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Carrion ecology in inland aquatic ecosystems: a systematic review

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ABSTRACT

Carrion ecology, i.e. the decomposition and recycling of dead animals, has traditionally been neglected as a key process in ecosystem functioning. Similarly, despite the large threats that inland aquatic ecosystems (hereafter, aquatic ecosystems) face, the scientific literature is still largely biased towards terrestrial ecosystems. However, there has been an increasing number of studies on carrion ecology in aquatic ecosystems in the last two decades, highlighting their key role in nutrient recirculation and disease control. Thus, a global assessment of the ecological role of scavengers and carrion in aquatic ecosystems is timely. Here, we systematically reviewed scientific articles on carrion ecology in aquatic ecosystems to describe current knowledge, identify research gaps, and promote future studies that will deepen our understanding in this field. We found 206 relevant studies, which were highly biased towards North America, especially in lotic ecosystems, covering short time periods, and overlooking seasonality, a crucial factor in scavenging dynamics. Despite the low number of studies on scavenger assemblages, we recorded 55 orders of invertebrates from 179 families, with Diptera and Coleoptera being the most frequent orders. For vertebrates, we recorded 114 species from 40 families, with birds and mammals being the most common. Our results emphasise the significance of scavengers in stabilising food webs and facilitating nutrient cycling within aquatic ecosystems. Studies were strongly biased towards the assessment of the ecosystem effects of carrion, particularly of salmon carcasses in North America. The second most common research topic was the foraging ecology of vertebrates, which was mostly evaluated through sporadic observations of carrion in the diet. Articles assessing scavenger assemblages were scarce, and only a limited number of these studies evaluated carrion consumption patterns, which serve as a proxy for the role of scavengers in the ecosystem. The ecological functions performed by carrion and scavengers in aquatic ecosystems were diverse. The main ecological functions were carrion as food source and the role of scavengers in nutrient cycling, which appeared in 52.4% ($N = 108$) and 46.1% ($N = 95$) of publications, respectively. Ecosystem threats associated with carrion ecology were also identified, the most common being water eutrophication and carrion as source of pathogens (2.4%; $N = 5$ each). Regarding the effects of carrion on ecosystems, we found studies spanning all ecosystem components ($N = 85$), from soil or the water column to terrestrial vertebrates, with a particular focus on aquatic invertebrates and fish. Most of these articles found positive effects of carrion on ecosystems (e.g. higher species richness, abundance or fitness; 84.7%; $N = 72$), while a minority found negative effects, changes in community composition, or even no effects. Enhancing our understanding of scavengers and carrion in aquatic ecosystems is crucial to assessing their current and future roles amidst global change, mainly for water–land nutrient transport, due to changes in the amount and speed of nutrient movement, and for disease

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control and impact mitigation, due to the predicted increase in occurrence and magnitude of mortality events in aquatic ecosystems.

Key words: aquatic subsidy, carcass, freshwater, land–water interface, ecological process, nutrient cycling, nutrient-rich resource, scavenger, wetland.

CONTENTS

I. INTRODUCTION

Carrion ecology involves the carrion itself (i.e. dead animal biomass), the scavengers (i.e. living organisms that are carrion consumers), and the interactions between them. Although the study of carrion decomposition has received less attention than dead plant matter (Barton *et al.*, 2019), there has been an increase in studies on scavengers and carrion in the last two decades (Olea, Mateo-Tomás & Sanchez-Zapata, 2019; Hyndes *et al.*, 2022; Newsome *et al.*, 2023), that highlight the key ecological role of scavengers in ecosystems (Barton *et al.*, 2013). Carrion is a sporadic and usually unpredictable but highly nutritious resource (Carter, Yellowlees & Tibbett, 2007) that functions as a biodiversity hotspot for taxa from microbes to top predators (Carter, Yellowlees & Tibbett, 2008; Bump *et al.*, 2009*c*; Mateo-Tomás *et al.*, 2015), increasing macronutrients in the soil and also on vegetation (Bump, Peterson & Vucetich, 2009*a*), not only in the short term, but for decades afterwards (Keenan & Beeler, 2023). Moreover, it can become an extremely abundant resource, which can drive the functioning of ecosystems (Barton *et al.*, 2013; Subalusky *et al.*, 2017). In a large-scale quantitative study, Morant *et al.* (2022) estimated ungulate (livestock and wild ungulates) carrion biomass production in Spain at 18,000 kg/ha/year. Large amounts of carrion also are generated in aquatic ecosystems. For example, Weber & Brown (2016) found up to 403 kg/ha of common carp (*Cyprinus carpio* Linnaeus) carrion in some USA lakes and Sousa *et al.* (2012) reported more than 102,250 kg/ha of bivalve carrion in Portuguese rivers, with both studies taking place in winter (over 3 months). In addition, scavengers are present in almost half of all trophic links (Wilson & Wolkovich, 2011) and are therefore essential in stabilising the food web and maintaining biodiversity. Furthermore, by consuming carrion, scavengers perform key ecosystem functions, such as disease control, nutrient recirculation (Beasley *et al.*, 2019), and nutrient transport between aquatic and terrestrial ecosystems (Hocking & Reimchen, 2006; Dunlop *et al.*, 2021).

Inland aquatic ecosystems (hereafter, aquatic ecosystems) constitute highly productive environments that are critically important for biodiversity conservation (Keddy *et al.*, 2009), hosting a disproportionate number of species compared to the area they cover (Strayer & Dudgeon, 2010; Reid *et al.*, 2019). Moreover, aquatic ecosystems sustain key ecological processes, such as biogeochemical cycling or hydrological buffering (Junk *et al.*, 2013) and therefore are crucial for supporting human well-being (Zedler & Kercher, 2005; Clarkson, Ausseil & Gerbeaux, 2013). Worryingly, they show one of the highest rates of both habitat and biodiversity loss, with more than 85% of global wetland (inland aquatic ecosystems together with coral reefs) area lost since 1700 (IPBES, 2019). Some of the most important processes threatening aquatic ecosystems and their biodiversity, such as overexploitation or water pollution (Dudgeon *et al*., 2006), are persistent with well-known effects including biodiversity loss, water eutrophication or emerging diseases (Reid *et al*., 2019). Other threats such as climate change, salinisation, microplastics or light and noise pollution are emergent with still unknown effects (Junk *et al*., 2013; Taylor *et al*., 2021). These threats are expected to become more severe under future climatic scenarios (Junk *et al*., 2013; Reid *et al*., 2019). While aquatic ecosystems should constitute a research priority due to the threats they face and their importance for biodiversity, the scientific literature is still biased towards terrestrial ecosystems, with less than 20% of articles focused on aquatic species (Di Marco *et al*., 2017). Furthermore, many ecosystem processes have been understudied in aquatic ecosystems, including long-term responses to anthropogenic stressors, parasitism and mutualism, plant–insect relationships and trophic networks, and especially those related to carrion ecology (Anderson & Wallace, 2019).

