



Barton, P. S., Evans, M. J., Foster, C. N., Pechal, J. L., Bump, J. K., Quaggiotto, M.-M. and Benbow, M. E. (2019) Towards quantifying carrion biomass in ecosystems. *Trends in Ecology and Evolution*, 34(10), pp. 950-961.

There may be differences between this version and the published version. You are advised to consult the publisher's version if you wish to cite from it.

<http://eprints.gla.ac.uk/221216/>

Deposited on: 3 August 2020

Enlighten – Research publications by members of the University of Glasgow  
<http://eprints.gla.ac.uk>

1 **Towards quantifying carrion biomass in ecosystems**

2

3 Philip S. Barton<sup>1\*</sup>, Maldwyn J. Evans<sup>1</sup>, Claire N. Foster<sup>1</sup>, Jennifer L. Pechal<sup>2</sup>, Joseph K.

4 Bump<sup>3</sup>, M.-Martina Quaggiotto<sup>4</sup>, M. Eric Benbow<sup>2,5</sup>

5

6 <sup>1</sup> Fenner School of Environment and Society, Australian National University, Canberra, ACT,  
7 2601, Australia.

8 <sup>2</sup> Department of Entomology, Michigan State University, East Lansing, MI, USA

9 <sup>3</sup> Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota,  
10 Saint Paul, Minnesota, 55108, USA

11 <sup>4</sup> Institute of Biodiversity, Animal Health and Comparative Medicine, University of Glasgow,  
12 Scotland, G12 8QQ

13 <sup>5</sup> Department of Osteopathic Medical Specialties, Michigan State University, East Lansing,  
14 MI, USA

15 \*Corresponding author: [philip.barton@anu.edu.au](mailto:philip.barton@anu.edu.au)

16

17

18 **Abstract**

19 The decomposition of animal biomass (carrion) contributes to the recycling of energy and  
20 nutrients through ecosystems. Whereas the role of plant decomposition in ecosystems is  
21 broadly recognised, the significance of carrion to ecosystem functioning remains poorly  
22 understood. Quantitative data on carrion biomass is severely lacking and there is no clear  
23 pathway towards improved knowledge in this area. Here we present a framework to show  
24 how quantities derived from individual carcasses can be scaled up using population metrics,  
25 allowing for comparisons among ecosystems and other forms of biomass. Our framework  
26 facilitates the generation of new data that is critical to building a quantitative understanding of  
27 carrion's contribution to trophic processes and ecosystem stocks and flows.

28

29

30 **Keywords:** animal, biogeochemical cycling, carcass, decomposer, decomposition, detritus,  
31 necrobiome, necromass, scavenger

32

33

34

---

35 **GLOSSARY**

36 **Autotrophic biomass** - Organic matter derived from primary producers via photosynthesis.

37 **Carcass** – Intact or partially consumed body of a dead animal, including invertebrates and  
38 vertebrates.

39 **Carrion** – The dead tissues from whole or part of an animal.

40 **Decomposition** – Process of decay and breakdown of organic matter.

41 **Heterotrophic biomass** – Organic matter derived from animals or other consumers.

42 **Necrobiome** - The community of decomposers and their interactions associated with  
43 decomposing organic matter.

---

#### 44 **The overlooked role of carrion in ecosystems**

45 The **decomposition** of organic matter disperses energy and nutrients concentrated by living  
46 organisms back into the biosphere [1, 2]. The critical importance of decomposition for  
47 ecosystems is made conspicuous by the absence of substantial accumulated dead biomass in  
48 most ecosystems [3, but cf. peatlands 4]. Yet there is a significant lack of data on ecosystem  
49 inputs from dead animal biomass (**carrion**, see Glossary) – a distinct form of **heterotrophic**  
50 **biomass**. This means we are unable to answer the question of whether carrion contributes  
51 fundamentally to ecosystem nutrient budgets and functioning. Currently we know that animal  
52 carcasses (including collective invertebrate carrion) enhance ecosystem heterogeneity by  
53 adding unusually concentrated resource hotspots [5-7], and support a suite of highly  
54 dependent species that provide valuable ecosystem services by consuming and recycling  
55 carrion [5, 8-10]. These contributions of carrion to biodiversity and ecosystem processes are  
56 distinct in key ways from plants, e.g. the timescale of biomass turnover [5, 6], suggesting a  
57 need to quantify carrion biomass and its role in ecosystem function. The data to answer this  
58 question are scarce, however, and there exists no framework to guide research in this area. For  
59 this reason, carrion remains a ‘hidden’ resource that has not been adequately incorporated into  
60 ecosystem models of resource stocks and flows [1, 11], and its importance is largely  
61 overlooked except following unusual or notable cases of mass mortality [12-14]. A critical  
62 first step to bridging this gap is to develop approaches to derive quantitative estimates of  
63 carrion inputs to ecosystems, and thus generate the data necessary to include heterotrophic  
64 biomass beside **autotrophic biomass** in ecosystem models.

65 We describe a framework that links knowledge gained from studies of individual  
66 **carcasses** to population-, community-, and ecosystem-level processes, enabling new estimates  
67 of carrion biomass at different ecological scales. We think that such estimates will be critical  
68 to emerging research on: how carrion enters an ecosystem detritus pool [14, 15]; the speed  
69 and mechanisms by which carrion nutrients are released [13, 15, 16]; the transfer of resources

70 among ecosystems [17-19]; and the contribution of carrion to ecosystem services [8, 20] and  
71 global biodiversity [6, 7, 12, 21-23].

72

### 73 **What do we know about carrion biomass in ecosystems?**

74 Theoretical models of ecosystem energetics and trophic structure that incorporate dead  
75 biomass have historically focused on the contribution of plant-derived biomass and  
76 downplayed (or ignored) the contribution of animal-derived biomass [e.g. 1, 3, 24], [but see  
77 11]). Yet, application of these resource models still requires quantitative estimates of biomass,  
78 and such estimates are broadly lacking for carrion.

79 Globally, animal biomass is estimated to be 2 Gt, which is a fraction of global biomass  
80 of plants (450 Gt), bacteria (70 Gt), or fungi (12 Gt) [25]. Within terrestrial ecosystems,  
81 estimates of 30,400 kg/km<sup>2</sup> of animal biomass (0.03 % of total biomass) have been given for  
82 an east African savanna [26], 20,000 kg/km<sup>2</sup> of animal biomass (0.02 % of total biomass) in a  
83 central Amazonian rainforest [27], and 434 kg/km<sup>2</sup> of vertebrate biomass (0.06 % of  
84 aboveground biomass) in a shrub–steppe ecosystem of the USA [28]. While animals clearly  
85 constitute a small relative percentage of total biomass, their effect on ecosystems via the  
86 production of carrion is likely to be disproportionate relative to equivalent amounts of plant  
87 biomass. This is because quantity alone does not predict impact, with biomass quality,  
88 quantity, and rate of turnover also affecting ecosystem structure and function [29]. The  
89 nutrient-rich and dynamic properties of carrion, and the numerous specialist species that it  
90 supports [5], mean that for a full understanding of ecosystem function it is critical to treat this  
91 heterotrophically-derived resource separately from plant biomass. But how much carrion  
92 biomass is there, and how might we find out?

