

The role of carrion in maintaining biodiversity and ecological processes in terrestrial ecosystems

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23 **Abstract**

24 Carrion provides a resource for a subset of animal species that deliver a critical ecosystem
25 service by consuming dead animal matter and recycling its nutrients. A growing number of
26 studies have also shown various effects of carrion on different plant and microbial
27 communities. However, there has been no review of these studies to bring this information
28 together and identify priority areas for future research. We review carrion ecology studies
29 from the last two decades and summarise the range of spatial and temporal effects of carrion
30 on soil nutrients, microbes, plants, arthropods, and vertebrates. We identify key knowledge
31 gaps in carrion ecology, and discuss how closing these gaps can be achieved by focusing
32 future research on the (i) different kinds of carrion resources, (ii) interactions between
33 different components of the carrion community, (iii) the ways that ecosystem context can
34 moderate carrion effects, and (iv) considerations for carrion management. To guide this
35 research, we outline a framework that builds on the ‘ephemeral resource patch’ concept, and
36 helps to structure research questions that link localised effects of carrion with their
37 consequences at landscape scales. This will enable improved characterisation of carrion as a
38 unique resource pool, provide answers for land managers in a position to influence carrion
39 availability, and establish the ways that carrion affects the dynamics of species diversity and
40 ecological processes within landscapes.

41

42

43 **Key-words:** animal, carcass, detritus, ecosystem, nutrient cycling, spatial, temporal

44

45 **Introduction**

46

47 The decomposition of organic matter is central to the cycling of energy and matter in all
48 ecosystems (Swift et al. 1979; Moore et al. 2004). Up to 90 % of organic matter generated by
49 plants is not consumed when living and enters the detritus pool (Swift et al. 1979; Gessner et
50 al. 2010). Animals consume the remaining 10%, incorporate this into new tissue for growth
51 and development, and eventually return these nutrients to the detritus pool as excreta and
52 carrion. Carrion, the focus of this review, is a nutrient-rich resource for a large variety of
53 facultative scavengers and predators (Schoenly and Reid 1983; Braack 1987; Schoenly 1991;
54 Parmenter and MacMahon 2009; Wilson and Wolkovich 2011). It can also affect soils (Bump
55 et al. 2009b), microbes (Yang 2004) and plants (Towne 2000). Carrion can therefore have
56 direct and indirect effects on many parts of an ecological community, and contribute to the
57 dynamics of species diversity and nutrient cycling (Hocking and Reynolds 2011; Beasley et
58 al. 2012).

59 Research on the role of carrion in ecological communities is often narrowly focused
60 on two different areas: successional patterns associated with determination of post-mortem
61 interval (e.g. Horenstein et al. 2010; Matuszewski et al. 2011), or spatial patterns of energy
62 and nutrient flow at ecosystem scales (e.g. Polis et al. 1997; Marcarelli et al. 2011). A recent
63 review by Carter et al. (2007) highlighted the neglected state of carrion decomposition
64 research from an ecological perspective, and two other reviews have showed the importance
65 of carrion in providing a distinct and probably underestimated resource in ecosystems
66 (DeVault et al. 2003; Wilson and Wolkovich 2011). Despite this, there have been few
67 comprehensive empirical studies of the role of carrion in supporting biodiversity and distinct
68 food webs in terrestrial ecosystems (Parmenter and MacMahon 2009; Wilson and Wolkovich
69 2011). Thus, while the decomposition process is well understood, and it is becoming

70 increasingly known that carrion is an important resource for many species, there has been no
71 review of the literature to bring this information together and identify new areas for research.
72 Our aim in this paper is to broaden the conceptual awareness of the way carrion affects the
73 spatial and temporal dynamics of ecological communities. We review the literature on carrion
74 ecology from the last two decades and identify some key knowledge gaps. We then describe a
75 framework to guide future research on the role of carrion in maintaining biodiversity
76 dynamics.

77

78 **Carrion is a unique resource**

79

80 Although carrion represents only a small part of the total detritus pool in most ecosystems
81 (Swift et al. 1979; Parmenter and MacMahon 2009), its role in nutrient cycling and
82 community dynamics is disproportionate compared with plant detritus for two reasons. First,
83 carrion is nutrient-rich whereas plant litter is typically nutrient-poor and low in key
84 macronutrients such as nitrogen and phosphorus (Swift et al. 1979; Moore et al. 2004).
85 Second, carrion decomposes at much faster rates than plant litter, perhaps up to three orders
86 of magnitude faster (Parmenter and MacMahon 2009). These two key qualities of accelerated
87 temporal dynamics and high nutrient concentration make carrion a distinct component of the
88 detritus pool in ecosystems.

89 Carrion is also a spatially patchy resource, with each carcass forming a “cadaver
90 decomposition island” (sensu Carter et al. 2007). This has the effect of creating a spatially
91 distinct hotspot of biological and chemical activity that becomes more pronounced for large
92 vertebrate animals. The processes occurring during the different phases of vertebrate
93 decomposition (see for example Mégnin 1894; Bornemissza 1957; Carter et al. 2007) provide

94 the underlying mechanisms by which large carcasses affect their surroundings and associated
95 organisms.