Carrion ecology in aquatic ecosystems has important links with terrestrial ecosystems. It is well known that the transport of nutrients derived from carrion can occur between different ecosystems due to the mobility of scavengers (Payne & Moore, 2006). This is particularly important in aquatic ecosystems, as terrestrial scavengers often consume carrion originating from aquatic environments, such as brown bears (*Ursus arctos* Linnaeus) or terrestrial arthropods feeding on salmon carcasses (Collins & Baxter, 2014; Lincoln, Wirsing & Quinn, 2021), or terrestrial vertebrate scavengers consuming common carp carcasses, the most abundant fish in many wetlands (Orihuela-Torres *et al*., 2022). To some extent, the exchange can also take place in the opposite direction when aquatic scavengers consume terrestrial subsidies such as American alligators (*Alligator mississippiensis* Daudin) consuming large amounts of carrion in waterfowl breeding colonies (Gabel, Frederick & Zabala, 2019). Aquatic subsidies are of vital importance for terrestrial ecosystems, affecting all trophic levels, from primary producers (Ben-David, Hanley & Schell, 1998; Irick *et al*., 2015) to top predators (Rose & Polis, 1998; Darimont, Paquet & Reimchen, 2008; Escobar-Lasso *et al*., 2016). Similarly, terrestrial nutrients may be essential subsidies for the aquatic environment. For example, mass inputs of wildebeest (*Connochaetes taurinus* Burchell) carrion from drowned individuals are known to influence nutrient cycling in the Mara River (Subalusky *et al*., 2017). Many scavengers play a key role in these subsidies by incorporating and transporting nutrients among ecosystems (Quinn *et al*., 2009). However, studies assessing the importance of scavenging in inland aquatic ecosystems are scarce. Furthermore, most studies on carrion ecology at the water–land interface have been conducted at the marine/ocean shoreline (Huijbers *et al*., 2013; Brown *et al*., 2015; Gilby *et al*., 2023). Therefore, there remains a large knowledge gap on the consumption and ecology of carrion in most aquatic ecosystems [but see Hyndes *et al*. (2022) for carrion on beaches]. In addition, mass-mortality events, mostly associated with biotoxicity and emerging diseases, may add large amounts of nutrients to terrestrial ecosystems (Fey *et al*., 2015; Ulloa *et al*., 2023). As these events are expected to increase in frequency, the relevance of scavenging and its related consumption and recirculation of nutrients from large carrion pulses may also grow (Barton *et al*., 2023).

In this review, we summarise the ecological role of carrion and scavengers in aquatic ecosystems, identifying the main knowledge gaps and providing future directions. To do so, we conducted a systematic review of existing information on carrion ecology studies in aquatic ecosystems. We structure the review in three parts: (*i*) 'when, where and how?' by carrying out a spatial–temporal bibliographic analysis of the relevant literature and identifying the types of aquatic ecosystems studied, carrion types and carrion locations (inside or outside of the water); (*ii*) 'who?', by identifying the taxonomic distribution of scavenger species (invertebrates and vertebrates) at different levels (up to family and species level respectively); and (*iii*) 'what?', by evaluating the main topics of these studies, the ecological functions and ecosystem threats related to carrion and scavengers, as well as the effects of carrion on ecosystem functioning (e.g. soil properties, primary production, or secondary production) and the direction of these effects (i.e. positive, negative, turnover and no effect). To the best of our knowledge, this review is the first attempt to compile this kind of information for inland aquatic systems, and allows us to identify knowledge gaps and propose future research avenues to advance our understanding on the importance of the ecological roles of scavengers and carrion in aquatic ecosystems.

II. METHODS

We conducted a systematic literature review of peer-reviewed scientific articles on scavengers and carrion in aquatic ecosystems, which included a wide variety of natural habitats such as rivers, streams, lakes, estuaries, marshes, bogs, swamps, fens, everglades, and also man-made habitats such as artificial wetlands, farm ponds, reservoirs or channels, but excluding marine ecosystems (i.e. coastal marine and off-shore zones). Our review included aquatic habitats with fresh, saline or brackish water. We followed the guidelines for systematic reviews by Pullin & Knight (2009), including a strict protocol for article searching and inclusion criteria to ensure transparency and minimise bias, and following the PRISMA EcoEvo checklist (O'Dea *et al*., 2021; see online Supporting Information, Appendix S1). We used both the *Web of Science* and *Scopus* databases. We developed a search string that combined several terms related to carrion and scavenging ('*scaveng**' *OR 'carrion' OR 'carcass'*) combined with terms related to inland aquatic ecosystems (*'wetland' OR 'freshwater' OR 'lake' OR 'pond' OR 'stream' OR 'river' OR 'marsh' OR 'swamp' OR 'bog' OR 'fens' OR 'everglade' OR 'reservoir' OR 'canal' OR 'channel' OR 'riparian'*) (see Appendix S2 for details).

The search was applied to the title, abstract and key words of peer-reviewed articles (i.e. we excluded book chapters and conference papers) published in English up to December 2020, yielding 8,204 articles (6,173 articles after eliminating duplicates). To identify relevant studies out of these 6,173 articles, we carried out a two-stage review process (e.g. Hevia *et al.*, 2017; Dressel, Ericsson & Sandström, 2018; Appendix S3): (*i*) initial screening by examining the title and abstract; and (*ii*) full-text screening of the articles. We applied five inclusion criteria. Specifically, we selected articles in English (criterion 1) that empirically (criterion 2) investigated scavenging by vertebrates, invertebrates or microbial communities and/or carrion–ecosystem effects (criterion 3) in aquatic ecosystems (criterion 4) and that were not historical studies (i.e. palaeoecological studies) (criterion 5) (see Appendix S4 for full details of inclusion criteria). The two-stage review process was carried out by A. O.-T. and Z. M.-R. (double-checked for a subset of articles which there was some doubt to confirm that similar decisions were made) to ensure that all potentially eligible studies were identified. We identified 287 articles as eligible for full-text screening after examining the title and abstract. Finally, 206 articles fulfilled the five inclusion criteria and therefore were selected for detailed analysis (see Database S1).

Following a systematic approach, we developed a coding scheme to organise the database. We particularly examined the following research questions related to carrion and scavenging and identified eight sets of variables that represent the main themes of this review (see Table S1 for complete list of variables): (1) when, where and how? (*i*) *Temporal and geographical distribution* of the considered studies (i.e. publication year, study lasting, country and continent); (*ii*) *Ecosystem type* where the study took place (Table S1); (*iii*) *Carcass type* (i.e. amphibian, bird, fish, salmonid, mammal, reptile, invertebrate or eggs) and *carcass location* (i.e. inside/outside water); (2) who? (*iv*) *Scavenger assemblages* (invertebrates were recorded to the order and/or family level and vertebrates to the species level); (3) what? (*v*) *Study topic* (Table 1); (*vi*) *Ecological functions* of carrion and scavengers (e.g. carrion as food for animals, nutrient cycling, water quality regulation; Table S2); (*vii*) *Ecosystem threats* associated with carrion and scavengers (e.g. water eutrophication, carrion as source of pathogens; Table S3); (*viii*) *Ecosystem effects of carrion* on all biodiversity components from soil microbiomes to vertebrate assemblages, and the direction of these effects (i.e. positive, negative, turnover and no effect; Table S4). A positive effect can be at the individual (e.g. fitness improvement), population (e.g. increased abundance or density) or community (e.g. increased species richness) level. Negative effects refer to a decline in the targeted component (e.g. negative effects associated with oxygen depletion, heavy metals, water pollution, mortality risk, etc.). We define as 'turnover' effects involving changes in community species composition. When no effects of carrion on the targeted ecosystem component were identified, we assigned the category 'no effect' (Table S4).

III. RESULTS

(1) When, where and how?