93 We examined the literature for reports of carrion biomass in ecosystems (see  
94 Appendix 1). We found 26 studies that presented information about the number, density, or  
95 biomass of animal carcasses, with biases towards fish in freshwater systems, ungulates in

96 terrestrial systems, and episodic, mass die-offs (e.g. following salmon spawning or insect  
97 emergence events) (Appendix 2 and Appendix 3). Estimates that included spatial information  
98 ( $n = 19$ ) showed there is little knowledge of the carrion biomass of most taxa from the  
99 majority of biomes (see Figure 1, Appendix 2).

100 Carrass size ranged over 10 orders of magnitude, from marine copepods (0.00003 g)  
101 up to moose (400,000 g) (Figure 1a). We found that carcass densities were highest for very  
102 small animals (e.g. 10 billion copepods/km<sup>2</sup>) and lowest for larger animals (e.g. 1 moose or  
103 impala/km<sup>2</sup>). Notable densities relative to body size included salmon (1 million  
104 carcasses/km<sup>2</sup>) and bivalves (1 billion carcasses/km<sup>2</sup>). Such densities were often localized to  
105 particular hotspots, such as specific reaches of streams and rivers, and represent an  
106 extraordinary concentration and release of nutrients.

107 When expressed as biomass density (kg/km<sup>2</sup>), bivalves, salmon, and midges  
108 represented the upper end of the range of 100,000 to 10,000,000 kg of carrion/km<sup>2</sup> (Figure 1b,  
109  $n = 17$ ). By contrast, copepods and ungulates were at the lower end of the range (between 10  
110 and 1000 kg/km<sup>2</sup>), despite being vastly different in body size. Studies of invertebrate  
111 carcasses were rare, but included measurement of midge density emerging from lakes, with  
112 estimates of up to 150,000 kg/km<sup>2</sup> [30]; scirtid beetle carcasses weighing 0.0004 g  
113 supplemented leaf litter as food for mosquito larvae [31]; and mass emergence and die-off of  
114 cicadas, each weighing 0.73 g, and their effect on arthropod scavenger communities [32] and  
115 forest soils [12]. Studies of vertebrate carrion gave estimates of moose carcasses resulting  
116 from human hunting contributing carrion at densities of up to 857 kg/km<sup>2</sup> [33]. There were  
117 several studies of migratory salmon biomass input to North American streams (Appendix 2).

118 Several studies reported large episodic inputs of carrion or mass mortality events [e.g.  
119 13, 14, 34] demonstrating how large, concentrated inputs of carrion can have important and  
120 long-term impacts on ecosystems, including via spatial resource subsidies [13, 35]. Yet these  
121 examples are in many ways the exception, and provide little insight into the significance of

122 the more widespread, constant, and hidden inputs of carrion biomass occurring within  
123 ecosystems.

124

### 125 **Carrion is hidden because scavenging and decomposition is fast and efficient**

126 The unique contribution of carrion biomass to ecosystem energetics, structure, and function is,  
127 in part, a result of its high concentration of nutrients, and the speed at which these nutrients  
128 are returned to the ecosystem. The carbon:nitrogen ratio is typically much lower for carrion  
129 than plant material [36], and carrion tissues are more metabolically rewarding than the  
130 majority of plant tissues. This makes carrion highly sought after by a diversity of efficient  
131 decomposer and scavenger organisms that comprise the **necrobiome**. These organisms are  
132 responsible for consuming, metabolizing, assimilating, excreting, and dispersing carrion  
133 tissues. Rapid turnover is also a key reason why carrion is typically not around long enough to  
134 be noticed or measured, and why it should not be grouped with plant detritus resource pools.

135 Mass loss of organic matter is typically quantified using a negative exponential

136 equation:  $y = e^{-kt}$ , where  $y$  is the mass, and  $k$  is the rate of decay per unit time ( $t$ ) [16, 24].

137 Rates of decay of plant leaf litter usually range between  $k = 0.1$  and  $4$  [37], whereas carrion-  
138 derived nutrients are typically released back into the biosphere at rates 10-100 times faster.

139 For example, decay rates of  $k = 0.008$  to  $0.014$  have been reported for rats (*Rattus rattus*)

140 [16],  $k = 0.046$  for cicadas (*Magicicada* sp.) [32],  $k = 0.088$  for salmon (*Oncorhynchus* sp.)

141 [38], and  $k = 0.058$  for ducks (*Anas acutas*) or  $k = 0.061$  for trout (*Oncorhynchus mykiss*)

142 [39]. A large body of literature also exists in the forensic sciences, where decay rates are

143 reported for different mammal species under different environmental conditions [e.g. 40, 41],

144 but often these studies include vertebrate scavenger exclusion, a potential confounding

145 variable in extrapolating decay rates to more natural conditions. The above examples

146 highlight that nutrient recycling and trophic processes occur on much faster timescales for

147 carrion than most plant tissues.

148

149 **A new framework to guide estimation of carrion in ecosystems**

150 We present a framework that links knowledge derived from individual carcasses to  
151 populations, communities, and ecosystems (Figure 2). Our broad goal is to show how carrion  
152 biomass can be estimated at a range of ecological scales within ecosystems. This can help  
153 researchers to answer fundamental questions about quantities of carrion, how carrion is  
154 distributed spatially and temporally, how it is partitioned among consumers and the  
155 environment, or how much is available at any particular point in time or space (Outstanding  
156 Questions). This can give critical perspective to local-scale studies of carrion decomposition  
157 or scavenging by placing them into a broader ecosystem context. Our framework also  
158 reinforces the need to measure carrion biomass in a consistent way, within defined spatial and  
159 temporal boundaries, to generate data useful for models of ecosystem energetics and function.

