate of decay; and they are

740 known to affect the recruitment of exogenous macro-saprotrophs (i.e., invertebrate

741 decomposers), in time frames ranging from minutes to years after death (Mądra et al. 2015,

742 Ulyshen 2016). In leaf litter decomposition, microbial communities are known to markedly

743 contribute to the production of associated VOC profiles (Gray et al. 2010). Ultimately,

744 decomposition is achieved by species that directly consume necromass or produce the enzymes

745 that catabolize compounds and degrade dead tissues. However, members of the necrobiome also

746 affect decomposition through physical alterations to the necromass, as well as intra- and inter-

747 specific species interactions that generate complex inter-dependencies among organisms. Among

748 the latter, interactions between invertebrates and microbes are particularly important. We

749 describe below major functions performed by community members of the necrobiome that both

750 directly and indirectly affect decomposition and compare and contrast functions occurring at

751 plant and animal necromass.

752

753 **Digestion**

754

755 Many organisms can perform the primary function of digestion with respect to relatively labile

756 animal tissues. The primary digesters at animal necromass are specialist carrion flies (Payne

757 1965), although there can be minor contributions from other insect groups, such as beetles or

758 ants (Barton and Evans 2017). Vertebrates should also be considered digesters as they will

759 consume entire carcasses before invertebrates are able to proliferate and participate in this

760 function (DeVault et al. 2003). For plant necromass, wood-feeding invertebrate symbionts and

761 saprophytic fungi and microbial communities in the stomachs of ruminant mammals (Hungate

762 1966) are capable of completely degrading the lignocellulose of plant cell walls to perform a

763 digestion function (Swift et al. 1979). Digestion by saprophytic fungi and microbes is performed

764 via the production of extra-cellular enzymes in ruminants (Refsnider and Janzen 2010) and is an

765 external process rather than internal as for insects and vertebrates.

766

767   **Fragmentation/penetration**

768

769 Physical alterations brought about by animals that act to fragment or tunnel into dead material

770 can strongly affect decomposition. The activities of carrion-feeding vertebrate scavengers and

771 vertebrates foraging for insects in dead wood act to fragment large necromass resources.

772 Fragments decompose more quickly than intact pieces due to increased surface area and

773 coverage of microbial biofilms, as well as improved aeration (e.g., Boddy 1983). Penetration of

774 the outer protective layers of dead animals and plants (e.g., skin or bark) is another important

775 physical alteration brought about by animal activity, which facilitates colonization by microbes

776 and other organisms (Connell and Slatyer 1977, Mann et al. 1990). In animal necromass this

777 activity is performed by larger scavenging animals (e.g., crows, vultures and hyenas) that pick at

778 parts of a carcass and enable entry by insects and microbes. In decomposing logs, insects that

779 create holes through bark and tunnel into the heartwood (Leach et al. 1937) play a particularly

780 important role in facilitating the establishment of rot fungi. Some vertebrates, such as aardvarks

781 (*Orycteropus afer*) in Africa or echidnas (*Tachyglossus aculeatus*) in Australia, also play a role

782 in the fragmentation of logs when searching for ant or termite nests. Although there are many

783 insect species that perform a fragmentation or penetration functional role in terrestrial habitats,

784 there are fewer major groups of xylophagous macroinvertebrates in freshwater systems

785 (Anderson et al. 1978), contributing to the slow rates of wood decomposition in these habitats.

786 Certain molluscs perform this function in marine environments and can cause a great deal of

787 damage to wooden boats and pilings (Nair and Saraswathy 1971). Another consequence of

788 fragmentation can be changes in microbial community composition. The production of fine

789 woody particulate material by many wood-boring insects is thought to favor bacterial

790 communities (Swift and Boddy 1984, van der Wal et al. 2007), including free-living N-fixers

791 (Ausmus 1977).

792

793 **Nutrient and microbe transport and dispersal**

794

795 Organisms within the necrobiome play a role in moving nutrients away from decaying

796 necromass through both passive and biological means (Figure 1). The microbes and elements of

797 decaying organic matter can move by direct translocation of microbial cells or along elemental

798 concentration gradients within the biomass and into, onto and within contiguous substrata. This

799 transfer is perhaps best visualized by the process of purging, whereby fluids and gases from a

800 decaying animal escape into soil or the atmosphere. Nutrients and particles also are dispersed by

801 mobile micro- (e.g., fungi, protists) or macro-saprotrophs (e.g., flies) that act as vectors of the

802 organic matter, microbes, and elements. The dispersal of these materials can occur in multiple

803 ways: 1) trophic transfer where the microorganisms and elements are ingested but not

804 assimilated, and then egested after saprotroph movement away from the necromass source; 2)

805 trophic transfer where the microorganisms and elements are ingested and assimilated, and

806 released after saprotroph movement and then death either through predation or decomposition; 3)

807 external attachment to the saprotroph by physical or chemical means during movement; and 4)

808 by being aerosolized or passively dispersed by winds, rainfall, water currents, or thermal energy

809   (e.g., convection). Additional discussion is given below of how members of the necrobiome

810   interact in networks to transport and disperse microbes and nutrients.