96 The flow of energy and nutrients in a carrion-centred food web is summarised in Figure
97 1. Environmental variables, such as temperature and moisture, have strong controlling effects
98 on rates of carrion decay (Carter et al. 2007; Parmenter and MacMahon 2009; Carter et al.
99 2010), and are especially critical to the rates of cycling of nutrients through microbial
100 decomposers. However, the dispersal of nutrients away from carrion is largely driven by the
101 activity of arthropod and vertebrate detritivores and scavengers, and their predators (Payne et
102 al. 1968; Putman 1978a; Braack 1987; DeVault et al. 2003; Schmitz et al. 2008; Parmenter
103 and MacMahon 2009). Carrion nutrients are channelled through below-ground pathways by
104 bacteria and fungi, which sequentially degrade the large and complex organic molecules
105 making up the various tissues of an animal (Bornemissza 1957; Carter et al. 2008). Some loss
106 of energy occurs through the release of gases from a carcass, such as carbon dioxide (Putman
107 1978b). The mineralisation of key nutrients by microbes, such as nitrogen and phosphorus,
108 make them available for uptake by plants (Towne 2000). These recycled carrion nutrients are
109 incorporated into plant tissues, which may then be consumed by herbivores (Yang 2008) and
110 their predators (Moore et al. 2004). Importantly, all animals, regardless of trophic position,
111 will ultimately re-enter the carrion pool in an ecosystem upon their death, unless they are first
112 consumed by a predator. Thus, the ecology of carrion is a central unifying concept that links
113 all animals to the cycling of energy and nutrients through their ecosystem.

114

115 **Ecological theory**

116

117 The dynamic temporal decomposition and patchy spatial occurrence of carrion produces
118 distinct effects on ecological communities, and provides the theoretical foundation for many

119 studies of carrion ecology. Most notable among these are temporal succession theory
120 (Schoenly and Reid 1987) and spatial aggregation and coexistence theory (Ives 1991), which
121 are often used by researchers to provide a set of expectations to test and explain their
122 observations. Succession theory is concerned with the predictable change in species
123 composition through time. However, succession in carrion ecology is different from
124 succession in plant ecology, as there is no equilibrium or climax community reached after the
125 carrion resource is depleted (Schoenly and Reid 1987). Nevertheless, it has been widely
126 documented that there are dynamic changes in the composition of organisms that visit carrion
127 during its different phases of decomposition (Schoenly and Reid 1987; Boulton and Lake
128 1988; Schoenly and Reid 1989; Moura et al. 2005; Matuszewski et al. 2011). Specifically, this
129 is usually documented as the arrival and departure of species (especially arthropods) through
130 time or at particular stages of decomposition. For this reason, succession theory is used
131 widely as a basis for determining the time since death of animal and human cadavers (e.g.
132 Mégnin 1894; Bornemissza 1957; Payne 1965; Moura et al. 2005; Tomberlin et al. 2011b).
133 Aggregation and coexistence theory is concerned with explaining the division of finite
134 resources among organisms (e.g. Hanski 1987; Ives 1991; Woodcock et al. 2002). This theory
135 has been used to understand and predict the dynamics of abundance and richness of organisms
136 present at carrion due to changes in inter- and intra-specific competition (Ives 1991; Kouki
137 and Hanski 1995; Woodcock et al. 2002). In particular, stochastic colonisation of carcasses by
138 organisms plays an important role in competition and coexistence dynamics, and therefore
139 species dominance. Although both theories are aimed at understanding community structure,
140 aggregation and coexistence theory has a focus on explaining species spatial occurrences,
141 whereas succession theory has a focus on explaining species temporal occurrences.

142 Efforts to synthesise a general understanding of the dynamics of carrion communities
143 have focused on the spatial and temporal properties of carrion. This has led to carrion being

144 conceptualised as discrete patches of concentrated energy and nutrients that are spread across
145 the landscape (Doube 1987). Such a perspective, encapsulated by the term “ephemeral
146 resource patch” has been further developed in greater detail by Finn (2001), with some
147 additional detail from Carter et al. (2007). This single idea captures many of the concepts
148 underpinning succession and aggregation theory. For example, the rapid change in carrion
149 quality during the process of decomposition drives the succession of species through time
150 (Schoenly and Reid 1987; Moura et al. 2005; Matuszewski et al. 2010), and the rare
151 occurrence of carrion produces intense inter- and intra-specific competition for a limited
152 resource through space (Kneidel 1984; Ives 1991; Kouki and Hanski 1995). Thus, the
153 ephemeral resource patch concept provides a general framework for how carrion resources
154 can affect the spatio-temporal dynamics of species populations or communities, and
155 ecological processes. This also highlights key conceptual parallels between carrion resources
156 and other spatially discrete and ephemeral resources, such as dung pads (Doube 1987), fungal
157 fruiting bodies (Heard 1998) and fruits (Sevenster and VanAlphen 1996), suggesting a
158 broader empirical basis exists to develop further the theory surrounding carrion ecology.

159

160 **The range of effects of carrion on communities and ecosystems**

161

162 **Methods**

163

164 To assess recent progress in knowledge of carrion ecology, we searched the ISI Web of
165 Knowledge (Science Citation Index) for English language studies published from 1990 to
166 2010 that examined the ecological effects of carrion on different taxa and ecosystem
167 properties. We focused on the last 20 years to capture the more recent progress in the field of
168 carrion ecology, but also refer to several foundational papers in our discussions (e.g.

169 Bornemissza 1957; Payne 1965; Coe 1978; Braack 1987; Schoenly and Reid 1987). We used
170 the following search terms in the topic search option, which includes title, abstract, and author
171 keywords: ‘carrion AND ecolog*’, ‘carcass AND ecolog*’, and ‘cadaver AND ecolog*’. We
172 supplemented this search by examining the reference lists of two recent papers by Parmenter
173 and MacMahon (2009) and Carter et al. (2007). From this pool of papers, we then selected
174 studies by searching the titles and abstracts of each publication for keywords in five broad
175 categories: (i) soil nutrients, (ii) below-ground bacteria and fungi, (iii) plants and vegetation,
176 (iv) arthropods, and (v) vertebrates. For each category, we restricted our search to empirical
177 studies on ecological communities in terrestrial ecosystems, thus reviews and taxonomic
178 checklists were excluded, as were studies on single species, and studies in aquatic or marine
179 systems.