160

161 *a) Individual carcasses*

162 The foundation to understanding resource effects on ecosystem structure and function is  
163 knowledge of both biomass and its turnover [29]. For carrion, it must necessarily begin at the  
164 scale of individual carcasses, with data on body mass, its consumers, and decay rate essential  
165 to estimating carrion quantity, how it is partitioned through consumers and the environment,  
166 and its turnover (Figure 2a, 2d). Body mass of individual carcasses provides the basic unit for  
167 multiplication to larger scales. The pathways by which carcass nutrients re-enter the  
168 environment include: consumption by vertebrates [42, 43] or invertebrates [10, 44, 45];  
169 assimilation by microbes present on the carrion or nearby substrates [46-48]; entering the soil  
170 [7, 16, 49, 50]; entering the water column [15, 39]; or entering the atmosphere [51]. This  
171 information is valuable because it allows for extrapolation from the individual carcasses to  
172 estimates of population-level inputs for a defined area (Box 1).

173           The paucity of studies that have examined the multiple pathways of carrion nutrient  
174 flow into different consumer groups or the environment is a major hurdle to the development  
175 of empirical and conceptual models of carcass effects on ecosystems. A broader knowledge  
176 base is needed to understand how the importance of each pathway changes in different  
177 ecosystem or scavenger community contexts. For example, some carcasses of animals might  
178 be entirely consumed by scavengers, whereas others may only be partly consumed [52, 53],  
179 take much longer to be consumed [42] or have more recalcitrant parts of the body (e.g., bones  
180 or shells). Simple models can be helpful to partition a carcass into its different environmental  
181 sinks and consumers pathways [e.g.  $carcass = soil + insects + vertebrates + atmosphere$ ].  
182 This formula is deliberately general, and can easily be applied to total mass (including  
183 moisture) or to single components of interest such as carbon, nitrogen, phosphorus, or other  
184 nutrients [16, 54]. The equation can also incorporate time (e.g. a differential balance approach  
185 to quantify rates of loss and gain) to understand how carcass components are differentially  
186 recycled back into the environment. For example, a long-term study of nutrient cycling from  
187 drowned wildebeest revealed that soft tissues decomposed in 2-10 weeks, whereas bones took  
188 seven years [13]. Tough tissues such as bones and hair may comprise up to 50% of the dry  
189 mass of vertebrate carcasses, and soft tissues the other 50%, representing slow and fast  
190 nutrient inputs from animal decomposition, respectively [13, 55]. More accurate accounting  
191 of the carrion biomass and its rate of nutrient flow through different consumers or  
192 environmental pathways is necessary to understand its landscape-scale effects (Box 1).

193

#### 194       *b) Populations*

195 Demographic information allows for multiplication of individual carcass-level data by  
196 population size or annual turnover to estimate population-level carrion biomass quantities and  
197 turnover rates [e.g. 56, 57]. The spatial distributions of populations can give information  
198 about the geographic boundaries of the carrion resource pool, and identifies areas of

199 concentrated inputs [49]. To derive population-level estimates of carrion biomass, the average  
200 mass of a carcass of a species (or mass of a particular nutrient within the carcass) can be  
201 multiplied by the number of carcasses entering the carrion pool per unit area and time (e.g.  
202 kg/km<sup>2</sup>/yr) (Figure 2b). This approach has been used effectively in a study of nutrient flow  
203 from wildebeest carcasses in the Mara River, Kenya [13]; measurements of nutrients in  
204 individual carcasses were combined with the estimates of numbers of carcasses produced  
205 from annual mass drownings. Per year, approximately 50% of carrion-derived carbon from  
206 drowned wildebeest flowed into watershed foodwebs or was released into the atmosphere,  
207 whereas 95% of carrion phosphorus remained in bones [13]. This study made explicit the  
208 contribution of dead animals to ecosystem function and the subsequent maintenance of  
209 downstream fish communities.

210 Multiplicative approaches to scaling from local to landscape scales are frequently used in  
211 soil ecology literature [e.g. 58] and studies of ecosystem energetics [27, 29]. It is common  
212 practice to convert nutrient or biomass data into standardized units of mass per unit area and  
213 time (e.g. kg/km<sup>2</sup>/yr or kg/ha/yr), thus allowing for comparisons across contrasting systems  
214 (Box 2). A similar approach has long been used in studies of animal biomass and secondary  
215 production in aquatic ecosystems [59, 60]. A mass-per-unit-area approach should be applied  
216 to studies of carrion biomass in terrestrial systems so that data are presented consistently, the  
217 contribution of carrion to ecosystems is easily comparable across disparate taxa, and the  
218 importance of carrion is able to be accurately estimated relative to other resource pools [18,  
219 61].

220 Estimating the spatial and temporal patterns of mortality for animal populations can be  
221 particularly challenging due to the combination of demographic processes, predator-prey  
222 dynamics, and landscape factors [49, 56, 62]. There are ways to integrate prey behaviour and  
223 predation risk information into carrion biomass estimates [49, 63], and this can generate  
224 knowledge of the spatial distribution of carcass nutrient inputs across landscapes (Box 3).

225 Such studies demonstrate the role of behaviour and trophic linkages in determining carrion  
226 effects on ecosystems [64, 65]. Concepts such as the ‘landscape of fear’ [sensu 66] or  
227 ‘landscape of disgust’ [sensu 67] are therefore relevant to estimating population-level factors  
228 influencing carrion quality and quantity (Figure 2b), and could be incorporated into species-  
229 specific models of carcass inputs where predation risk is known to affect the spatial  
230 distribution of populations and animal deaths.

231

### 232 *c) Communities*

233 Animal communities consist of species spanning a wide spectrum of sizes, abundances, life  
234 history traits, and population dynamics. The general body size-abundance relationship  
235 illustrates that most animal species are small and only a few are large [68]. This relationship is  
236 a useful way to conceptualise the distribution and inputs of carrion in ecosystems (Figure 2c).  
237 Yet what is needed are generalisable body size – decay rate or time-to-consumption  
238 relationships (standardised by temperature and humidity). Such models do not yet exist,  
239 however, and would greatly benefit the scaling of carcass-level data to community levels. For  
240 example, approximate abundance and density profiles with decay rates could be assigned to  
241 different sized carcasses (e.g., size spectra), and scaling factors applied to move between  
242 carcass size classes. For example, a ‘small’ size class might be considered 100 times more  
243 abundant and decay at twice the rate as a ‘large’ carcass, which is 10 times the size. Similarly,  
244 smaller vertebrate carcasses are more likely to be consumed in their entirety in a short time  
245 frame (when scavengers are not satiated). Large vertebrate carcasses (e.g., ungulates,  
246 elephants, whales), on the other hand, are more likely to be only partially consumed by  
247 scavengers [42], with remains entering the ecosystem through distinct invertebrate and  
248 vertebrate consumers. Actual values of size-dependent effects still require empirical  
249 measurement for a range of species, but this principle would allow for coarse and rapid  
250 scaling of carrion inputs generated by whole animal communities across body size classes.