(*a*) *Temporal and geographical distribution of studies*

The oldest papers found in our review were published in the 1960s, and dealt with observations of the consumption of salmon carcasses in the USA (Moyle, 1966; Nicola, 1968). It was not until the 1990s that studies were published on carrion ecology in aquatic ecosystems outside North America, especially in Europe and to some extent in Australia (Hiraldo, Blanco & Bustamante, 1991; Hewson, 1995; Elliott, 1997). There has been a continuous increase in the number of studies published since then, with the last decade (2010–2020) alone accounting for 49% ($N = 101$) of the articles reviewed, and 2020 being the year with the largest number of articles (8.7%; $N = 18$; Fig. 1). Most of the studies were sporadic or carried out over very short periods in a single season, and there were very few (5.8%; $N = 12$) that covered at least an entire year. The vast majority of studies were conducted in North America (69.9%; $N = 144$), followed by Europe (14.1%; $N = 29$), Asia (7.8%; $N = 16$), South America (4.4%; $N = 9$), Oceania (2.4%; $N = 5$) and Africa (1.4%; $N = 3$; Fig. 1).

(*b*) *Inland aquatic ecosystem types*

Studies in lotic ecosystems were predominant, with streams and rivers accounting for more than 65% of studies (34% and 31.6%; $N = 70$ and 65, respectively). The next most studied aquatic ecosystem types were lakes (15.5%; $N = 32$), ponds (5.3%; $N = 11$) and marshes (3.9%; $N = 8$). Other aquatic ecosystem types (e.g. channels, reservoirs, dams, cave streams, swamps, canals, etc.) were studied in a very small proportion of the articles (<2.5% each).

(*c*) *Carcass types and locations*

Most articles (64%; $N = 119$) studied carrion inside water, while 24.2% ($N = 45$) placed carrion outside water and 11.8% ($N = 22$) used carrion both inside and outside water (Fig. 2). The carcasses used most often were from fish (67%; $N = 122$), of which the majority were salmonids (75.4%; $N = 92$). After fish, the most commonly used carrion was from mammals (13.7%; $N = 25$), invertebrates and birds (7.1%; $N = 13$ each), amphibians (2.2%; $N = 4$), and finally reptiles (1.6%; $N = 3$). Eggs were used in three studies (Fig. 2).

(2) Who?

(*a*) *Invertebrate scavenger studies*

We found 20 studies of scavenger invertebrate assemblages in aquatic ecosystems. Almost half were conducted in

Table 1. Description of the topics used for the classification of the articles that appeared in the systematic literature review on carrion ecology in aquatic ecosystems.

Topic	Description	References
Carcass movement	Articles studying how far the carcasses move.	Strobel *et al.* (2009); Muhametsafina *et al.* (2014)
Carcass persistence	Articles studying how long it takes for the carrion to disappear/decompose.	Linz *et al.* (1991); Weaver *et al.* (2015)
Ecosystem–carrion effects	Articles studying the effect of carrion in ecosystem functioning.	Bilby *et al.* (1998); Chaloner & Wipfli (2002); Weber & Brown (2013)
Foraging ecology of invertebrates	Articles where invertebrate species consume carrion either as a part of their diet or in a sporadic observation.	Nicola (1968); Velasco & Millán (1998)
Foraging ecology of vertebrates	Articles where vertebrate species consume carrion either as a part of their diet or in a sporadic observation.	Souza & Abe (2000); Gleason *et al.* (2005); Gleason (2007)
Forensic studies	Studies focusing on lesions and invertebrate succession in the carcass for forensic purposes. In many cases, human corpses are used.	Keiper *et al.* (1997); Haefner *et al.* (2004)
Invertebrate scavenger assemblages	Studies focusing on the invertebrate scavenger assemblage that consumes the carcasses and, in some cases, the consumption patterns.	Fenoglio *et al.* (2005); Richards *et al.* (2015)
Microbial communities	Studies focusing on the microbial communities that decompose the carcasses.	Tang *et al.* (2009); Pechal & Benbow (2016)
Nutrient transport by scavengers	Articles studying the role of scavengers in transporting nutrients.	Francis *et al.* (2006); Quinn *et al.* (2009)
Vertebrate scavenger assemblages	Studies focusing on assessing the vertebrate scavenger assemblage that consumes the carcasses and, in some cases, the consumption patterns.	Hewson (1995); Abernethy *et al.* (2017); Schlichting *et al.* (2019)
Others	The article focuses on a different topic than listed above.	Cliplef & Wobeser (1993); Sousa *et al.* (2012); Santori *et al.* (2020)

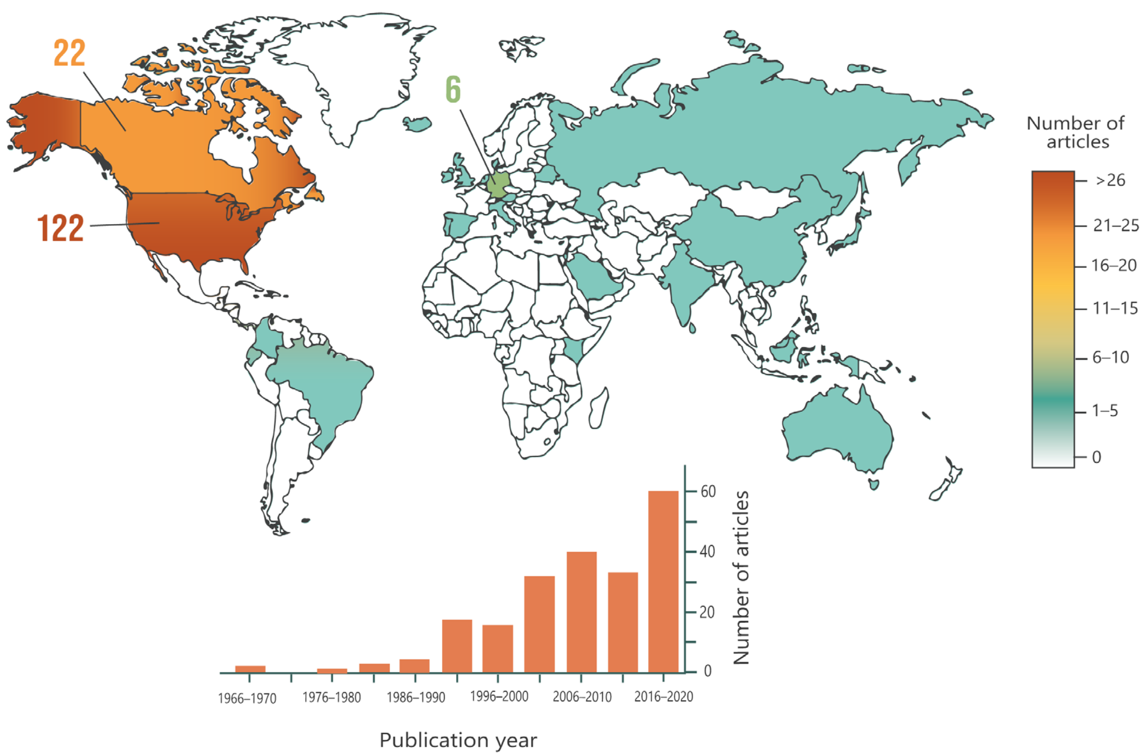

Fig. 1. Global spatial and temporal distribution of studies on carrion ecology in inland aquatic ecosystems according to publication year and country. Countries with no published studies are shown in white.