811

812   **Detoxification**

813

814   Non-structural secondary compounds are often present in heartwood and are known to be toxic

815   to many microbial decomposers and insects (Käärik 1974). The abundance of these compounds

816   can vary by as much as 50-fold among angiosperms and 20-fold among gymnosperms (Cornwell

817   et al. 2009), and the variance is thought to be largely responsible for the differences in decay

818   resistance observed among different wood species (Bultman and Southwell 1976). The protective

819   effects of these and other extractives diminish over time (Bultman and Southwell 1976);

820   however, bacteria and fungi both play a part in neutralizing these potentially toxic compounds

821   (Burnes et al. 2000, Dorado et al. 2000). Further, microbial symbionts of some insects associated

822   with detritus provide detoxification function of plant secondary compounds (Dowd 1992). As far

823   as we are aware, there are no analogous intrinsic toxins present associated with microbial

824   communities of animal necromass that retard microbial or insect activity. However, a burying

825   beetle, Nicrophorus vespilloides (Silphidae) (Arce et al. 2012), produces antimicrobial secretions

826   that compete with microbes on carrion. Overall, the detoxification pathways in plants suggest

827   this function is primarily the activity of microbial components of the plant necrobiome.

828   However, there are likely undiscovered analogous activities in animal necromass decomposition.

829

830   **Predation**

831

832   Predators are conspicuous and important members of the necrobiome. It is not uncommon for

833   predators to be among the most species-rich guilds in dead wood (Hammond et al. 2001, Wende

834   et al. 2017), as well as at carcasses (Barton and Evans 2017). Moreover, opportunistic predation

835   by non-predatory invertebrates is commonplace in decomposing wood. Termites are known to

836   feed on dead insect larvae and other invertebrate carcasses encountered while foraging in wood

837   (Thorne and Kimsey 1983, and examples therein), which includes cannibalizing dead or injured

838   nestmates (Wilson 1971). Many wood-boring beetle larvae are also known to prey on other

839   larvae encountered in dead wood (Soper and Olson 1963) and this probably relieves the

840   limitations imposed by the low nutritional quality of wood.

841

842   For carrion, cannibalism among fly larvae may be an adaptation to intense competition rather

843   than a nutritional requirement (e.g., the hairy maggot blow fly Chyrsomya rufifacies Macquart

844   1842) (Baumgartner 1993). Most predatory beetles and ants at carcasses tend to be generalists

845   and take advantage of the concentrated and abundant insects associated with carrion (Barton and

846   Evans 2017). Some species of predatory insect may also opportunistically scavenge on carcass

847   tissue, possibly due to the similar stoichiometric composition and easy switching between

848   resources. The function of predators (and parasitoids, not discussed here) in decomposition is

849   largely restricted to moderating the abundance of other decomposer organisms, and in most cases

850   probably does not alter the rate or pattern of decomposition to any notable degree. Predatory

851   ants, however, have been shown to dominate the insect community and retard rates of mass loss

852   of both wood (Warren and Bradford 2012) and animal carcasses (Barton and Evans 2017).

853   Indeed, Houston (1985) argued that ant communities in South America prolong carcass

854   availability to vertebrates by feeding on dipteran larvae that otherwise would quickly consume

855   the carcasses. Further, it is known that some invertebrate predators approach carrion specifically

856   to prey on other organisms and not necessarily the necromass (Payne 1965).

857

858   **NECROBIOME INTERACTIONS AND NETWORKS**

859

860   In addition to discussing the taxonomic and functional organization of the necrobiome, we

861   expand the necrobiome concept to also consider the complex biotic and abiotic mechanisms of

862   species and element (e.g., nutrients, carbon) translocation and dispersal from the decaying

863   necromass into adjacent substrates, the local habitat, and ultimately into the larger ecosystem, as

864   originally presented by Polis and Strong (1996). We argue that the decaying biomass holds a

865   community of microbial species that often follow elemental movement into and throughout the

866   environment, thus providing a way to track the dispersal of species, their genomes, metabolic

867   diversity and function after host death and through decomposition. While understudied, the

868   dispersal of genetic and metabolic information into the surrounding environments (Preiswerk et

869   al 2018) is arguably a potentially transformative way to view decomposition as an ecosystem

870   process through multiple disciplines and areas of scientific inquiry.

871

872   Many invertebrates act as vectors of microbial digesters from one resource to another. This

873   transfer by insects can disperse gut symbionts as well as those that passively carry microbes on

874   their bodies (Persson et al. 2009, Strid et al. 2014). Fungus-farming termites perform the reverse

875   role, where dead plant particles are transported back to nests containing ecto-symbiotic fungal

876   gardens (Wood and Thomas 1989). Blow flies and house flies are known to carry and transmit

877   pathogenic bacteria to and from decomposing organic matter (Greenberg and Bornsetein 1964,

878 Greenberg et al. 1970, Greenberg 1973, Macovei and Zurek 2006, Nayduch 2017). A recent

879 study by Weatherbee et al. (2017) showed that carrion associated microbial taxa consumed by

880 blow fly larvae are transferred into the gut of the larvae. Although it is not definitively known

881 whether microbes are passed transstadially to adults in all species (Singh et al. 2015), evidence

882 from adult flies suggests a high likelihood that some bacteria ingested from carrion are

883 assimilated by larvae, persist into the adults, and then are dispersed into the landscape

884 (Weatherbee et al. 2017).

885

886 In addition to vectoring microbes, many insects also carry other invertebrates from one

887 ephemeral or isolated resource patch to another. Phoresy is common among invertebrates

888 associated with dung and carrion (Krantz 1998), fungal fruiting structures (Fain and Ide 1976),

889 and dead wood. Examples of saproxylic insects from which phoretic passengers have been

890 recorded include bark beetles, click beetles, cerambycid beetles, passalid beetles and parasitic

891 wasps (Haack and Wilkinson 1986). As pointed out by Moser and Roton (1971), virtually all

892 relatively large insects capable of long distance dispersal serve as hosts for one or more phoretic

893 species. Many host species carry not just a single phoretic species but a whole community of

894 passengers. For example, at least eighteen species of mites are known to be phoretic on the bark

895 beetle Dendroctonus frontalis (Coleoptera: Curculionidae) in the southeastern United States

896 (Moser 1976). Although phoresy is often viewed as a form of commensalism where the phoretic

897 species benefits and the host is unaffected, this is not always the case with reports of both

898 negative (Lindquist 1969, Hodgkin et al. 2010) and positive impacts (Purrington and Drake

899 2008) on the host.