251

252 *d) Ecosystems*

253 Knowledge of carrion at ecosystem scales can be developed from scaling-up population- or  
254 community-level estimates directly or via models. This might be achieved by multiplying  
255 community or population data by the geographic area of the ecosystem of interest, while  
256 acknowledging the spatio-temporal variation in carrion inputs. This idea is complicated,  
257 however, by seasonality in animal populations, and the difficulty in surveying carrion biomass  
258 at any moment in time due to variable inputs and its rapid turnover rates. Plant litter surveys,  
259 by contrast, can be conducted using routine measures of litter depth, volumes, or density  
260 along transects because of relatively even spatial distribution and with long turnover rates.  
261 Analogous surveys of animal carcasses are not so straight forward, but might, for example, be  
262 achieved using bone surveys of larger vertebrates [69, 70]. One approach to scaling-up  
263 biomass production in ecosystems is the calculation of secondary production via the  
264 instantaneous growth rate method, whereby the mean growth rate of a population is multiplied  
265 by its collective living biomass [71]. This information can be used to estimate the energy  
266 channeled through populations into biomass production [72], and is used, for example, to  
267 quantify secondary production in aquatic systems and fisheries management [72, 73].  
268 Variation from steady state conditions can provide information about mortality rates and  
269 carrion production. Another option is to take a top-down approach. Ecosystem-scale studies  
270 of plant litter decomposition and carbon budgets have employed total and differential mass  
271 balance approaches [24, 74]. The mass balance equation [ $Input = Output + Accumulation$ ] is  
272 a simple mathematical expression of the principle of conservation of mass [74, 75]. When  
273 applied to carrion, this equation reveals that the quantity of carrion cycled through  
274 decomposition pathways should equal the annual production of carrion only if the mass of  
275 carrion present in the ecosystem remains constant. Both instantaneous growth rate and mass  
276 balance approaches are well-understood and robust starting points for conceptualizing the flux

277 of nutrients among resource pools of animal populations or communities in ecosystems [74,  
278 75]. Furthermore, these approaches are amenable to scaling with ecosystem net primary  
279 productivity (NPP) and total biomass (and thus ratios of animal/plant or dead/live, Figure 2).  
280 This means that a generalised carrion budget established for one ecosystem [e.g. 57, 65] could  
281 be compared to other ecosystems, if differences in NPP are known.

282

### 283 **Implications and concluding remarks**

284 Our framework allows for new questions to be asked about how carrion decomposition  
285 processes occurring at one scale have implications at other scales (see Outstanding  
286 Questions). For example, knowledge of the quantity of nitrogen flowing from a carcass into  
287 nearby plants [e.g. 7, 76], flies [e.g. 53, 77] or vertebrate scavengers [e.g. 43] can now be  
288 placed within a multiplicative framework to predict quantities and their short- and long-term  
289 consequences at larger scales. Further, our framework links a key set of ecological concepts  
290 that can be used to estimate the contribution of carrion biomass to ecosystems in terms of the  
291 quantity and quality of nutrients, the spatial density of carcasses, the timeframes of nutrient  
292 release, and the trophic pathways of nutrient transfer. This framework is essential for placing  
293 carrion on the same conceptual footing as plant-derived biomass, and the future development  
294 of more complete ecosystem models of resource stocks and flow.

295         Knowledge of ecosystem structure and function will benefit from a clearer  
296 understanding of resource biomass and turnover [29]. It is critical to expand our knowledge of  
297 carrion inputs to ecosystems, because inputs in some cases are changing drastically. For  
298 example, new estimates of the global distribution of animal biomass indicate a six-fold  
299 decrease in the mass of wildlife and a four-fold increase in humans and livestock over the last  
300 few hundred years [25]. This substantial redistribution of animal biomass has produced a  
301 massive but unquantified change in the contribution of carrion decomposition to nutrient  
302 cycling in the terrestrial biosphere. The same is true for marine systems, where commercial

303 whaling practices have led to one of the largest examples of wildlife exploitation by humans,  
304 resulting in a massive loss of animal biomass [78]. There are also other, more localised  
305 changes to carrion inputs in some ecosystems. For example, in Europe, carcasses of large  
306 vertebrate species and livestock are removed from grazing landscapes to meet veterinary or  
307 health regulatory requirements [79-81], thus leaving landscapes devoid of large carrion.  
308 Additionally, there has been an increase in frequency of wildlife mass mortality events due to  
309 disease outbreaks or starvation [14], extreme shifts in abiotic conditions [82], as well as  
310 greater attention to annual migrations and mass drownings [13]. Declines in apex predator  
311 populations around the world [83] also means that carrion inputs are changing, and in some  
312 cases contributing to an overabundance of large herbivores [56, 84, 85]. In all these cases,  
313 changes to the quantity, quality, location, or timing of inputs of carrion biomass to ecosystems  
314 have occurred. The consequences of available carrion due to these perturbations include shifts  
315 in nutrient pools, or changed pathways of nutrient flow through biotic communities, with  
316 further unknown ramifications for ecosystems (Outstanding Questions). Our conceptual  
317 framework, coupled with improved and standardized empirical methodology [13, 52, 57],  
318 provides a way to generate the data and calculations necessary to understand the implications  
319 of these changed carrion inputs for biogeochemical cycling and resource flow, and therefore  
320 ecosystem health and function [17, 86].

321         Once quantitative data from a range of biomes and animal taxa are derived, a new  
322 perspective becomes possible that allows heterotrophic biomass to be conceptualised in a  
323 similar way to autotrophic biomass. Future efforts to discover the contribution of carrion  
324 biomass to ecosystems is fundamental to a comprehensive, mechanistic, and predictive  
325 understanding of ecosystem functioning - one that allows the unique temporal and spatial  
326 properties of carrion to be incorporated into models of ecosystem resource stocks and flow.

327

328

329 **Acknowledgements**

330 PSB was funded by the Australian Research Council (DE150100026). JKB was supported by  
331 grants from the United States National Science Foundation (NSF ID#1545611, NSF  
332 ID#1556676).

333

334 **Additional information**

335 Supporting Information is available for this paper at xxxxxxxxx.

336

337 FIGURE TITLES

338

339 **Figure 1.** Summary of some quantitative estimates of carrion from the empirical literature,  
340 showing (a) the negative log-log relationship between published carcass size and density, and  
341 (b) estimates of carrion biomass for a range of different taxa. Different colours represent  
342 different taxa. Raw data is given in Appendix 3.