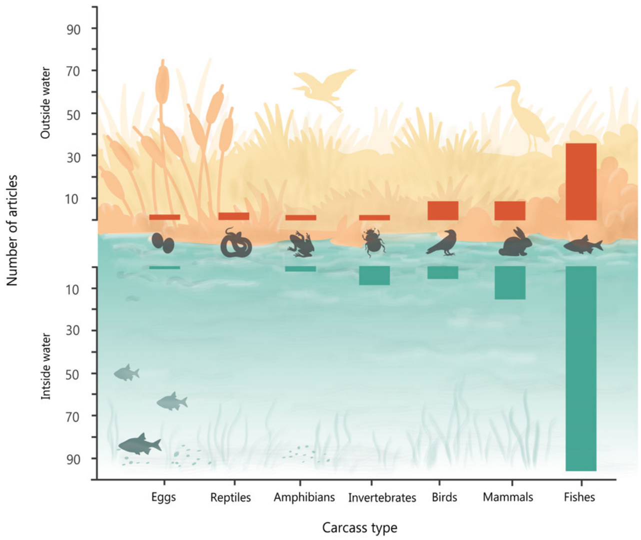

Fig. 2. Carrion types and locations (inside *versus* outside water) in the articles identified in the systematic literature review. Articles that used carrion both inside and outside water are included in both categories.

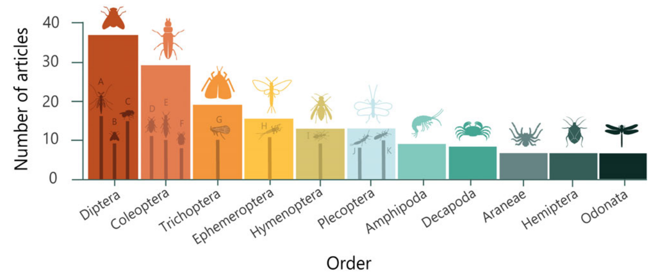

Fig. 3. Invertebrate scavengers identified in the systematic literature review. The 11 most common orders and families are shown. The wide bars show orders and the inset narrow bars show families: A, Chironomidae; B, Muscidae; C, Calliphoridae; D, Silphidae; E, Staphylinidae; F, Dytiscidae; G, Limnephilidae; H, Baetidae; I, Formicidae; J, Chloroperlidae; K, Nemouridae. See Tables S5 and S6 for all orders and families.

North America ($N = 9$), followed by Europe ($N = 5$), South America and Asia ($N = 3$ each). The most studied wetland type was streams ($N = 11$), followed by lakes and rivers ($N = 4$ each); marsh, ponds, cave streams and aquatic containers had one study each. Most studies placed carrion inside water ($N = 13$), while five studies used carrion outside of water, and two placed carrion both in and out of water. Fish carcasses were the most common carrion used ($N = 11$), followed by birds ($N = 4$), while amphibian, reptile and invertebrate carcasses appeared in one study each. The number of carcasses placed in each study ranged between one and 200, with an average of 46 carcasses per study. There were only six studies in which carrion consumption patterns (i.e. consumption rate and/or percentage of carrion biomass consumed) were reported.

The recorded invertebrate scavenger assemblages included an average of seven orders per article (range 1–17) and 16 families per article (range 1–46). Considering all invertebrate scavenger studies in aquatic ecosystems (i.e. invertebrate scavenger assemblages, forensic studies and foraging ecology of invertebrates) a total of 179 families and 55 different orders were listed (Fig. 3; Table S5 and S6). The orders that appeared in most articles were Diptera ($N = 37$), followed by Coleoptera ($N = 29$), Trichoptera ($N = 19$) and Ephemeroptera ($N = 14$; Fig. 3). The most frequently recorded families were Chironomidae ($N = 16$), Calliphoridae ($N = 14$), Baetidae and Silphidae ($N = 11$ each; Fig. 3).

(*b*) *Vertebrate scavenger studies*

We found only 15 articles focused on vertebrate scavenger assemblages. Similar to invertebrate studies, most of these were from North America ($N = 11$), with some in Europe ($N = 3$) and one in South America. All studies were conducted over fairly short periods of between one and six months. More than half were conducted in rivers ($N = 9$), and the most commonly used carrion type was fish ($N = 9$). The number of carcasses ranged from one to 945, and the number of scavenger species ranged from three in the study using one carcass to 22 in the study using the highest number of carcasses ($N = 945$), with an average of eight scavenger species per study. Only eight studies assessed the ecological functions of carrion consumption.

From all studies recording vertebrate scavenger species consuming carrion in aquatic ecosystems, we recorded 114 species from 40 families and 22 orders of the five existing classes of vertebrates (Table S7). The class with the highest number of scavenger species recorded was birds, with 55 species belonging to 12 families and nine orders (Fig. 4). Among birds, raptors (Accipitriformes) were the most species-rich order with 17 species. The second richest class was mammals with 32 species, 14 families and four orders (Fig. 4). Among mammals, the order Carnivora was the best represented with 17 species, especially the family Mustelidae with seven species (Table S7). In third place was fish (Actinopterygii), with 18 species belonging to seven families and five orders (Fig. 4), the family Salmonidae being the most represented with six species (Table S7). Reptiles were in fourth place, with eight species belonging to six families from three orders (Fig. 4), the order Testudines being the most important with four species (Table S7). Finally, for amphibians, only one species has been recorded consuming carrion, the two-toed amphiuma (*Amphiuma means* Garden).

In terms of the number of studies in which the different taxa appear, birds remain the main class ($N = 94$), followed by mammals ($N = 62$), fish ($N = 20$), reptiles ($N = 12$) and amphibians ($N = 1$; Fig. 4). However, for the different orders, Carnivora ($N = 46$) appeared in the most articles, followed by Accipitriformes ($N = 33$) and Passeriformes ($N = 26$; Table S7). In terms of families, the three most frequent