900

901   Interactions between decomposer organisms belonging to different kingdoms (or domains) are

902   quite common and warrant separate attention. Recent evidence indicates that microscopic species

903   interacting with higher organisms are playing a far greater role in regulating succession patterns

904   (Ezenwa et al. 2012). Interkingdom interactions between plants and microbes are prevalent, and

905   these interactions may also transect invertebrate communities. A specific example is with

906   Sphagnum mosses. These plant assemblages dominate peatland bog ecosystems and form a

907   unique and extreme habitat for microbes. This moss genus is well known for its preservative

908   properties and slow rate of decomposition, occupies one-third of land on the planet, and stores

909   more carbon than any other single genus of plant (Turetsky 2003). Highly acidic conditions

910   along with low concentrations of nutrients, together with specialized leaf structures with high

911   water content, lead to very specialized microbial colonization that is unique to Sphagnum species

912   (Opelt et al. 2007). Furthermore, Sphagnum moss species produce secondary metabolites, such

913   as phenolics, terpenoids, and tannins, and accumulate carbohydrates, that influence microbial

914   colonization and subsequently microbially-mediated decomposition. These plant specific factors

915   may facilitate peat accumulation through lowering of redox potential that leads to decreased

916   microbial decomposition rates (Belyea 1996). Methanotropic bacteria within the bogs themselves

917   are well documented with Burkholderia and Serratia to be among the most dominant bacteria

918   colonizing Sphagnum plants (Juottonen et al. 2005). Very few fungi colonize the actual plants, as

919   these hosts are known for their antifungal and antibacterial activity (Opelt et al. 2007). A recent

920   study showed that bacterial isolates from two Sphagnum species had antagonistic activities

921   against fungi, while also performing nitrogen fixation and lowering host plant ethylene levels

922   (Knorr et al. 2015). Despite these documented antimicrobial properties, a relatively large number

923   of fungal taxa have been identified on S. fuscum (Thormann et al. 2001). Thus, the overall

924 functioning of peat bog ecosystems is heavily influenced by interkingdom interactions occurring

925 among plants, bacteria, and fungi, as well as their associated chemicals associated with high

926 volumes of necromass.

927

928 Microbes have evolved complex strategies for outcompeting one another for resources available

929 within carrion. Although in the early stages of discovery, it is clear microbes associated with

930 carrion play important roles in regulation of arthropod attraction, colonization, and utilization of

931 the remains. Furthermore, recent evidence indicates within kingdom interactions (e.g., blow fly

932 predator v blow fly prey) are partially governed by their associated microbiome in carrion

933 (Crippen et al. 2015, Weatherbee et al. 2017) and other necromass decomposition networks

934 (Purahong et al. 2016, Deveau et al. 2018). Some compounds serve as a mechanism of

935 communication and group responses, better known as quorum sensing (Nealson and Hastings

936 1979), while others serve to disrupt communication. In both cases, these processes give a

937 competitive advantage to the producer of these compounds by reducing competition with other

938 microbes within the environment. For example, indole, a by-product of tryptophan degradation,

939 is a key molecule used by Escherichia coli (gut microbe of many vertebrate species) as a quorum

940 sensing molecule (Kim and Park 2015) and is a bacterial taxon commonly associated with

941 vertebrate carrion (Metcalf et al. 2016). In contrast, dimethyl disulphide (DMDS) is detected

942 during the later stages of vertebrate decomposition (Forbes and Perrault 2014) and is a quorum

943 quenching molecule for many Gram-negative species. In both instances, these compounds

944 regulate blow fly attraction (Ma et al. 2012, Tomberlin et al. 2012b). In addition to being an

945 attractant, the response of blow flies to these compounds tends to be sex and physical state (e.g.,

946 gravid v non-gravid) specific (Brundage et al. 2017).

947

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

949   scales to vertebrates and can affect vertebrate scavenger interactions (DeVault et al. 2003,

950   Beasley et al. 2015). For instance, temperature is known to impact invertebrate and microbial

951   activity (Vass 2001, Zhou and Byard 2011), and was later found to affect the percentage

952   consumption of small-mammal carcasses by vertebrate scavengers (DeVault et al. 2004a).

953   Although the mechanism of this interaction has not been tested, microbial and invertebrate

954   communities are known to affect the rate of decomposition (Simmons et al. 2010) and quality of

955   the carcass (Payne et al. 1968, Pechal et al. 2013, Pechal et al. 2014a), which likely influences

956   the quality and quantity of these resources available to vertebrate scavengers. The reciprocal

957   effect can be inferred from high vertebrate scavenging rates (DeVault et al. 2011) that eliminate

958   these resources via consumption of fresh carcasses as they become available and therefore

959   reducing persistence in the landscape (Jones et al. 2015). Additionally, there is some evidence

960   that microbes of carcasses and vertebrate scavengers may have co-evolved, as hyenas frequently

961   feed on ungulate carcasses that have died from anthrax without showing disease characteristics

962   (Villiers Pienaar 1969, Gasaway et al. 1991). There is precedent for evolved adaptations in avian

963   scavengers for competing with carrion microbial communities (Houston 1974, Houston and

964   Cooper 1975). These cross-kingdom scavenger interactions are important to ecosystems but are

965   often overlooked aspects of the ecology of animal decomposition (Wilson and Wolkovich 2011);

966   however, they constitute linkages that make up food webs, indirect predatory-prey effects, and

967   necrobiome community networks.