343

344 **Figure 2.** Linkages between individual carcasses, populations, communities, and ecosystems  
345 can facilitate the estimation of carrion biomass at each scale. (a) Individual carcasses provide  
346 the base unit for scaling up carrion biomass in ecosystems. *Key metrics:* Carcass mass, decay  
347 rate, and composition all provide information that might be of interest at larger scales. Carcass  
348 nutrients can be routed through different consumers or ecosystem compartments (e.g. insect  
349 vs. vertebrate scavengers, microbes, or liquids or gases into the soil or atmosphere). (b)  
350 Populations provide information about numbers of carcasses entering an ecosystem from  
351 different species of animals, as well as their distribution and temporal inputs. *Key metrics:*  
352 multiplication of carcass-level data by population-level data is the first step to scaling up  
353 carcass biomass that can be expressed as input rates. (c) Communities provide information  
354 about relative abundances and body sizes among species. *Key metrics:* multiplication of  
355 population-level inputs by community-level body size and decay rate factors can generate  
356 data about relative contributions by multiple species. (d) Ecosystem-scale estimates of carrion  
357 biomass can be developed from scaling up population- and community-level quantities via  
358 secondary production methods. Mass-balance approaches provide a top-down approach to  
359 estimate carrion biomass as a function of changes to steady-state conditions. *Key metrics:*  
360 ecosystem carrion estimates provide data about total quantities and turnover, and is critical for  
361 broader context when partitioning total biomass into live vs. dead or plant vs. animal.

362

---

363 **Box 1. Partitioning carcasses into resource pools - Rabbit carcasses and fly production.**

364 Rabbit (*Oryctolagus cuniculus*) populations have established in much of southern Australia,  
365 and now contribute to local ecosystem dynamics, including the production of carrion and  
366 resources for blow fly larvae (Calliphoridae). It is possible to estimate such ecosystem  
367 contributions by scaling up carcass-level biomass data. A hypothetical population of 100  
368 rabbits/km<sup>2</sup>, with a turnover of 50/yr, each with a mass of 1.5 kg, and assuming no direct  
369 predation, gives a total potential carrion input of 75 kg/km<sup>2</sup>/yr. It is possible to partition this  
370 resource pool into different nutrient components and recycling pathways [54, 77]. For  
371 example, one study showed 22% of the mass of a rabbit carcass was converted to fly larvae  
372 biomass, and 13.6% entered the soil as either moisture or nutrients [54]. From an input of 75  
373 kg/km<sup>2</sup>/yr, this represents 16.5 kg into fly larvae and 10.2 kg into soil. Further, the 16.5 kg of  
374 fly larvae biomass represents approximately 180,000 potential adult flies [54]. Partial  
375 consumption of carcasses by vertebrates could be estimated, and incorporated as a simple  
376 factor that modulates or down-scales these estimates.

377 We can extrapolate from the above case study to estimate: *What is the contribution of*  
378 *carrion biomass to invertebrate populations?* For example, kangaroo (*Macropus giganteus*)  
379 populations can reach densities of up to two kangaroos/ha in the same study area as the above  
380 rabbit example [87]. At 30 kg per animal, this equates to 6000 kg/km<sup>2</sup>/yr of live biomass. If  
381 10% of the kangaroo population turned over each year, the input of carrion would be 600  
382 kg/km<sup>2</sup>/yr eight times that of rabbits, equating to 132 kg of potential fly larvae biomass  
383 (assuming a similar conversion rate). This study begins to build a community-level profile of  
384 carrion inputs (Figure 2c). Scaling carrion to a standardized unit allows for comparisons with  
385 other forms of biomass (Figure 2d). In the same study system, for example, a dominant  
386 perennial grass is *Themeda australis*, with a mean biomass of 50.6 kg/ha [88], or 5,060  
387 kg/km<sup>2</sup>. In relative terms, therefore, rabbit and kangaroo carrion annual inputs of 675 kg/km<sup>2</sup>  
388 is approximately 1/8<sup>th</sup> that of a dominant grassland plant species. The general insight from our

389 framework is that multiplication of per-carcass data (Figure 2a) by population attributes  
390 (Figure 2b) within a spatial and temporal window allows for estimates of key resource stocks  
391 and flows, and can facilitate the comparison of resource types within an ecosystem.

---

392

---

393 **Box 2. Carrion and population demographics - Seal carrion on the Isle of May.**

394 The grey seal (*Halichoerus grypus*) colony on the Isle of May (45 hectares, Scotland, UK)  
395 generates substantial quantities of carrion in the form of placentae and dead seals. In late  
396 October, approximately 2000 pups are born, of which 13.3% die from natural causes [57].  
397 Aerial and ground surveys have been used to estimate the mean annual number of placentae  
398 and seal carcasses (both pups and adults) deposited into the island and littoral ecosystem  
399 during each pupping season [57]. A total of 6,893 kg of carrion was found to be generated  
400 every year [3,124.3 kg (74.9 SE) of placentae, 3,768.2 kg (713.7 SE) of carcasses]. This  
401 quantitative knowledge of carrion biomass is rare, and allows for additional calculations to  
402 determine the contribution of carrion to ecosystem processes. For example, the total carrion  
403 biomass corresponded to  $110.5 \times 10^3$  MJ/yr of energy, with  $68.1 \times 10^3$  MJ/yr (SE=1.64)  
404 delivered as placentae and  $42.4 \times 10^3$  MJ/yr (SE=10.42) as carcasses [57]. Further, they  
405 established that the total biomass scavenged by vertebrates (mostly gulls) was 1,032 kg, and  
406 this represented  $12.8 \times 10^3$  MJ of energy cycled through vertebrate consumers. Placed into our  
407 framework, a key insight is that multiplication of per-carcass data (and routed via vertebrate  
408 consumer pathways) (Figure 2a) by population attributes (Figure 2b), can yield new insights  
409 into carrion biomass acting as a resource for scavengers, and broader island food web  
410 dynamics.

411 The role of carrion biomass in the energetics and function of island ecosystems can  
412 often be disproportionate relative to other forms of biomass, and when compared to mainland  
413 ecosystems [18, 35]. This disparity is highlighted, for example, by the 22 times greater  
414 production of seal carrion (equivalent to  $15,317 \text{ kg/km}^2$ ) than the combined production of  
415 rabbit and kangaroo carrion described in the previous case study (i.e.,  $675 \text{ kg/km}^2$ ). This  
416 simple extrapolation of data, and comparison across environments, quickly highlights the  
417 relative importance of carrion in contrasting ecosystems.