180 Our search yielded 65 papers that presented 84 separate case studies of a measured
181 effect of carrion on one of the five categories (see electronic supplementary materials). Of the
182 84 case studies, 64% were on arthropods, and 72% were from the period 2001 to 2010 (ESM
183 Fig. 1). In contrast, only 23% were on soil, plant or microbial responses to carrion. For each
184 empirical case study on soil nutrients or organisms we asked the following questions: (1) In
185 what biome was the study conducted? (2) What were the main taxa of interest? (3) What type
186 of carrion was examined? (4) What were the main spatial or temporal contrasts? We
187 summarise our key findings separately for soils, bacteria and fungi, plants, arthropods, and
188 vertebrates.

189
190 Soil nutrients

191
192 A large proportion of carrion nutrients are consumed by animals and dispersed through the
193 landscape. Nevertheless, carcasses can have dramatic localised effects on soil properties

194 (Melis et al. 2007), including impacts on pH and nutrient content due to the direct leakage of
195 fluids and transfer of carrion tissue to the soil by invertebrates. Changes in soil nutrients
196 follow a predictable temporal pattern that closely matches the nutrient and mass loss of the
197 aboveground portion of the carrion (Carter et al. 2007). For example, a recent study
198 examining the role of carrion in nutrient cycling in a North American shrub-steppe ecosystem
199 showed that the sequence of peak nutrient transfer to the soil was first potassium and sodium,
200 followed by nitrogen and sulphur, then phosphorus and magnesium, and finally calcium
201 (Parmenter and MacMahon 2009).

202 Such comprehensive and quantitative studies on soil nutrient responses to carrion are
203 rare, however, and more typical are studies that focus on soil nitrogen (ESM Table 1). These
204 studies show no clear relationship between carcass size and depth of soil nitrogen change, and
205 the duration of this effect is quite variable. Earlier work by Coe (1978) showed that elephant
206 carcasses elevated nitrogen levels 40 cm below ground directly under the carcass, and 8cm
207 below ground 2 m away from the carcass, indicating some lateral movement of nutrients away
208 from the carcass. In contrast, frogs and sparrows can elevate soil nitrogen up to 15 cm below
209 ground (Parmenter and MacMahon 2009). It would seem reasonable, therefore, that carcass
210 size is an important factor, as it represents the quantity of nutrients available to move into the
211 local soil area. However, the apparently wide range of soil depth and duration measurements
212 in our sample of studies means that the magnitude of spatial and temporal effects of carrion
213 on soil nutrients remains largely unknown (but see Parmenter and MacMahon 2009).

214 Notably, we found only a single study that compared the quantity of animal biomass
215 to plant biomass in an ecosystem. Here, Parmenter & MacMahon (2009) estimated that 0.06%
216 of total aboveground biomass was vertebrate animal, compared with 99.94% plant biomass in
217 their semi-arid study site. This indicates that carrion may only contribute a trivial amount to
218 some ecosystem nutrient budgets. However, this estimate does not include abundant insects

219 such as ants, or below ground invertebrates such as earthworms or termites, and total carrion
220 biomass may be higher. We found no studies that described a nutrient budget accounting for
221 different forms of carrion in an ecosystem, indicating there is little quantitative knowledge of
222 the contribution of various forms of carrion to nutrient cycling.

223

224 Soil bacterial and fungal communities

225

226 We found very few studies that documented the response of below ground bacterial or fungal
227 communities to carrion outside a human forensic perspective. The effect of carrion on the
228 diversity and dynamics of microbial communities is therefore largely unknown (Stokes et al.
229 2009). Nevertheless, the few studies we found have demonstrated significant effects on both
230 microbial biomass and diversity below ground (ESM Table 2). At individual animal
231 carcasses, this is ultimately driven by the rapid and direct release of nutrients into the soil
232 from body fluids, as well as the transfer of other organic matter further into the soil from the
233 action of arthropods. This appears to have large impacts on microbes. For example, Carter *et*
234 *al.* (2008) recorded a 400% increase in microbial biomass under rat (*Rattus rattus*) carcasses
235 in a tropical savannah ecosystem in Australia. Although this species of rodent has a small
236 mass (200 g), it indicates that even a small carcass can have profound effects on soil
237 microbial communities. However, this phenomenon can have impacts at larger spatial scales.
238 For example, the addition of dead cicadas to plots in temperate forests of North America was
239 shown to increase bacterial abundance by 12%, and fungal abundance by 28% after one
240 month (Yang 2004). When multiplied across entire forested landscapes, such as during mass
241 cicada emergences and die-off, this represents an enormous change in the microbial biomass,
242 and highlights the significance of even very small insect carcasses as an important nutrient
243 cycling pathway. Another study on moose (*Alces alces*) showed that carcasses increased the

244 abundance of both bacteria and fungi communities 40 months after the death of the animal
245 (Bump et al. 2009a), indicating a long-lasting effect from a large carcass. Thus, carcasses of a
246 range of sizes can have significant effects on microbial communities when multiplied across a
247 landscape. The implications for ecosystem functioning are significant if the interaction
248 between soil bacteria and fungi with plant communities is recognised (van der Heijden et al.
249 2008). This includes the facilitation of nutrient uptake by plants (Towne 2000), and the
250 temporal availability of resources to below ground consumers (Wardle et al. 2004). Indeed,
251 the role of microbes at carrion in mediating trophic interactions and nutrient processing has
252 been identified as a critical issue relevant to both the fundamental ecology of food webs, and
253 the applied use of assemblage responses to inform human forensics (Tomberlin et al. 2011b).