968

969 The biotic structure and interactions among necrobiome taxa inherently give rise to network

970 structure that can be used to define the complex and dynamic nature of organic matter

971 decomposition. Foodwebs are biotic networks of interacting organisms, energy and nutrient flow

972 and define communities and metacommunities. The complexity of foodweb networks has been

973 studied in several systems (Polis and Strong 1996, Eklöf et al. 2013, Wende et al. 2017), and has

974 been proposed as a useful tool for developing a systems approach to understanding ecosystems

975 (Dunne et al. 2002). The necrobiome framework offers an opportunity to quantify a subset of

976 overall ecosystem foodweb networks and test novel hypotheses related to the strength of direct

977 and indirect interactions among species and trophic levels. Furthermore, the necrobiome

978 approach affords the opportunity to test hypotheses and further theory with evolutionary

979 importance of the decomposer communities, much like that argued for understanding the broader

980 importance of scavenging in foodweb research (DeVault et al. 2003, Wilson and Wolkovich

981 2011). The complexity and stability of plant and animal necromass networks likely arises, in

982 part, from the indirect (non-physical) interactions that involve evolved sensing, physiology and

983 behavior associated with finding and consuming decomposing resources (Tomberlin et al. 2011)

984 and direct interacions of the necrobiome.

985

986 **SPATIAL AND TEMPORAL DIMENSIONS OF THE NECROBIOME**

987

988 Dead wood and animal carcasses vary in size, spatial density, and temporal input and turnover,

989 adding another layer to necrobiome dynamics. Succession and related theory (Box 1) is well

990 documented for decomposer communities associated with plant and animal necromass

991 (Refsnider and Janzen 2010). Yet, scaling up these localized processes and integrating them into

992   the higher-level spatial and temporal dynamics occurring among multiple decomposer

993   communities at ecosystem scales is a significant challenge. Indeed, very few studies have yet to

994   document the large-scale dynamics of single sources of detritus (e.g., forest stand blow downs)

995   beyond ontogeny-based death events of anadromous fishes (e.g., Pacific salmon, Oncorhynchus

996   spp.), despite recent work demonstrating that large animal mass mortality events are increasing

997   in both magnitude and frequency globally (Fey et al. 2015). Empirical studies of large-scale

998   carrion effects include the mass emergence of cicadas (Magicicada spp.) in North American

999   forests (Yang 2004), the annual spawning runs of salmon (e.g., Oncorhynchus spp.) (Hocking

1000 and Reynolds 2011), and the mass drowning of wildebeest in the Mara River in Kenya

1001 (Subalusky et al. 2017). These studies have shown how substantial quantities of carrion can alter

1002 forest soil microbial communities (Yang 2004), change the biomass and composition of riparian

1003 plant communities (Hocking and Reynolds 2011), and subsidize 50% of the diet of fish

1004 communities (Subalusky et al. 2017). Such instances provide evidence of carrion and associated

1005 necrobiomes changing nutrient cycling in a way that alters ecosystem functioning. Examples of

1006 plant necromass altering ecosystems are more common, with litter fall and decomposition having

1007 critical role in the cycling of mega-tons of carbon annually (Gessner et al. 2010). Plant litter is

1008 ubiquitous in vegetated ecosystems, and associated decomposer communities are similarly

1009 widespread (Refsnider and Janzen 2010). Similar to the spatially discrete dead trees and coarse

1010 woody debris, there are fewer instances of analogous, highly recalcitrant, structures of animal

1011 carcasses (e.g., whale bones) that provide focal points for the assemblages of distinct necrobiome

1012 communities over long (e.g., years to decades) temporal scales. However, the impact of such

1013 spatially and temporally unpredictable events on bottom-up or top-down processes are still not

1014 fully understood.

1015

1016   Across a landscape are many dead logs and carcasses of different sizes and decay stages, with

1017   each stage having a different necrobiome defined by its attendant species and their interactions.

1018   This variability emphasizes the among-necromass dynamics of multiple necrobiomes.

1019   Succession is well documented (see Box 1) and tells us that any single necrobiome exists only

1020   for a certain window of time (Table 1), which might range from hours to days for carcasses in

1021   warm conditions (Payne 1965, Barton and Evans 2017) or months to years for some large fallen

1022   trees (Weedon et al. 2009) or mummified animal necromass in habitats such as dry deserts or

1023   peat bogs (Brothwell et al. 2002, Chapman 2015). Decomposer organisms searching for their

1024   next resource to continue their life-cycle are therefore not only looking for another log or

1025   carcass, but also a specific decay stage, thus further emphasizing the rapid temporal turnover of

1026   the necrobiome within a necromass source. For specialist decomposers in the necrobiome, their

1027   existence is entirely dependent on resource continuity through time, with continuity also

1028   dependent on spatial proximity due to dispersal limitation. Thus, the implications of high-level

1029   among-necromass necrobiome dynamics become apparent across multiple scales in ways that

1030   include: (i) the reproductive success and survival of individuals, and their subsequent dispersal

1031   and contribution to population genetics (Stokland et al. 2012); (ii) competition among species,

1032   coexistence, and community diversity and heterogeneity; (iii) the consumption and metabolic

1033   breakdown of necromass via microbes and saprophytes; and (iv) dispersal of necromass energy,

1034   genomes and elements through the environment as new living biomass.