---

418

---

419 **Box 3. Carrion and landscape heterogeneity - Wolf predation & moose carrion on Isle**

420 **Royale, USA.**

421 On Isle Royale, USA, the moose (*Alces alces*) population has varied between approximately  
422 500 and 2,000 animals over the last 60 years (1958 to 2018), and the predation rate  
423 [proportion of moose killed annually by wolves (*Canis lupus*)] has been greater than 20% in  
424 some years. Studies of the localized effects of carcasses on soil and plants have shown that  
425 wolf kill sites exhibit elevated soil nutrients, microbial biomass, and leaf nitrogen at levels  
426 ~40-300% greater than reference sites (Figure I) [49]. Combining these localized ‘per-  
427 carcass’ data with information about carrion distribution and wolf killing success can generate  
428 landscape-level knowledge of carrion effects on ecosystems [49]. This example of local to  
429 landscape carrion scaling is embedded within our framework (linkages between panels Figure  
430 2a > 2b > 2c > 2d), and shows how principles from population biology can be linked with  
431 data of localized nutrient inputs to reveal novel interpretation and estimates of carrion  
432 biomass.

433 Additional insight can be gained when scaling via our framework is combined with  
434 behavioral concepts. Studies have shown that the ‘fear’ of predation can in some contexts  
435 exceed the effects of local resource availability on prey, and lead to changes in the way they  
436 use a landscape [e.g. 89, 90]. This means that apex predators not only shape carrion effects on  
437 ecosystems via kill sites directly, but predation risk can decouple carcass locations from prey  
438 distribution patterns and create hotspots of carrion occurrence over time [91]. This has  
439 important consequences for maintaining ecological processes, such as the generation of  
440 mosaics of resource heterogeneity that help maintain microbial and plant diversity [49, 92].

441

442 **Figure I.** Scaling of local to landscape carrion effects was undertaken at Isle Royale National  
443 Park, USA, by quantifying the long-term (~1958-2016) influence of wolves on carrion  
444 resource heterogeneity via moose carcass distribution. Localized carcass effects (**upper left**)

445 included elevated soil nutrients (N, P, & K), microbial biomass (bacterial and fungal  
446 phospholipids fatty acids, PLFAs) and plant foliar nitrogen [49]. Understanding how wolves  
447 contributed to carcass effects across the island landscape (**lower and upper right**) was  
448 achieved by relating carcasses from wolf kills versus natural starvation. Values >1 indicate  
449 areas where carcass distribution is more influenced by wolves and values <1 indicate where  
450 carcass distribution is more influenced by moose starvation (values of 1 indicate equal  
451 influence). Wolves travel along shorelines which results in higher predation close to the  
452 water, such as (A) a river drainage, (B) an isthmus, (C) a harbour, and (D) a peninsula.

---

453

454 **References**

- 455 1. Moore, J.C., *et al.* (2004) Detritus, trophic dynamics and biodiversity. *Ecol Lett* 7, 584-600
- 456 2. Handa, I.T., *et al.* (2014) Consequences of biodiversity loss for litter decomposition across  
457 biomes. *Nature* 509, 218–221
- 458 3. Gessner, M.O., *et al.* (2010) Diversity meets decomposition. *Trends Ecol Evol* 25, 372-380
- 459 4. Belyea, L.R. (1996) Separating the effects of litter quality and microenvironment on  
460 decomposition rates in a patterned peatland. *Oikos* 77, 529–539
- 461 5. Benbow, M.E., *et al.* (2019) Necrobiome framework for bridging decomposition ecology of  
462 autotrophically- and heterotrophically-derived organic matter. *Ecol Monogr* 89, e01331
- 463 6. Barton, P.S., *et al.* (2013) The role of carrion in maintaining biodiversity and ecological  
464 processes in terrestrial ecosystems. *Oecologia* 171, 761-772
- 465 7. Bump, J.K., *et al.* (2009) Ungulate carcasses perforate ecological filters and create  
466 biogeochemical hotspots in forest herbaceous layers allowing trees a competitive advantage.  
467 *Ecosystems* 12, 996-1007
- 468 8. Mateo-Tomas, P., *et al.* (2017) Both rare and common species support ecosystem services in  
469 scavenger communities. *Glob Ecol Biogeogr* 26, 1459-1470
- 470 9. Hill, J.E., *et al.* (2018) Effects of vulture exclusion on carrion consumption by facultative  
471 scavengers. *Ecology and Evolution* 8, 2518-2526
- 472 10. Barton, P.S., and Evans, M.J. (2017) Insect biodiversity meets ecosystem function: differential  
473 effects of habitat and insects on carrion decomposition. *Ecol Entomol* 42, 364-374
- 474 11. Getz, W.M. (2011) Biomass transformation webs provide a unified approach to consumer-  
475 resource modelling. *Ecol Lett* 14, 113-124
- 476 12. Yang, L.H. (2004) Periodical cicadas as resource pulses in North American forests. *Science* 306,  
477 1565-1567
- 478 13. Subalusky, A.L., *et al.* (2017) Annual mass drownings of the Serengeti wildebeest migration  
479 influence nutrient cycling and storage in the Mara River. *Proc Natl Acad Sci U S A* 114, 7647-  
480 7652
- 481 14. Fey, S.B., *et al.* (2015) Recent shifts in the occurrence, cause, and magnitude of animal mass  
482 mortality events. *Proc Natl Acad Sci U S A* 112, 1083-1088
- 483 15. Beasley, J.C., *et al.* (2012) Carrion cycling in food webs: comparisons among terrestrial and  
484 marine ecosystems. *Oikos* 121, 1021-1026
- 485 16. Parmenter, R.R., and MacMahon, J.A. (2009) Carrion decomposition and nutrient cycling in a  
486 semiarid shrub-steppe ecosystem. *Ecol Monogr* 79, 637-661
- 487 17. Gounand, I., *et al.* (2018) Meta-ecosystems 2.0: rooting the theory into the field. *Trends Ecol*  
488 *Evol* 33, 36-46
- 489 18. Polis, G.A., and Hurd, S.D. (1996) Linking marine and terrestrial food webs: Allochthonous  
490 input from the ocean supports high secondary productivity on small islands and coastal land  
491 communities. *Am Nat* 147, 396-423