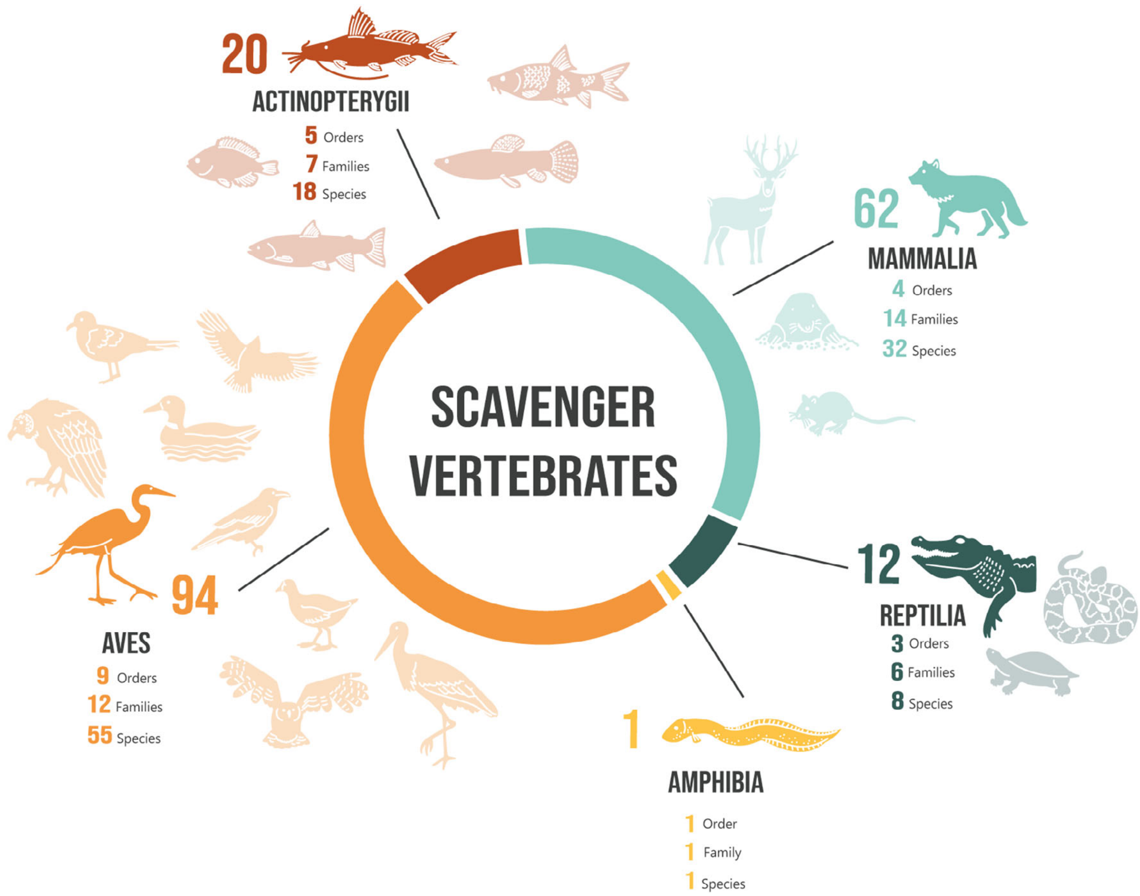

Fig. 4. Number of articles per class of vertebrate scavengers identified in the systematic literature review. For each class, the number of orders, families and species included in the respective set of studies are shown. Silhouettes represent the orders that appeared in each class.

were all bird families (Accipitridae, Corvidae and Laridae; $N = 33$, 21 and 18 articles, respectively), while the next three are mammals (Canidae, Ursidae and Mustelidae, $N = 13$, 13 and 12 articles, respectively). The individual scavenger species recorded in the most articles were the bald eagle (*Haliaeetus leucocephalus* Linnaeus; $N = 13$) and the American black bear (*Ursus americanus* Pallas; $N = 10$; Table S7).

(3) What?

(a) *Topics*

About half of the reviewed articles focused on ecosystem–carrion effects (41.3%; $N = 85$). The next most common topic was foraging ecology of vertebrates (23.3%; $N = 48$), followed by invertebrate scavenger assemblages (9.7%; $N = 20$), vertebrate scavenger assemblages (7.3%; $N = 15$) and forensic studies (4.9%; $N = 10$), while all the remaining topics were investigated to a lesser extent (Fig. 5). Specific topics appearing in less than three articles (e.g. facilitation of carcass colonisation, effects of industrial disturbances on invertebrate scavengers, or water quality regulation by scavengers) were grouped in the topic 'others' (5.7%; $N = 12$; Fig. 5).

(b) *Ecological functions*

The ecological functions performed by carrion and scavengers in aquatic ecosystems were diverse. The two main ecological functions were carrion as food source and the role of scavengers in nutrient cycling, which appeared in 52.4% ($N = 108$) and 46.1% ($N = 95$) of the articles, respectively (Fig. 6). A much smaller number of articles focused on the ecological function of nutrient transport by scavengers (4.9%; $N = 10$) and water quality regulation (1.9%; $N = 4$). Lastly, only two articles dealt with carrion as breeding place, pathogen regulation, and facilitation process of breeding place and colonisation (1%; $N = 2$ each; Fig. 6).

(c) *Ecosystem threats*

Although most articles did not identify ecosystem threats derived from carrion or scavengers, they did appear in a few ($N = 18$). The most common ecosystem threats were water eutrophication

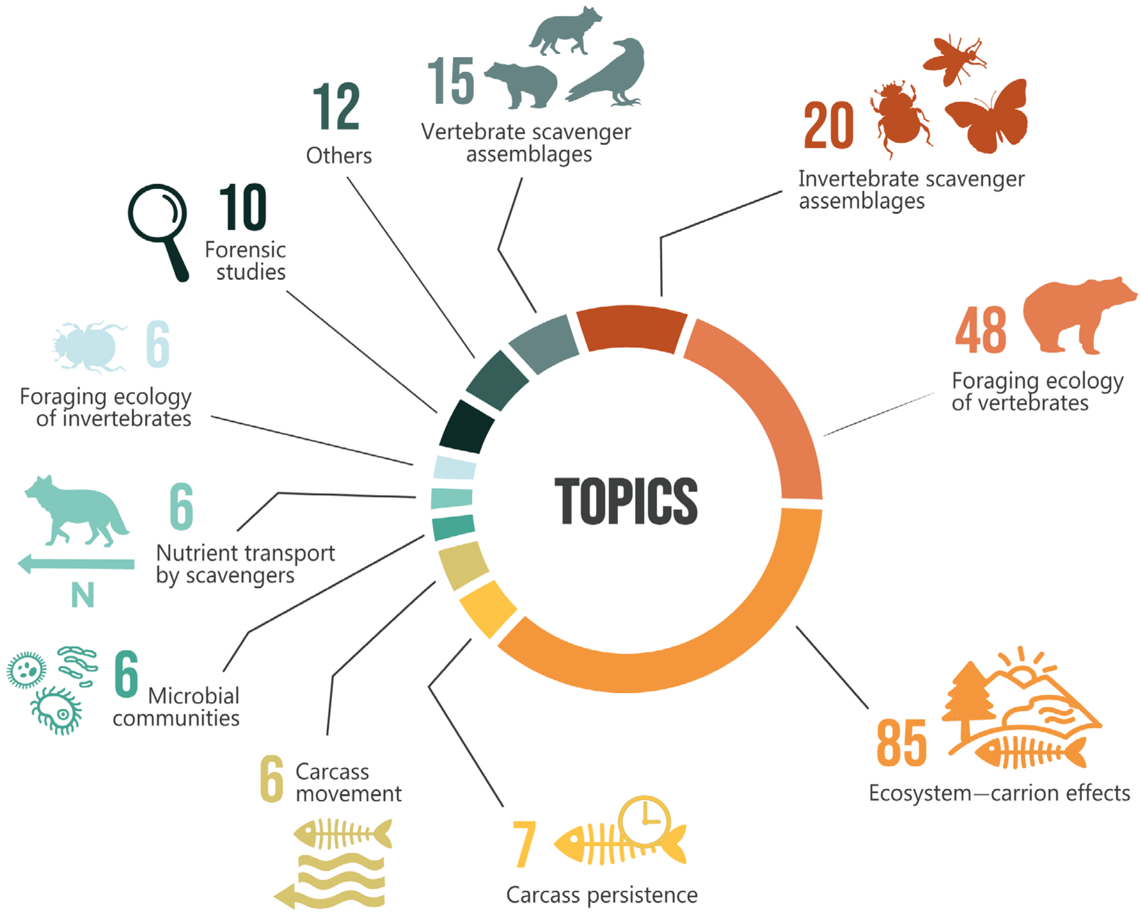

Fig. 5. Topics used for the classification of the reviewed articles and number of articles per topic.

and carrion as source of pathogens (2.4%; $N = 5$ each) followed by nest predation (1.5%, $N = 3$), oxygen depletion (1%; $N = 2$), transport of contaminants by scavengers (1%; $N = 2$) and alteration of leaf litter decomposition (0.5%; $N = 1$: Fig. 6).