1035

1036   There are gaps in our knowledge of ecosystem-scale responses to plant and animal necromass,

1037   and many fundamental questions remain. A framework that joins patch-scale phenomena with

1038   ecosystem-scale consequences is therefore needed to fully appreciate the cross-scale dynamics of

1039   the necrobiome. We synthesize in Figure 4 previous work that has attempted to conceptualize

1040   among-carcass dynamics (Barton et al. 2013a, Benbow et al. 2015b), but which also applies

1041   conceptually to leaf litter, dead trees and course woody debris. We suggest that the spatial and

1042   temporal dimensions of the dynamic necrobiome are best conceptualized hierarchically, with

1043   community dynamics occurring spatially and temporally within necromass sources as well as

1044   spatially and temporally among multiple sources of necromass (Figure 4).

1045

1046   **BUILDING THEORY IN DECOMPOSITION ECOLOGY**

1047

1048   The necrobiome framework illustrates the links and interactions among decomposer organisms

1049   associated with defined substrates, and the key interactions with each other and the environment

1050   over a range of spatial and temporal scales. For example, microbes and necrophagous insects

1051   interact on individual carcasses and come into direct contact with one another (Crippen et al.

1052   2015). Similarly, phoretic mites interact directly with their insect hosts and carcasses, which

1053   provides focal points for their movement via necrophilous insects across landscapes (Perotti and

1054   Braig 2009). Yet these examples of direct contact that occur over relatively small spatial and

1055   temporal scales can have implications at much larger scales by altering metacommunity structure

1056   and the rate and pathway of nutrient and genome movement through ecosystems. The

1057   necrobiome allows for clearer conceptualization of the links between groups of species and their

1058   environmental context, and we believe this can help to develop empirical tests of ecological

1059   theory related to decomposition. For example, for many forms of necromass, especially large and

1060   recalcitrant forms, the decomposition process is characterized by a succession of species (see

1061 Box 1). Succession is, in part, guided by colonization history and priority effects as early

1062 colonizers can have facilitative or inhibitory effects on later colonizers (Connell and Slatyer

1063 1977). In addition to direct interactions among decomposers coexisting at the same time and

1064 place, the indirect priority effects among species across time are known to be of great importance

1065 to the development of these communities as well as to their collective effects on decomposition.

1066 In Sweden, for example, Weslien et al. (2011) showed that colonization of Norway spruce (Picea

1067 abies L. Karst.) by two beetle species within one year of cutting influenced the occurrence of

1068 another beetle species a decade later in a way that was mediated through a species of wood-

1069 decaying fungi.

1070

1071 The examination of species traits can also benefit from the necrobiome concept by understanding

1072 what traits mediate key functions or processes. Greater general understanding of species and

1073 assemblage and food web responses to decomposition is necessary to improve the transferability

1074 of findings across geographic regions with different sets of species, which is a source of variation

1075 among applied research, such as forensics, using these ecological concepts (Tomberlin et al.

1076 2012a). For example, dispersal is a key trait that determines species ability to search and

1077 colonize different forms of necromass (Tomberlin et al. 2011) but has not been widely examined

1078 among carrion-associated arthropods (Barton et al. 2013b). Additionally, the feeding traits of

1079 species are closely related to specialization and arrival dynamics (Barton and Evans 2017), can

1080 be associated with tissue quality (Ulyshen 2016), and drive competition and interactions among

1081 insects and microbial species (Burkepile et al. 2006). These complex interactions form ecological

1082 networks upon which ecosystem functions rest. There is a need for a unified ecological theory

1083   building upon the previous knowledge from plant and animal necromass across ecosystems to

1084   more comprehensively understand decomposition ecology.

1085

1086   **IMPLICATIONS AND CONCLUSIONS**

1087

1088   The proposed necrobiome framework provides a general template to conceptualize the structure

1089   and function of decomposer communities. A set of questions naturally arises from the

1090   necrobiome framework and its spatial and temporal dimensions. For example, what is the

1091   functional outcome for decomposition by adding or subtracting different biotic components of

1092   the necrobiome? What is the effect of altered interactions in the presence or absence of these

1093   biotic components and are the responses consistent among necromass types? Landscape

1094   consequences extend from these localized questions, such as: How does altered necrobiome

1095   structure and function lead to altered rates and pathways of genomic, element, and nutrient

1096   movement through ecosystems? Manipulative experiments have shown that excluding insects

1097   from carrion (Payne 1965, Pechal et al. 2014a) and plant matter (Heneghan et al. 1998, Wall et

1098   al. 2008, Ulyshen 2014, Stoklosa et al. 2015) resulted in changes to necromass loss rates. But

1099   what about experiments that change various functional components, or enhance fragmentation by

1100   insects, or manipulate the internal or external microbial communities, such as excluding

1101   detoxifying bacteria? Necromass varies along important gradients of nutrient quality, size, and

1102   digestibility, and decomposition progresses as a function of the attendant necrobiome and

1103   surrounding abiotic template. Clarity in our understanding of these controlling parameters means

1104   that future research on decomposition can soon be standardized across resource types. Future

1105   experimental studies that control for these parameters can then focus on manipulating key

1106   functional groups or interactions within the necrobiome to reveal the consequences for

1107   decomposition, food webs and ecosystem services.