254

255 Plant communities

256

257 Similar to soil microbial communities, plants are not mobile and do not actively seek out
258 carrion. As a result, the response of plants to carrion is largely passive, and will depend on
259 their ability to exploit fluxes in soil nutrient loading and pH, and subsequent changes in the
260 soil microbial community. Few studies have documented plant responses to carrion (ESM
261 Fig. 1), but most of them reported changes in either foliar nitrogen or biomass (ESM Table 3).
262 It is widely understood that plant available nitrogen in soils is closely related to soil microbial
263 activity (Schimel and Bennett 2004), and this is why some studies measure nitrogen levels in
264 both plant leaves and soil (Melis et al. 2007; Bump et al. 2009a). The use of stable isotopes
265 has confirmed this nutrient cycling pathway (Yang 2004; Bump et al. 2009a). Very few
266 studies have examined compositional dynamics of plants in response to carcass addition
267 (Towne 2000; Melis et al. 2007), and we found only a single study that documented the
268 competitive advantage given to some plants by the increased nutrient availability associated

269 with carcass decomposition (Bump et al. 2009b). Thus, it remains largely unknown if
270 carcasses are generally important by providing opportunities for disturbance specialist plant
271 species in ecosystems. Importantly, some studies have explicitly compared the responses of
272 plants next to carcasses with that of plants further away, thereby revealing the spatial extent as
273 well the magnitude of the hotspot effect of a carcass on plants (Danell et al. 2002; Bump et al.
274 2009b). At landscape scales, it has been demonstrated that regular and large-scale inputs of
275 carrion resources, such as mass insect die-off (Yang 2004), or annual contributions of
276 migrating salmon (Hocking and Reynolds 2011), can affect plant communities. This shows
277 that carrion, in its many different forms, can affect plant growth and composition across a
278 wide range of temporal and spatial scales.

279

280 Arthropod communities

281

282 Other than microbes, arthropods are typically the most species-rich and abundant organisms
283 found at carrion (Braack 1987). Functionally, arthropods are a critical component of carrion
284 food webs and contribute to the consumption, recycling and dispersion of carrion nutrients
285 (Parmenter and MacMahon 2009). The comminution of carrion by arthropods is not widely
286 documented, unlike plant detritus where comminution is a key mechanism for decomposition
287 by microbes (Hattenschwiler et al. 2005). Instead, carrion tissue appears to be directly
288 consumed and assimilated by arthropods. However, in the absence of arthropods, such as
289 when arthropods are experimentally excluded, the decomposition of carrion can be
290 significantly delayed (Payne et al. 1968; Parmenter and MacMahon 2009). This is especially
291 the case during warmer months of the year when blowflies dominate carrion consumption
292 (Payne 1965; Putman 1978c). There is a long history of arthropod succession studies,
293 including the seminal work of Mégnin (1894), Bornemissza (1957), Putman (1978c), and

294 Payne (1965), culminating in the development of the ‘continuum of change’ succession
295 paradigm by Schoenly and Reid (1987). Detailed reviews of this area of research can be found
296 elsewhere (Amendt et al. 2004; Tomberlin et al. 2011b). Therefore, in the following section
297 we focus on the broader ecological effect of carrion on arthropod communities.

298 The majority of studies on the ecology of carrion involved arthropods (ESM Fig. 1,
299 ESM Table 4). Most investigations focused on estimation of post-mortem interval with
300 application to human forensics. These provided location-specific details of arthropod
301 visitation patterns at carrion of different animals, but typically the pig *Sus scrofa*, which has
302 been used as a model for human cadavers in forensic work (ESM Fig. 3). Although studies
303 have examined arthropods at carrion of different animal species such as rodents or ungulates,
304 we found only one study that explicitly compared arthropod communities at carcasses of
305 different animal species (Watson and Carlton 2005). This offers an avenue for future research,
306 as there is some evidence that larger carcasses can host more diverse arthropod communities
307 than small carcasses (Schoenly and Reid 1983), and the wide variety of carrion resources in
308 ecosystems may provide resources to distinct components of arthropod communities. There
309 also was a bias towards conducting carrion arthropod studies in forested areas (ESM Fig. 2),
310 suggesting a need for studies on carrion in a wider range of vegetation types. This is
311 important because it is not clear whether carrion arthropod communities differ fundamentally
312 in structure between ecosystems or biomes. Most arthropod studies involved either a spatial or
313 temporal contrast, and only a few studies had simply documented species present at carrion
314 and attempted no comparisons across habitats or seasons (ESM Fig. 3). Most studies
315 examined both flies and beetles at carrion, and many also examined three or more taxa
316 (typically flies, beetles and ants). We found one published study that explicitly compared the
317 abundance and species richness of beetles (at a deer carcass) with a nearby control site in a
318 coniferous forest in Norway. In their study, Melis et al. (2004) found a higher diversity of

319 beetles at the carcass, thereby demonstrating its localised biodiversity ‘hotspot’ effect. While
320 many studies have repeatedly demonstrated the importance of carrion as a driver of temporal
321 change in arthropod communities (Moura et al. 2005; Matuszewski et al. 2010), very few
322 studies have explicitly examined the role carrion has in driving spatial variation in species
323 richness and abundance (Melis et al. 2004). The fact that so few studies have quantified this
324 hotspot effect, or examined community heterogeneity among carcasses, suggests there is a
325 significant gap in our knowledge of how many arthropod species carrion supports in different
326 environments, which may be relevant to biodiversity conservation.

327

328 Vertebrate communities

329

330 In some ecosystems, vertebrate scavengers are among the first to arrive at an animal carcass
331 (after blowflies), and can be responsible for consuming the majority of carrion (DeVault et al.
332 2003; Wilson and Wolkovich 2011). In many ecosystems, it is likely that more energy is
333 transferred through scavenging of carrion than through predation of live animals (Wilson and
334 Wolkovich 2011), and this represents a major underestimation of the importance of carrion as
335 a resource to vertebrate communities, and perhaps in ecosystems generally (DeVault et al.
336 2003).