(*d*) *Ecosystem–carrion effects*

Regarding the effects of carrion on ecosystems, we found studies spanning all ecosystem components ($N = 85$), from soil (i.e. sediment under water and terrestrial soil) to water column, but also biofilm and vegetation, with a particular focus on both invertebrate and vertebrate scavenger assemblages. In addition, we also found studies assessing the effect of carrion on ecological processes (i.e. litter and wood decomposition). Although the effects were very different, overall, the majority of articles found positive effects (84.7%; $N = 72$), a minority found negative effects (10.6%; $N = 9$), five articles found turnover effects (i.e. changes in community species composition) and 11 articles found no effects.

The most frequently studied organisms were aquatic invertebrates ($N = 24$), which were usually positively (e.g. increased abundance/biomass) affected by carrion in most cases ($N = 22$). In a few cases, aquatic invertebrates were negatively impacted [e.g. increased mercury (Hg) in macroinvertebrates, or decline in adult aquatic invertebrates' biomass] by carrion ($N = 3$), or carrion had no effects ($N = 2$) or caused a turnover in the aquatic invertebrate assemblage ($N = 1$; Fig. 7). Effects on fish were the next best studied ($N = 15$; Fig. 7). Most studies found a positive effect (e.g. increase on individual growth, or on population abundance) of carrion on fish ($N = 11$), while negative effects (e.g. oxygen depletion in the water leading to embryo mortality) were reported in one study, with three studies where carrion had no effect on fish (Fig. 7). Effects on other organisms were studied to a lesser extent (Fig. 7). A total of 17 studies explored the effects of carrion on different components of the food web as a whole (i.e. three or more components), in all cases reporting a positive effect of carrion (e.g. individual fitness improvement, increased abundance/density or species richness of the different components and ecosystem levels) on the food web (Fig. 7).

IV. DISCUSSION

(1) What do we know

Research into carrion ecology in aquatic ecosystems has experienced exponential growth in recent years demonstrating a

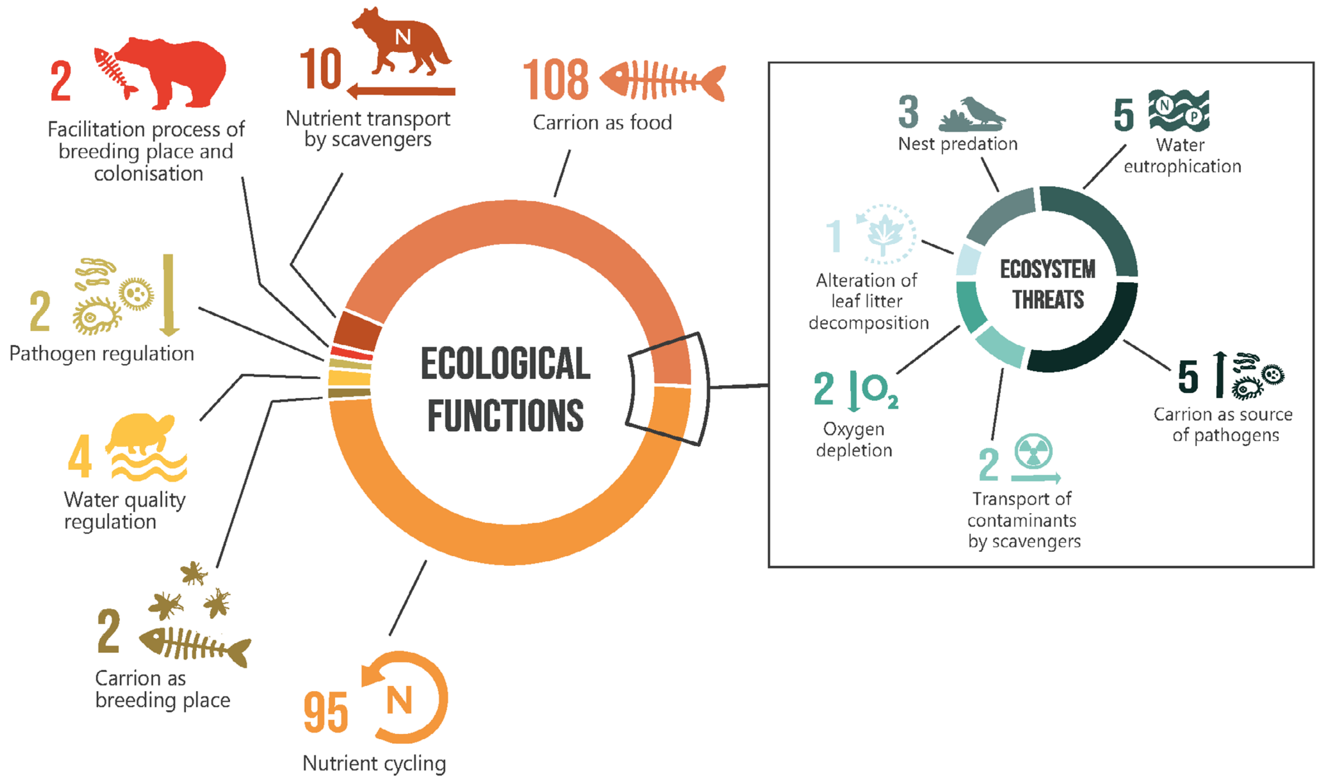

Fig. 6. Ecological functions and ecosystem threats of carrion and scavengers identified in the systematic literature review and number of articles where each ecological function and ecosystem threat was identified. The black outlined segment shows the ratio of studies reporting ecosystem threats to those reporting ecological functions.

growing interest of scientists in this field of ecology. Lotic systems in North America have garnered the most extensive attention, particularly regarding the significance of fish carrion within aquatic environments. Nevertheless, numerous research gaps and challenges persist. It is paramount to emphasise the vital roles that scavengers and carrion play in the functioning of aquatic ecosystems, and we call for additional research in this field.

In contrast to other disciplines where most studies focus on vertebrates, invertebrate scavenger assemblages have historically been more the subject of study due to their forensic value, and their successional stages in carrion are relatively well understood, especially for terrestrial species (Payne, 1965; Payne & King, 1974; Anderson & VanLaerhoven, 1996). Early studies on invertebrate assemblages in aquatic ecosystems also had a forensic approach (Vance, VanDyk & Rowley, 1995; Keiper, Chapman & Foote, 1997), although since the 2000s studies on invertebrate scavengers have shifted towards an ecological focus (Chaloner, Wipfli & Caouette, 2002; Fenoglio *et al.*, 2005). The most frequently occurring order in the reviewed literature was Diptera, followed by Coleoptera. In terrestrial ecosystems, Diptera are the first invertebrates to arrive to carrion and tend to be the most abundant and consume the most biomass (Blackith & Blackith, 1990; Davies, 1999), while Coleoptera consume carrion at later stages of decomposition, or can be predators of carrion insects (Archer, 2014). Overall, there is an extensive and diverse community of invertebrates that benefits from carrion in aquatic ecosystems.