1108

1109   The necrobiome concept and the further development of decomposition theory have implications

1110   to disciplines ranging from ecosystem restoration to forensics. In restoration ecology, new

1111   comparative work could examine the effects of manipulation of plant and animal necromass to

1112   return key processes critical to decomposition and nutrient cycling and broader ecosystem-scale

1113   functioning. Using the necrobiome framework, functional and biotic components can be

1114   identified that enhance or slow nutrient cycling, change community network stability, generate

1115   ecosystem heterogeneity, or add biodiversity per se. In the field of forensics, insects are the

1116   primary source of evidence used by practitioners for death cases requiring legal action. Although

1117   the dynamics of forensically important insects are rooted in ecological theory (e.g., community

1118   assembly, succession, priority effects, metacommunities, perturbation impacts, biodiversity, and

1119   patch dynamics) (Benbow et al. 2015a), there must be an expansion of this basic knowledge and

1120   potential use to other constituents of the necrobiome (e.g., microbes). The necrobiome concept

1121   provides a strong conceptual basis to further both theoretical and empirical endeavors.

1122

1123   **ACKNOWLEDGEMENTS**

1129   M.E.B. and P.S.B contributed equally to leading this paper, and P.S.B. can be contacted as a

1130   corresponding author via email (philip.barton@anu.edu.au). Points of view in this document are

1131   those of the authors and do not necessarily represent the official position or policies of the U.S.

1132   Department of Justice.

1133

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2102   **DATA AVAILABILITY**

2103   Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.pp5bs35

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2105 **Table 1.** Decomposer components and characteristics of heterotrophically- and autotrophically-

2106 derived necromass decomposition with representative studies for each component. Microbial

2107 communities include prokaryotes and microscopic protists, fungi and eukaryotes. Temporal

2108 scales range from ecologically relevant scales related to the life history traits of decomposer

2109 species to plant and animal biomass protected from decomposer species over geological time

2110 scales of decades or centuries (e.g., peat bog mummies).

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, Pechal et al. 2014b, Metcalf et al. 2016)	(Swift and Boddy 1984, Arnold et al. 2000, Persson et al. 2009, Voříšková and Baldrian 2013)
Macroinvertebrate-Saprotrophs	Blow flies (e.g., Diptera: Calliphoridae, Sarcophagidae) and Beetles (e.g., Coleoptera:	Wood boring and detrital insects (e.g., Coleoptera: Curculionidae): (Hickin 1963, Wallace et al. 1997, Haila and Niemelä 1999, Lieutier et

	Staphylinidae and Silphidae): (Fuller 1934, Chapman and Sankey 1955, Bornemissza 1957, Payne 1965, Greenberg 1971a, b,)	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)	Localized (0.1 – 100 m): (Lussenhop 1992, Strickland et al. 2009a)
	Diffuse (100-1000 m): (Houston 1974, Holland et al. 2017)	Diffuse (100 – 10,000 m): (Polis and Hurd 1996, Jiménez et al. 2017)
Temporal Scale Context	Ecologically Short (minutes to days): (DeVault et al.	Ecologically Short (minutes to days): Leaching rates (Nykvist

2004b, Farwig et al. 2014, Smith et al. 2017)	1959 a,b, 1963, Cummins et al 1973, Kuiters and Sarink 1986)
Ecologically Long (weeks to years): (Danell et al. 2002, Barton et al. 2016)	Ecologically Long (weeks to years): (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)	Geological (decades to centuries): (Van Geel 1978, Middeldorp 1986, Barthelmes et al. 2006, Kvavadze and Kakhiani 2010, Ronkainen et al. 2013)

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2113   **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 (Leroux and Loreau 2008, Gravel, et al. 2010, Polis, et al. 1997). 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 carcasses 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. 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.

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2116   **Figure Captions**

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2118   **Figure 1.**

2119   The necrobiome is the community of organisms associated with necromass decomposition, and

2120   includes their interactions with the necromass, with each other, and with their surrounding

2121   habitat and ecosystem. This concept is general across plant, fungi, dung/frass/feces or animal

2122   necromass types, and in both terrestrial and aquatic realms. (a) Various qualities of necromass

2123   have strong controlling effects on its associated necrobiome. (b) The decomposing necromass is

2124   host to a microbiome while alive, both internal (endonecrotic) and external (epinecrotic), and

2125   these communities begin to change after death and during the course of decomposition. The

2126   changing microbiomes use the organic matter as habitat and for energy and nutrients. As decay

2127   progresses, the organic matter and associated activities of the microbes facilitate the attraction of

2128   invertebrate and vertebrate saprophages that directly consume the necromass and the microbial

2129   communities. (c) All of these biotic components of the necrobiome interact in ways that give rise

2130   to pathways of microbial and elemental dispersal away from the decaying necromass into

2131   adjacent soil or water media, as well as to the surrounding ecosystem at both localized and broad

2132   spatial scales. (d) The necrobiome and its functions operate within a complex network of

2133   interactions that are constrained by its terrestrial or aquatic context, the regional species pool,

2134   and gradients of abiotic factors. Critically, all these aspects of the necrobiome are interlinked,

2135   and the relative importance of each component of the necrobiome, and their function, will

2136   depend on the intrinsic qualities of decaying necromass and the extrinsic controlling

2137   environmental factors (e.g., temperature, moisture, latitude).

2138

2139 **Figure 2.** Examples of necromass types occurring in ecosystems showing differences in size and

2140 heterogeneity. (a) Log cross section showing different rates of decay at edges versus center, (b)

2141 millipede carcass exoskeleton remains, (c) leaf litter, and (d) vertebrate carcass showing

2142 endoskeleton remains. Despite the contrasting physical appearance of necromass types, the broad

2143 structure of the necrobiome at each necromass type can be conceptualized in a similar way.