337 The importance of vertebrates in carrion removal varies among ecosystems, but it is
338 clear that vertebrates accelerate carrion decomposition rates (DeVault et al. 2003; Parmenter
339 and MacMahon 2009). Indeed, this was a dominant theme among many of the vertebrate
340 scavenger studies we found (ESM Table 5). Most vertebrate studies also were biased towards
341 the responses of mammals or birds to carrion, with only a single study documenting the use of
342 carrion by reptiles (Read and Wilson 2004). Together, these studies show there is a distinct
343 set of vertebrate scavengers on each major continent, but that some scavenger guilds are more

344 diverse than others. For example, some scavenger guilds are dominated by only a few large
345 scavenger vertebrates, such as dingos and raptors in arid Australia (Read and Wilson 2004).
346 But some have a diverse scavenger guild, such as lions, hyenas, jackals and vultures in the
347 Serengeti of Africa (Hunter et al. 2007), or wolves, coyotes and bears in Yellowstone
348 National Park, USA (Wilmers et al. 2003). This kind of research is critical to understanding
349 the degree of overlap among scavenger species, and the resilience underpinning carrion
350 consumption by scavenger vertebrate communities in different landscapes (Olson et al. 2012).

351

352 **Knowledge gaps**

353

354 It is clear from our review that most empirical studies to date have focused on localised,
355 descriptive, and location-specific effects of carrion. We believe the key knowledge gap in
356 carrion ecology is therefore a clear understanding of whether carrion is important to terrestrial
357 ecosystems beyond its localised effects (Yang 2004; Bump et al. 2009a; Hocking and
358 Reynolds 2011). Thus, there remain a number of unanswered questions and gaps in our
359 knowledge of the role of carrion in maintaining biodiversity and ecological processes, and the
360 spatial and temporal scales over which this occurs. We suggest four broad areas as priorities
361 for future carrion ecology research: (i) carrion resources, (ii) community interactions, (iii)
362 ecosystem context, and (iv) carrion management. Below we discuss key questions that
363 explore the spatial and temporal dimensions of these four priority research areas (Table 1).

364

365 Carrion resources

366

367 An increased understanding of its important sources is fundamental to furthering our
368 knowledge of the ecology of carrion. A key question is therefore: What is the net contribution

369 of differently sized animal carcasses to the total carrion resource pool? Answering this
370 question requires an understanding of the composition and abundance dynamics of the animal
371 communities that will contribute to the carrion pool. Focusing first on vertebrate carrion, it is
372 clear that some species contribute disproportionately to carrion input in terms of overall
373 biomass. For example, sea birds on islands may dominate carrion input (Polis and Hurd
374 1996), whereas a deer may be only one of several species of ungulate contributing to the
375 carrion pool in a grassland prairie (Towne 2000). Further, the input of vertebrate carrion can
376 vary widely from such massive (but rare) quantities of millions of kilograms per square
377 kilometre recorded during the mass starvation of elephants in Kenya (Coe 1978), to thousands
378 of kilograms per square kilometre of moose in Michigan, USA (Bump et al. 2009a).

379 Although most studies on carrion focus on vertebrate carcasses (see DeVault et al.
380 2003; Parmenter and MacMahon 2009), it is widely understood that invertebrate biomass
381 exceeds that of vertebrates in many ecosystems. This is exemplified in some tropical systems,
382 where 90% of the estimated 200 kg.ha⁻¹ of aboveground animal biomass consists of
383 invertebrates (Wilson 1987). Soil invertebrate biomass may be even higher in some
384 ecosystems, ranging from 51 kg.ha⁻¹ in cropped land, to 205 kg.ha⁻¹ in temperate forests, and
385 732 kg.ha⁻¹ in pastures (Lavelle et al. 1997). Invertebrates also have shorter life spans, and are
386 recycled through ecosystems at faster rates than vertebrates. They also are comparatively
387 more uniformly distributed than vertebrates. This has different ecological implications. For
388 example, within the root system of a single individual plant, soil invertebrate deaths and
389 decomposition will provide a continuous source of nutrients throughout a growing season. In
390 contrast, the nutrient gain for the same plant from a decomposing vertebrate carcass is a lower
391 probability “hit or miss” scenario. Animal biomass in terrestrial ecosystems will always be
392 tiny compared with plant biomass (Fahey et al. 2005; Parmenter and MacMahon 2009).
393 Nevertheless, an understanding of the relative biomass of different kinds of carrion from both

394 vertebrates and invertebrates, and their input rates, will provide for a more objective approach
395 and give a fuller picture of the different kinds of carrion in ecosystems.

396

397 Community interactions

398

399 Ultimately, it is the action of microbes, invertebrates and vertebrates that facilitate the
400 decomposition and dispersion of carrion nutrients through an ecosystem (Carter et al. 2007;
401 Parmenter and MacMahon 2009; Beasley et al. 2012). Yet how these different components of
402 the carrion community interact is poorly understood. Further, there is a poor understanding of
403 how the interactions between carrion and its consumers relates to ecosystem functioning
404 (Tomberlin et al. 2011a; Wilson and Wolkovich 2011). A key question therefore is: How are
405 carrion resources partitioned among the carrion community? The competitive interactions
406 between microbial decomposers and vertebrate carrion consumers has been known for some
407 time (Janzen 1977; DeVault et al. 2003). However, it is only more recently that examples
408 have been documented for the competitive exclusion of arthropods by bacteria (Burkepile et
409 al. 2006) and bacteria by arthropods (Hoback et al. 2004; Rozen et al. 2008). This competitive
410 dynamic might have significant ramifications for the fate of carrion nutrients in ecosystems.
411 This is because nutrients can be dispersed large distances by insects, whereas they are simply
412 converted in the soil via bacteria and fungi at the site of a carcass. This highlights the lack of
413 studies that have compared communities of multiple taxa such as arthropods, birds and
414 carnivores (but see Read and Wilson 2004; Selva and Fortuna 2007; Parmenter and
415 MacMahon 2009).