- 492 19. Quaggiotto, M.M., *et al.* (2018) Seal carrion is a predictable resource for coastal ecosystems.  
493 *Acta Oecol* 88, 41-51
- 494 20. Morales-Reyes, Z., *et al.* (2015) Supplanting ecosystem services provided by scavengers raises  
495 greenhouse gas emissions. *Scientific Reports* 5, 7811
- 496 21. Hocking, M.D., and Reynolds, J.D. (2011) Impacts of salmon on riparian plant diversity.  
497 *Science* 331, 1609-1612
- 498 22. Steyaert, S., *et al.* (2018) Special delivery: scavengers direct seed dispersal towards ungulate  
499 carcasses. *Biol Lett* 14, 20180388
- 500 23. Moleón, M., *et al.* (2015) Carcass size shapes the structure and functioning of an African  
501 scavenging assemblage. *Oikos* 124, 1391-1403
- 502 24. Swift, M.J., *et al.* (1979) *Decomposition in terrestrial ecosystems*. Blackwell Scientific  
503 Publications
- 504 25. Bar-On, Y.M., *et al.* (2018) The biomass distribution on Earth. *Proceedings of the National  
505 Academy of Sciences (USA)* 115, 6506-6511
- 506 26. Hendrichs, H. (1970) Estimates of ungulate biomass in the thornbush savanna north and west of  
507 the Serengeti steppe in East Africa following a new procedure and remarks on the biomass of  
508 other herbivorous species. *Saugetierk. Mitt.* 18, 237-255
- 509 27. Fittkau, E.J., and Klinge, H. (1973) On biomass and trophic structure of the central amazonian  
510 rain forest ecosystem *Biotropica* 5, 2-14
- 511 28. Parmenter, R.R., and MacMahon, J.A. (2009) Carrion decomposition and nutrient cycling in a  
512 semiarid shrub-steppe ecosystem. *Ecol Monogr* 79, 637-661
- 513 29. Odum, E.P. (1962) Relationships between structure and function in the ecosystem. *Jpn J Ecol*  
514 12, 108-118
- 515 30. Dreyer, J., *et al.* (2012) Lake-derived midges increase abundance of shoreline terrestrial  
516 arthropods via multiple trophic pathways. *Oikos* 121, 252-258
- 517 31. Harshaw, L., *et al.* (2007) Decaying invertebrate carcasses increase growth of *Aedes triseriatus*  
518 (Diptera : Culicidae) when leaf litter resources are limiting. *J Med Entomol* 44, 589-596
- 519 32. Yang, L.H. (2006) Interactions between a detrital resource pulse and a detritivore community.  
520 *Oecologia* 147, 522-532
- 521 33. Lafferty, D.J.R., *et al.* (2016) Moose (*Alces alces*) hunters subsidize the scavenger community  
522 in Alaska. *Polar Biol* 39, 639-647
- 523 34. Dreyer, J., *et al.* (2015) Quantifying aquatic insect deposition from lake to land. *Ecology* 96,  
524 499-509
- 525 35. Polis, G.A., and Hurd, S.D. (1995) Extraordinarily high spider densities on islands: flow of  
526 energy from the marine to terrestrial food webs and the absence of predation. *Proc Natl Acad  
527 Sci U S A* 92, 4382-4386
- 528 36. Carter, D.O., *et al.* (2007) Cadaver decomposition in terrestrial ecosystems.  
529 *Naturwissenschaften* 94, 12-24

- 530 37. Zhang, D., *et al.* (2008) Rates of litter decomposition in terrestrial ecosystems: global patterns  
531 and controlling factors. *Journal of Plant Ecology* 1, 85-93
- 532 38. Scheuerell, M.D., *et al.* (2005) A new perspective on the importance of marine-derived nutrients  
533 to threatened stocks of Pacific salmon (*Oncorhynchus* spp.). *Can J Fish Aquat Sci* 62, 961-964
- 534 39. Parmenter, R.R., and Lamarra, V.A. (1991) Nutrient cycling in a freshwater marsh: the  
535 decomposition of fish and waterfowl carrion. *Limnol Oceanogr* 36, 976-987
- 536 40. Sutherland, A., *et al.* (2013) The effect of body size on the rate of decomposition in a temperate  
537 region of South Africa. *Forensic Sci Int* 231, 257-262
- 538 41. Matuszewski, S., *et al.* (2014) Effect of body mass and clothing on decomposition of pig  
539 carcasses. *International Journal of Legal Medicine* 128, 1039-1048
- 540 42. Moleón, M., *et al.* (2015) Carcass size shapes the structure and functioning of an African  
541 scavenging assemblage. *Oikos* 124, 1391-1403
- 542 43. Wilson, E.E., and Wolkovich, E.M. (2011) Scavenging: how carnivores and carrion structure  
543 communities. *Trends Ecol Evol* 26, 129-135
- 544 44. Payne, J.A. (1965) A summer carrion study of the baby pig *Sus scrofa* Linnaeus. *Ecology* 46,  
545 592-602
- 546 45. Britton, J.C., and Morton, B. (1994) Marine carrion and scavengers. *Oceanography and Marine*  
547 *Biology* 32, 369-434
- 548 46. Lauber, C.L., *et al.* (2014) Vertebrate decomposition is accelerated by soil microbes. *Appl*  
549 *Environ Microbiol* 80, 4920-4929
- 550 47. Singh, B., *et al.* (2018) Temporal and spatial impact of human cadaver decomposition on soil  
551 bacterial and arthropod community structure and function. *Frontiers in Microbiology* 8, 2616
- 552 48. Metcalf, J.L., *et al.* (2016) Microbial community assembly and metabolic function during  
553 mammalian corpse decomposition. *Science* 351, 158-162
- 554 49. Bump, J.K., *et al.* (2009) Wolves modulate soil nutrient heterogeneity and foliar nitrogen by  
555 configuring the distribution of ungulate carcasses. *Ecology* 90, 3159-3167
- 556 50. Barton, P.S., *et al.* (2016) Substantial long-term effects of carcass addition on soil and plants in  
557 a grassy eucalypt woodland. *Ecosphere* 7, e01537
- 558 51. Putman, R.J. (1978) Patterns of carbon dioxide evolution from decaying carrion. 1.  
559 Decomposition of small mammal carrion in temperate systems. *Oikos* 31, 47-57
- 560 52. Putman, R.J. (1978) Flow of energy and organic matter from a carcass during decomposition. 2.  
561 Decomposition of small mammal carrion in temperate systems. *Oikos* 31, 58-68
- 562 53. Hocking, M.D., and Reimchen, T.E. (2006) Consumption and distribution of salmon  
563 (*Oncorhynchus* spp.) nutrients and energy by terrestrial flies. *Can J Fish Aquat Sci* 63, 2076-  
564 2086
- 565 54. Barton, P.S., *et al.* (2019) Nutrient and moisture transfer to insect consumers and soil during  
566 vertebrate decomposition. *Food Webs* 18, e00110