2144

2145 **Figure 3.** Some examples of the range of necromass sizes (L) and nutritional quality (C:N) for

2146 carrion, dung, leaf and wood substrates. Red points represent examples where there is volume

2147 data available in the literature, whereas white points are examples for which there is no volume

2148 data available. Data used for this figure were deposited the Dryad Digital Repository

2149 (doi:10.5061/dryad.pp5bs35).

2150

2151 **Figure 4.** The spatial and temporal dimensions of the necrobiome among multiple necromass

2152 patches introduce an additional level of dynamics important to understanding ecosystem-scale

2153 processes. (1) Each item of necromass decomposes from fresh (F) to dry (D), and the attendant

2154 necrobiome changes in diversity and composition through time. (2) This creates time windows

2155 for colonization and dispersal by specialist decomposers and their predators as they search for

2156 the next similar decay stage. (3) Multiple necromass resources occur at any one time and

2157 generates a range of decay states with different necrobiomes. (4) This creates a shifting spatial

2158 mosaic of necrobiome patches over time, each with unique levels of diversity, composition, and

2159 types of interactions and processes.

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

Habitat and ecosystem

Saprophage community

External microbiome

Internal microbiome

Necromass

Substrate microbial community

(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)
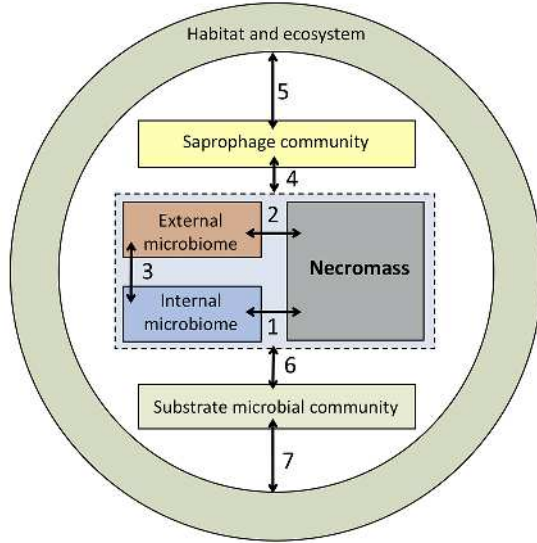
(c) Necrobiome interactions and functions

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
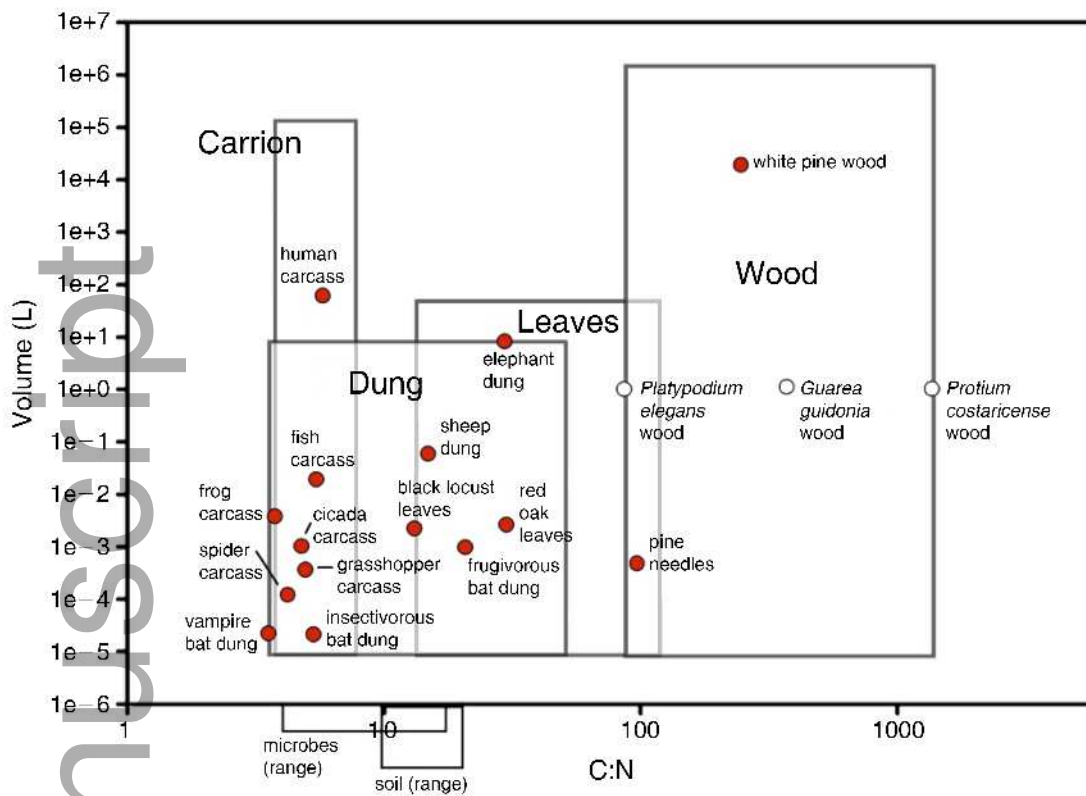7. Dispersal of microbes and elements into broader ecosystem via trophic and physical pathways