416 Changes to land use and habitat also may affect the composition of carrion communities
417 (Klein 1989; DeVault et al. 2011). When this happens, some consumers of carrion may be
418 lost. This in turn may affect the process of carrion decomposition (Klein 1989). A key

419 question is therefore: Where and when is there functional redundancy among carrion
420 consumers? It is already known that many vertebrates will opportunistically scavenge on
421 carrion (DeVault et al. 2003), and there is evidence that some intra-guild compensation occurs
422 when dominant scavengers are removed (Olson et al. 2012). Similarly, several species of
423 blowfly co-occur at carcasses (Lang et al. 2006), and inter- and intra-specific competition may
424 affect carrion consumption rates. However, far less is known about redundancy among other
425 arthropod or microbial components of carrion food webs. An increased understanding of how
426 carrion resources are partitioned among carrion communities, and the spatial and temporal
427 overlap of consumers, will allow for a greater appreciation of the consequences to species loss
428 to carrion decomposition processes.

429

430 Ecosystem context

431

432 Carrion nutrients represent a subset of the much larger detritus nutrient pool in an ecosystem
433 (Moore et al. 2004), albeit greatly concentrated in discrete carcasses (small and large
434 carcasses), and with an accelerated turnover among a subset of organisms. This information
435 needs to be placed into ecosystem context, where background nutrient levels and productivity
436 will mediate the impact of carrion on soils and organisms. A key question is therefore: How
437 does the contribution of carrion to nutrient budgets vary among ecosystems? For example,
438 Barton et al. (in review) found that patterns of plant colonisation on kangaroo carcasses
439 depended on whether the carcass was added to native-dominated or exotic-dominated
440 grassland (Fig. 2). Similarly, Hocking & Reynolds (2011) found that the effect of salmon
441 carcasses on riparian plant communities was attenuated by overall productivity of the
442 catchment. These examples show two kinds of context dependency for carrion effects on plant
443 communities. This provides a foundation for the estimation of the consequences of changes in

444 carrion brought about by both natural processes, such as disease and starvation, as well
445 anthropogenic processes such as hunting and culling of wild herbivores.

446

447 Carrion management

448

449 The loss of top predators (Estes et al. 2011) and changes to populations of large wild
450 herbivores (Côté et al. 2004; Gordon et al. 2004), can alter the supply and distribution of
451 carrion in ecosystems (Wilmers and Post 2006; Wilson and Wolkovich 2011). A key question
452 is therefore: How do anthropogenic changes to carrion affect nutrient cycling and
453 biodiversity? For example, a commonly applied management response to large populations of
454 wild herbivores is hunting or culling, with carcasses often taken off-site for disposal or
455 consumption by humans. When this occurs, nutrients become unavailable to animal and
456 microbial consumers and are not recycled through food webs and the broader ecosystem. This
457 may have significant consequences for high-level food web dynamics (Wilmers and Post
458 2006; Wilson and Wolkovich 2011; Beasley et al. 2012). Where carrion resources have been
459 reduced, alternative sources may need to be supplied to provide spatial and temporal
460 continuity in resources and allow the persistence of carrion-dependent species in a given
461 landscape, such as has occurred for some species of vulture in the Pyrenees mountains of
462 Europe (Margalida et al. 2009; Margalida et al. 2011). Leaving carrion in ecosystems may be
463 one of the most effective short-term ways of managing for a component of biodiversity
464 associated with the nutrient cycling process. Of course, there are likely to be several
465 impediments to the management of carrion in landscapes, including cultural, legal and
466 economic factors (Dupont et al. 2012). Recognising them in the first place, however, may help
467 to mitigate some of these challenges.

468

469 **A framework for carrion research in landscapes**

470

471 Several ecological concepts rooted in the spatial and temporal dynamics of organisms and
472 nutrients have been applied to carrion, such as metapopulations (Hanski 1987) and resource
473 pulses (Yang et al. 2008), but are also applied to many other areas of ecology. In contrast, the
474 ‘ephemeral resource patch’ concept described by Doube (1987) and Finn (2001) specifically
475 relates to carrion, and captures the distinct spatial and temporal properties of this resource.

476 We propose a framework to facilitate future carrion ecology research that builds on these
477 theoretical ideas and the ephemeral resource patch concept. We believe this concept can be
478 used to build a general framework for scaling-up the localised effects of carrion to landscapes.

479 There are many similarities, for example, between the succession of carrion beetles or spike in
480 soil nitrogen at an individual vertebrate carcass (Barton et al. in review), and the change in
481 soil microbes and nitrogen in an entire forest due to the mass emergence of cicadas (Yang
482 2004). In both scenarios, carrion generates patchiness in biodiversity and ecological

483 processes, but at different spatial scales. The landscape-scale analogue to the ephemeral
484 resource patch concept is the idea of ‘landscape fluidity’. This idea was proposed as a way of
485 viewing the ebb and flow of organisms in landscapes through time (Manning et al. 2009). It is
486 described as a tool to conceptualise the dynamics of landscapes, and how processes such as
487 changes in the connectivity of habitat will affect the movement and persistence of organisms.

488 Most notably, with particular relevance to carrion ecology, the concept encapsulates the
489 continuity of species presence both within sites, and between sites across a given landscape
490 through time. It is this idea of continuity and overlap in carrion patches that has been not been
491 fully developed in the carrion ecology literature, and where we believe our framework can
492 contribute. We suggest that merging the concepts of landscape fluidity and ephemeral
493 resource patches can provide a unifying framework for conceptualising carrion dynamics and

494 testing hypotheses about the role of carrion in maintaining continuity in biodiversity and
495 ecological processes across multiple spatial and temporal scales (Fig. 3). For example, it is
496 widely documented that different decay phases drive temporal succession in carrion
497 assemblages (Fig. 3a). This means that two carcasses at different stages of decay host more
498 species than if two carcasses at the same stage of decay. Similarly, different habitat types host
499 spatially distinct carrion consumer species (Fig. 3b), and two carcasses in different habitats
500 might be expected to support more species than two carcasses in the same habitat. Thus, a
501 question emerging from our new framework is: What spatio-temporal arrangement of carrion
502 patches promotes the persistence of the highest diversity of carrion consumers within a
503 landscape? (Fig. 3c). Answering this question requires the explicit linking of local carrion
504 community dynamics with landscape-scale carrion resource dynamics. Simulation models
505 might be used to extrapolate alternate scenarios of carrion resource availability based on
506 population abundance, recruitment and mortality data (Wilmers and Getz 2004). This could
507 then be combined with data on assemblage composition dynamics observed across different
508 kinds of carcasses (Schoenly and Reid 1987; Parmenter and MacMahon 2009). Further
509 development of this into a more formal mathematical framework would require the
510 integration of succession theory with aggregation and coexistence theory (Ives 1991;
511 Schoenly 1992). A fully developed research agenda that combines our framework with
512 existing succession models and simulations of carrion availability would be able to
513 quantitatively predict how differing scenarios of carrion input, density, and decay stage might
514 lead to differing biodiversity and nutrient cycling outcomes.