- 567 55. Smith, C.R., and Baco, A.R. (2003) Ecology of whale falls at the deep-sea floor. *Oceanography*  
568 *and Marine Biology* 41, 311-354
- 569 56. Wilmers, C.C., and Getz, W.M. (2004) Simulating the effects of wolf-elk population dynamics  
570 on resource flow to scavengers. *Ecol Modell* 177, 193-208
- 571 57. Quaggiotto, M.-M., *et al.* (2018) Seal carrion is a predictable resource for coastal ecosystems.  
572 *Acta Oecol* 88, 41-51
- 573 58. Macdonald, B.C.T., *et al.* (2014) Carrion decomposition causes large and lasting effects on soil  
574 amino acid and peptide flux. *Soil Biol Biochem* 69, 132-140
- 575 59. Waters, T.F. (1969) Turnover ratio in production ecology of freshwater invertebrates. *Am Nat*  
576 103, 173-185
- 577 60. Waters, T. (1977) Secondary production in inland waters. *Adv Ecol Res* 10, 91-164
- 578 61. Polis, G.A., *et al.* (1997) Toward an integration of landscape and food web ecology: The  
579 dynamics of spatially subsidized food webs. *Annu Rev Ecol Syst* 28, 289-316
- 580 62. Pereira, L.M., *et al.* (2014) Facultative predation and scavenging by mammalian carnivores:  
581 Seasonal, regional and intra-guild comparisons. *Mammal Rev* 44, 44-55
- 582 63. Wilmers, C.C., and Post, E. (2006) Predicting the influence of wolf-provided carrion on  
583 scavenger community dynamics under climate change scenarios. *Glob Change Biol* 12, 403-409
- 584 64. Hawlena, D., *et al.* (2012) Fear of Predation Slows Plant-Litter Decomposition. *Science* 336,  
585 1434-1438
- 586 65. Wilmers, C.C., *et al.* (2003) Trophic facilitation by introduced top predators: grey wolf  
587 subsidies to scavengers in Yellowstone National Park. *J Anim Ecol* 72, 909-916
- 588 66. Kohl, M.T., *et al.* (2018) Diel predator activity drives a dynamic landscape of fear. *Ecol Monogr*  
589 88, 638-652
- 590 67. Weinstein, S.B., *et al.* (2018) A landscape of disgust. *Science* 359, 1213-1214
- 591 68. White, E.P., *et al.* (2007) Relationships between body size and abundance in ecology. *Trends*  
592 *Ecol Evol* 22, 323-330
- 593 69. Behrensmeyer, A.K. (1978) Taphonomic and ecologic information from bone weathering  
594 *Paleobiology* 4, 150-162
- 595 70. Miller, J.H. (2012) Spatial fidelity of skeletal remains: elk wintering and calving grounds  
596 revealed by bones on the Yellowstone landscape. *Ecology* 93, 2474-2482
- 597 71. Hynes, H.B.N., and Coleman, M.J. (1968) A simple method of assessing annual production of  
598 stream benthos. *Limnol Oceanogr* 13, 569-&
- 599 72. Kimmerer, W.J. (1987) The theory of secondary production calculations for continuously  
600 reproducing populations. *Limnol Oceanogr* 32, 1-13
- 601 73. Allen, K.R. (1971) Relation between production and biomass. *Journal of the Fisheries Research*  
602 *Board of Canada* 28, 1573-1581
- 603 74. Olson, J.S. (1963) Energy storage and balance of producers and decomposers in ecological  
604 systems. *Ecology* 44, 322-&

- 605 75. Schlesinger, W.H. (1977) Carbon balance in terrestrial detritus. *Annu Rev Ecol Syst* 8, 51-81
- 606 76. Towne, E.G. (2000) Prairie vegetation and soil nutrient responses to ungulate carcasses.  
607 *Oecologia* 122, 232-239
- 608 77. Putman, R.J. (1977) Dynamics of the blowfly, *Calliphora erythrocephala*, within carrion. *J.*  
609 *Anim. Ecol.* 46, 853-866
- 610 78. Clapham, P.J., *et al.* (2008) Determining spatial and temporal scales for management: lessons  
611 from whaling. *Mar Mamm Sci* 24, 183–201
- 612 79. Margalida, A., *et al.* (2011) Can wild ungulate carcasses provide enough biomass to maintain  
613 avian scavenger populations? An empirical assessment using a bio-inspired computational  
614 model. *PLoS ONE* 6, e20248
- 615 80. Margalida, A., and Colomer, M.A. (2012) Modelling the effects of sanitary policies on  
616 European vulture conservation. *Scientific Reports* 2, 753
- 617 81. Morales-Reyes, Z., *et al.* (2017) Evaluation of the network of protection areas for the feeding of  
618 scavengers in Spain: from biodiversity conservation to greenhouse gas emission savings. *J Appl*  
619 *Ecol* 54, 1120-1129
- 620 82. McDowell, W., *et al.* (2017) Mass mortality of a dominant invasive species in response to an  
621 extreme climate event: Implications for ecosystem function. *Limnol Oceanogr* 62, 177-188
- 622 83. Estes, J.A., *et al.* (2011) Trophic downgrading of planet earth. *Science* 333, 301-306
- 623 84. Gordon, I.J., *et al.* (2004) The management of wild large herbivores to meet economic,  
624 conservation and environmental objectives. *J Appl Ecol* 41, 1021-1031
- 625 85. Cote, S.D., *et al.* (2004) Ecological impacts of deer overabundance. *Annual Review of Ecology,*  
626 *Evolution and Systematics* 35, 113-147
- 627 86. Gounand, I., *et al.* (2018) Cross-ecosystem carbon flows connecting ecosystems worldwide.  
628 *Nature Communications* 9, 4825
- 629 87. Barton, P.S., *et al.* (2011) Experimental reduction of native vertebrate grazing and addition of  
630 logs benefit beetle diversity at multiple scales. *J Appl Ecol* 48, 943-951
- 631 88. McIntyre, S., *et al.* (2015) Restoration of eucalypt grassy woodland: effects of experimental  
632 interventions on ground-layer vegetation. *Aust J Bot* 62, 570-579
- 633 89. Valeix, M., *et al.* (2009) Behavioral adjustments of African herbivores to predation risk by  
634 lions: Spatiotemporal variations influence habitat use. *Ecology* 90, 23-30
- 635 90. Willems, E.P., and Hill, R.A. (2009) Predator-specific landscapes of fear and resource  
636 distribution: effects on spatial range use. *Ecology* 90, 546-555
- 637 91. Laundre, J.W., *et al.* (2001) Wolves, elk, and bison: reestablishing the "landscape of fear" in  
638 Yellowstone National Park, USA. *Can J Zool* 79, 1401-1409
- 639 92. Stein, A., *et al.* (2014) Environmental heterogeneity as a universal driver of species richness  
640 across taxa, biomes and spatial scales. *Ecol Lett* 17, 866-880

641