(a) Necromass qualities include the size, nutrient content, and digestibility of the resource
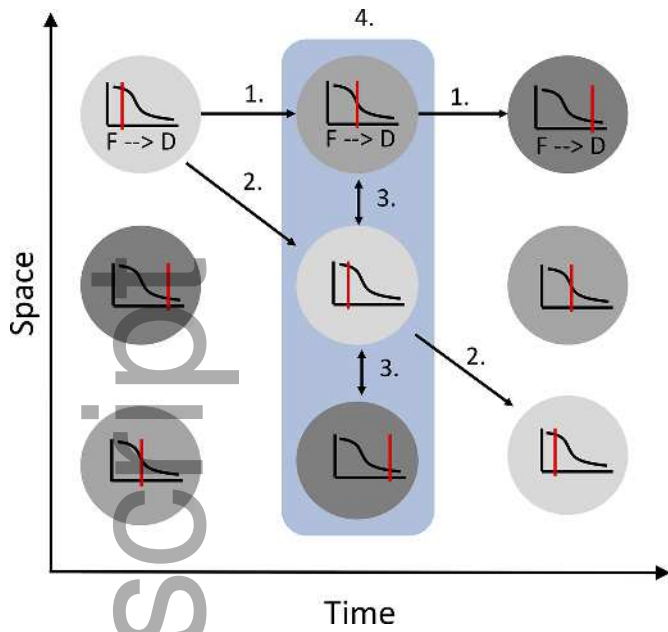
ecm_1331_f1.tif
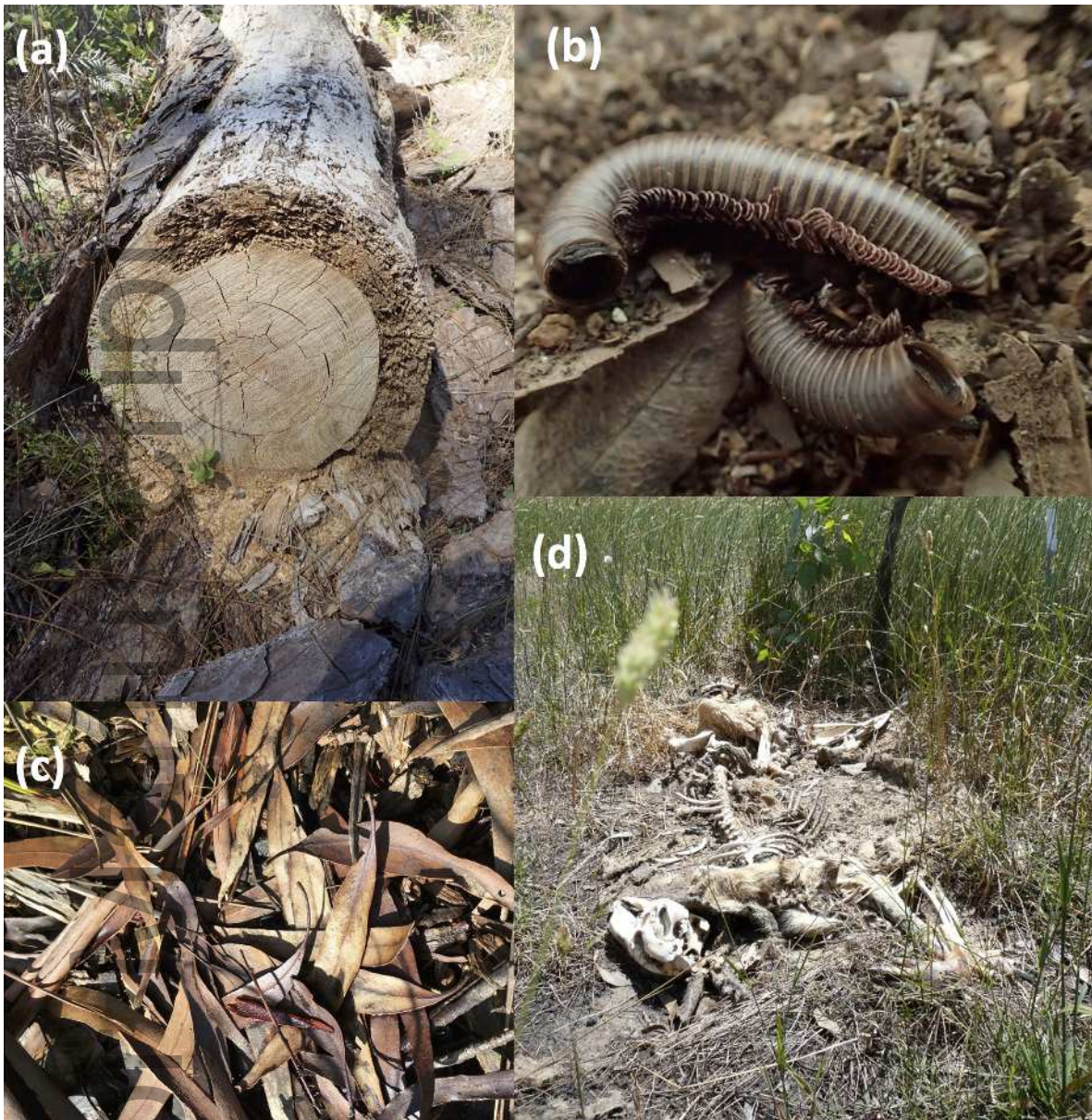
ecm_1331_f2.tif

ecm_1331_f3.tif

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 as they search for the next similar decay stage.

3. Multiple necromass resources occur at any one time, and generates a range of decay states with different necrobiomes.

4. The creates a shifting spatial mosaic of necrobiomes over time, each with unique levels of diversity, composition, and types of interactions and processes.

ecm_1331_f4.tif