515

516 **Conclusions**

517

518 Although there are a growing number of studies on carrion in terrestrial ecosystems, there
519 remain many aspects of carrion ecology that are open to future research. It is clear from these
520 studies that carrion has profound bottom-up effects on a wide range of organisms and
521 communities, with further effects on nutrient cycling. Nevertheless, there remains much to be
522 done to increase our understanding of how these localised phenomena driven by carrion
523 decomposition result in larger scale maintenance of biodiversity and ecological processes.
524 Advancing this knowledge can be achieved by tackling important questions surrounding the
525 supply and distribution of all kinds of animal carrion, the interactions and linkages among
526 different components of the carrion fauna. The question of whether carrion is important
527 beyond localised scales will ultimately be answered by performing more comprehensive
528 studies on carrion nutrient budgets, and by quantifying experimentally how much diversity
529 and heterogeneity is added to communities through the dynamics of multiple carrion patches.
530 Such knowledge will not only enhance our understanding of the role of carrion in supporting
531 biodiversity and nutrient cycling processes, but also help to provide answers for land
532 managers in a position to influence how much carrion is supplied, and where and when it is
533 available in landscapes.

534

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536

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541

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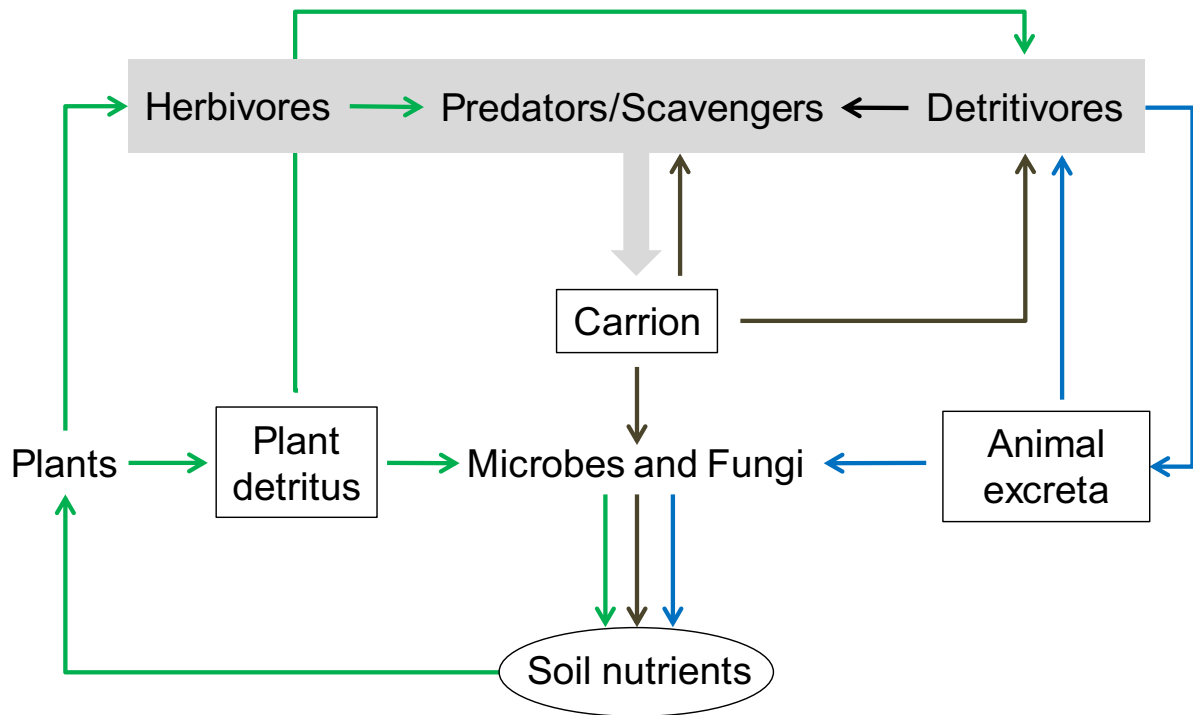
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753 **Table 1.** A list of four broad knowledge gaps, key questions, and some of their spatial and
 754 temporal dimensions, that might be used to guide future carrion research.

KNOWLEDGE GAP	KEY QUESTIONS	SPATIAL AND TEMPORAL DIMENSIONS
1. Carrion resources	a) What is the net contribution of differently sized animal carcasses to the total carrion resource pool?	<ul style="list-style-type: none"> • What is the spatial density of differently sized carcasses, such as insects versus mice? • When are the biggest temporal inputs of invertebrate and vertebrate carrion?
2. Community interactions	a) How are carrion resources partitioned among the carrion community? b) Is there functional redundancy among carrion consumers?	<ul style="list-style-type: none"> • How far do flies and scavenging carnivores disperse carrion nutrients through the landscape? • Where is there spatial and temporal overlap of among carrion consumer species ?
3. Ecosystem context	a) Does the contribution of carrion to nutrient budgets vary among ecosystems?	<ul style="list-style-type: none"> • Are carrion nutrients recycled more slowly in low-productivity ecosystems?
4. Carrion management	b) How do anthropogenic changes to carrion affect nutrient cycling and biodiversity?	<ul style="list-style-type: none"> • Does hunting or culling result in the spatial transfer or loss of carrion nutrients?