Vertebrate scavengers have historically received less attention, leading to an underestimation of their ecological importance. Wilson & Wolkovich (2011) found that scavenging was underestimated by 16-fold in food web research, and Sebastián-González *et al.* (2023) determined that more than a half of the scavenger species identified in their database were not assigned as carrion-consumers in the Elton Traits database, one of the most complete diet databases (Wilman *et al.*, 2014). However, recent studies show that a wide range of organisms, including omnivores, carnivores and other feeding guilds, consume carrion to varying degrees (Sebastián-González *et al.*, 2023). Despite the smaller number of studies on vertebrate scavenging in aquatic ecosystems, our database included more than a hundred vertebrate scavenger species consuming carrion, highlighting the importance of this group for food web stabilisation and nutrient transport at the water–land interface (Escobar-Lasso *et al.*, 2016; Schlichting *et al.*, 2019). The majority of studies documenting vertebrates consuming carrion involved sporadic observations. However, in a few cases the species composition of the vertebrate scavenger assemblage in an

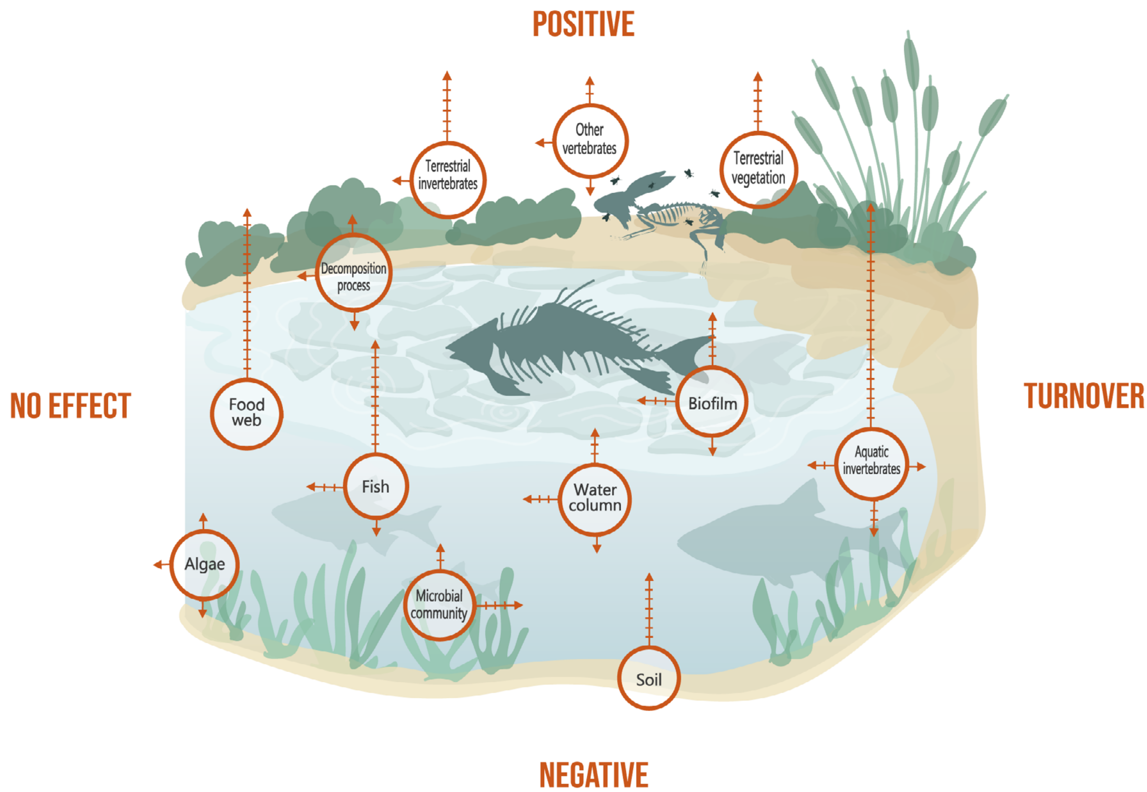

Fig. 7. Ecosystem effects of carrion and effect direction (positive, negative, turnover or no effect) on the different components of the ecosystem identified in the systematic literature review. Each segment within the arrow represents one article.

area was investigated, or the study systematically assessed carrion consumption patterns by vertebrates. For example, Schlichting *et al.* (2019) and Gabel *et al.* (2019) reported that vertebrates consumed most monitored carcasses (85% and 89.5%, respectively). By contrast, Abernethy *et al.* (2017), using amphibian and reptile carcasses, reported that vertebrates consumed less than 20% of the carrion, with invertebrates being the main carrion consumers. Studying scavenging dynamics in more detail will help us to deepen our understanding of the importance of this guild in aquatic ecosystems.

This review highlights that studies related to carrion ecology in aquatic ecosystems focused most often on the effects of carrion on the ecosystem, especially for aquatic invertebrates and fish, as well as on terrestrial components such as terrestrial vegetation or invertebrates, evidencing the importance of nutrients from aquatic carrion for terrestrial ecosystems (Quinn *et al.*, 2018). Particularly noteworthy is the considerable amount of research on the effects of salmon carcasses in North America (60.7% of the ecosystem–carrion effects articles), perhaps motivated by economic interests, as this species generates millions of dollars of revenue annually (Tveteras & Asche, 2008), and also because of the large carrion biomass that these post-reproductive mass-mortality events regularly produce (Gende *et al.*, 2004). The second most common topic covered by studies was the foraging ecology of vertebrates, which was mostly evaluated through sporadic observations of carrion in the diet. Several recent studies of vertebrate scavenger assemblages in lentic systems in Spain (Orihuela-Torres *et al.*, 2022; Orihuela-Torres, Sebastián-González & Pérez-García, 2023) and Canada (Etherington *et al.*, 2023) where 26 and five scavenger species were recorded respectively, and in Norway (Dunlop *et al.*, 2021) where six scavenger species consumed carcasses in a lotic system, show that vertebrate scavenger assemblages are much more limited than those in terrestrial ecosystems, as is also the case for invertebrate scavenger assemblages (Olea *et al.*, 2019).

Despite the bad reputation of many scavenging species (Margalida & Donázar, 2020), our review of the literature showed that ecological functions such as carrion as food source or the role of scavengers for nutrient cycling in aquatic ecosystems far outweigh (by 12-fold) the ecosystem threats they pose. In addition, these threats often result from ecosystem imbalances due to a lack of scavenging. If carrion is not consumed, it will remain for longer periods and in greater amounts in ecosystems and then can act as a source of pathogens or promote water eutrophication (Evelsizer, Clark & Bollinger, 2010; Weber & Brown, 2013). However, the vast majority of studies reported positive effects of carrion on ecosystems (e.g. increased species richness, abundance or fitness) reaching all levels of the food web.

(2) Critical research gaps

Despite significant advances in carrion ecology research, substantial knowledge gaps regarding scavenging dynamics remain. Our review highlights the particularly limited information available in the context of aquatic ecosystems. Geographical disparities are very pronounced compared to previous systematic reviews in other disciplines (Lozano *et al.*, 2019; Loss *et al.*, 2022; Festa *et al.*, 2023). Efforts should be concentrated on less-studied regions such as tropical areas, and Africa, Asia, and Oceania. Consequently, caution must be exercised when interpreting the conclusions of our review, as most studies originated from North America. Furthermore, while studies on carrion ecology in aquatic ecosystems have increased in the last decade, research covering periods of up to a full year and considering the effects of seasonality (Parmenter & Macmahon, 2009; Walker *et al.*, 2021) remains rare. To enhance our understanding of carrion's roles and significance in these vulnerable ecosystems, future research should be designed to extend over longer periods.