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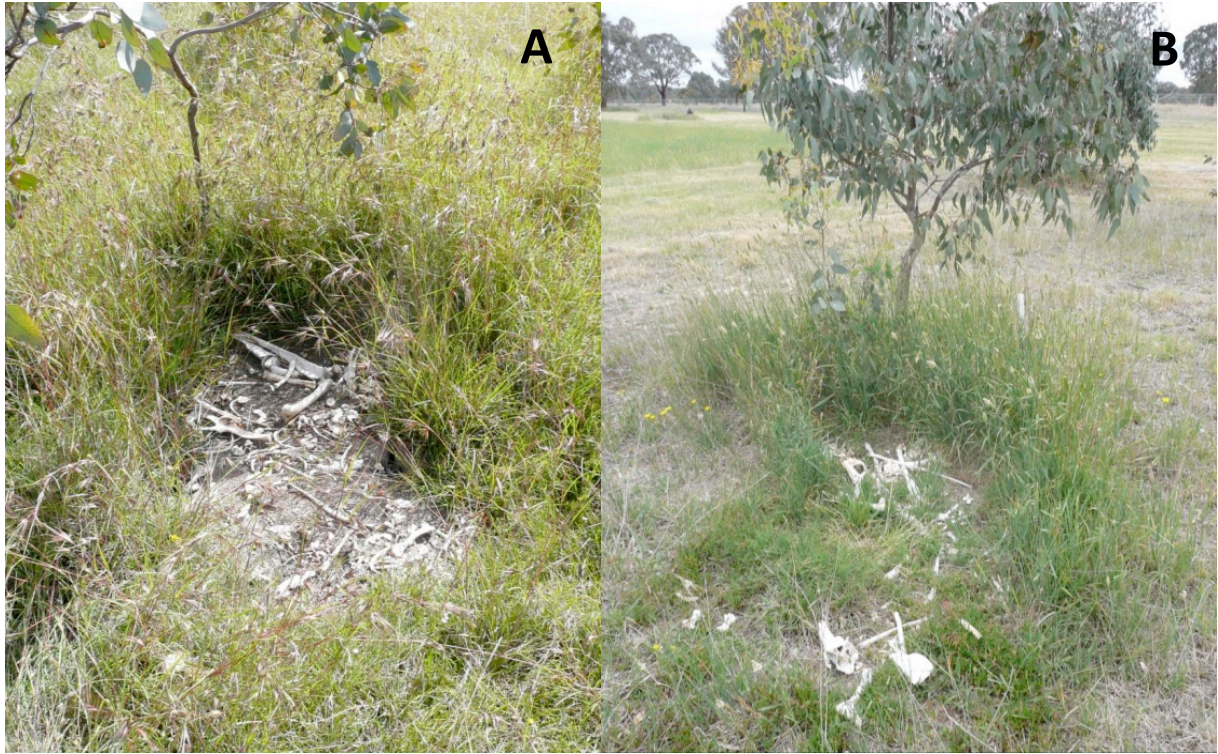


757

758 **Figure 1.** Simplified pathways of energy and nutrient flow in a carrion-centred food web. The
 759 grey box represents all living animals and their potential contribution to the carrion pool in an
 760 ecosystem upon their death. Brown arrows depict the flow of energy and material from
 761 carrion resources through vertebrate scavengers and invertebrate detritivores, and the
 762 channelling of carrion nutrients through microbes and fungi into the soil nutrient pool. Blue
 763 arrows show the transfer of energy from live animals to excreta into detritivores and
 764 microbes. The green arrows depict the flow of nutrients via plants, starting with the uptake of
 765 nutrients from soil, and their flow through herbivores and their predators. Most plant biomass
 766 is not consumed by animals, and forms a distinct and very large resource pool that is also
 767 channelled through detritivores and microbes.

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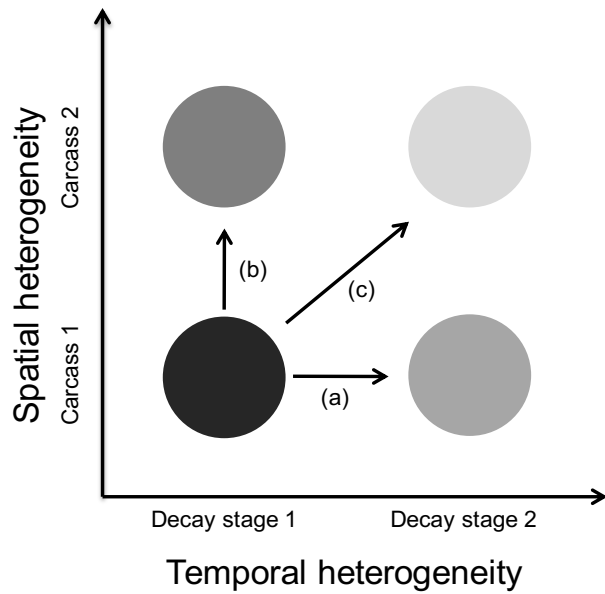
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Figure 2. An example of how ecosystem context mediates localised responses of plant communities one year after addition of carcasses. (A) Very little recolonisation has occurred in native-dominated grassland, whereas (B) recolonisation has progressed significantly in an exotic-dominated grassland a few kilometres away but after the same period of time. Source: (Barton et al. in review).



779
 780 **Figure 3.** The ephemeral resource patch concept allows for the scaling-up of localised effects
 781 of carrion on to better understand their consequences at landscape scales. This framework
 782 builds on widely documented links between (a) the temporal change in structure and nutrient
 783 content of carrion and assemblage succession (Schoenly and Reid 1987), and (b) the spatial
 784 differences in habitat affinities and stochastic colonisation (Kavazos and Wallman 2012). This
 785 information can be used to test hypotheses about (c) what spatio-temporal arrangements of
 786 carrion promote biodiversity and ecological processes within landscapes.

787

788