Research within the field of carrion ecology has been predominantly focused on rivers and streams, which are lotic systems characterised by the presence of flowing water for a significant portion of the hydrological year. These systems exhibit distinct functioning and biodiversity compared to lentic systems, which include standing water bodies like lakes, ponds, and marshes where surface flow is absent (Likens, 2010; Allan, Castillo & Capps, 2021). It is likely that the processes and significance of carrion consumption and decomposition in these two main system types will differ significantly. Therefore, it is crucial to prioritise studies in lentic systems to obtain a greater understanding of the role of carrion and scavengers in all aquatic ecosystems.

In addition, most studies focused on carcasses inside the water column and mostly used fish carcasses, with few studies monitoring other types of carcasses. It is known that carcass type is decisive in structuring the scavenger assemblage (Olson, Beasley & Rhodes, 2016), in the decomposition process, and in the nutrients they input into the ecosystem (Parmenter & Lamarra, 1991). Carcass location is also a key determinant of the scavenger species that consume them, as scavenger assemblages are completely different inside and outside the water (Redondo-Gómez *et al.*, 2022) and carrion decomposition processes may also vary substantially (Wallace, 2016). To advance our understanding of the ecology of carrion in aquatic ecosystems, it will be important to carry out studies with different types of carrion at the same time, both inside and outside the water, to assess the role of terrestrial scavengers that consume carrion of aquatic origin and incorporate nutrients into the terrestrial ecosystem (Hewson, 1995; Orihuela-Torres *et al.*, 2022), or in the opposite direction, i.e. scavengers consuming terrestrial carcasses and incorporating the nutrients into the aquatic environment.

Another interesting result of this review relates to the very few studies assessing carrion consumption patterns. This type of study would allow us to measure quantitatively the ecological role of scavengers as biomass recyclers, so we recommend that future work incorporates variables such as consumption rates (carrion biomass consumed per time unit), the duration of carcass removal, and the number of carcasses completely consumed or percentage of biomass consumed. Furthermore, studying the scavenging dynamics of vertebrates and invertebrates together will allow us to obtain a deeper knowledge about the relative roles of each scavenger group under different circumstances.

We also identified a lack of comprehensive quantitative assessments on the ecological functions that scavengers perform (e.g. nutrient recirculation, disease control, water quality regulation) (Santori *et al.*, 2020; Maslo *et al.*, 2022; Inagaki *et al.*, 2022) in aquatic ecosystems. This is especially relevant under current trends of population reductions of large animal species in both aquatic and terrestrial ecosystems (e.g. cetaceans, large freshwater fish and large terrestrial mammals), potentially slowing down the recirculation and transport of nutrients, such as the movement of phosphorus between aquatic and terrestrial ecosystems (Doughty *et al.*, 2016). However, many populations of scavenger species [e.g. gulls, red foxes (*Vulpes vulpes* Linnaeus), wild boar (*Sus scrofa* Linnaeus)] in aquatic ecosystems are increasing, due to their plasticity and ability to take advantage of anthropogenic subsidies (Podgórski *et al.*, 2013; Reshamwala *et al.*, 2021; Vez-Garzón *et al.*, 2023). In this context, vertebrate scavengers may play an essential role in aquatic ecosystems, as they consume large amounts of carrion and are able to move them long distances through ecosystems (Payne & Moore, 2006; Orihuela-Torres *et al.*, 2022). Therefore, improving our knowledge on the ecological role of vertebrate scavengers in aquatic ecosystems and the implications of defaunation on nutrient cycling and transport across ecosystems should be a priority for future studies.

Aquatic ecosystems are affected by global changes, where threats such as water pollution by industrial and agricultural discharges or direct human impacts such as tourism and outdoor recreation are increasing. These threats may have adverse effects on scavengers, disrupting the assemblage composition and negatively affecting carrion removal (Orihuela-Torres *et al.*, 2023). However, we found few studies assessing the effects of these threats on invertebrate and vertebrate scavenger assemblages and their ecological functions (e.g. Knight, Anderson & Verne Marr, 1991; Silva *et al.*, 2020). Understanding the effects of global change scenarios in aquatic ecosystems is essential for their effective management and for maintaining healthy populations of scavengers, thus preserving their ecological functions within these endangered ecosystems.

(3) Future challenges

Unravelling the role of scavengers, particularly in the context of nutrient transfer between water and land in aquatic ecosystems presents a deep challenge. First, it will be crucial to determine the quantity of carrion consumed by scavengers, and then how these nutrients are distributed throughout aquatic ecosystems and their subsequent impact on terrestrial and aquatic environments. However, obtaining accurate data on the amount of carrion consumed by individual organisms through traditional diet studies is virtually impossible (Sebastián-González *et al.*, 2023). To estimate the amount of carrion consumed by scavengers in aquatic ecosystems, it is necessary to develop experimental designs using different methods, such as camera traps for vertebrates, or exclusion cages for invertebrates. New analytical techniques such as DNA analyses or stable isotope studies, in combination with fieldwork may also help to clarify the role of carrion in the diet of scavengers in aquatic ecosystems (Nielsen *et al.*, 2018).

There may be fundamental differences between terrestrial and aquatic scavengers. For example, terrestrial ecosystems tend to have more specialised scavengers that rely exclusively on carrion for their life cycle, but such specialists appear to be absent from aquatic ecosystems (Fenoglio, Merritt & Cummins, 2014). However, due to the inherent technological and logistical challenges associated with studying underwater ecosystems, there has been only limited investigation into aquatic scavenging assemblages. It is very difficult to monitor lentic systems, where waters are often turbid and aquatic cameras cannot be used (Anderson & Wallace, 2019). Therefore, it will be important to conduct studies of scavenger assemblages with carrion submerged in the water to understand better the different stages of succession in aquatic scavengers, as well as to study consumption patterns to determine their efficiency in carrion removal and nutrient recirculation.

Mass-mortality events are increasing in occurrence and magnitude in aquatic ecosystems due to increased disease emergence, biotoxicity, and events produced by multiple interacting stressors (Fey *et al.*, 2015). Scavengers are likely to play a key role in disease mitigation and nutrient cycling by consuming large amounts of carrion in these ecosystems (Barton *et al.*, 2023). In most aquatic ecosystems, especially in lentic systems, a large part of carrion is generated as large pulses, i.e. mass-mortality events (e.g. botulism, avian influenza, pond drying). These events represent a drastic change in the availability of carrion both spatially and temporally. However, studies on how scavengers respond to mass-mortality events in aquatic ecosystems and the effects they have are scarce, partly because they are relatively unpredictable and also demanding to simulate experimentally. It is essential for future work to explore how the spatial and temporal availability of carrion affects the ability of scavengers to remove carcasses, prevent the spread of pathogens and recirculate nutrients in the ecosystem (Tomberlin *et al.*, 2017).

V. CONCLUSIONS

(1) Given the significant biases detected in this review in terms of regions, target ecosystems and temporal coverage, future research should prioritise understudied regions, lentic systems and extend coverage across different seasons in order to understand scavenging dynamics better in aquatic ecosystems.

(2) Considering the scarcity of studies on scavenger assemblages, both vertebrate and invertebrate, a major concern is the lack of quantitative data addressing carrion consumption patterns. Such data serve as a proxy for assessing the ecological functions performed by scavengers, and its absence hampers our ability to obtain a comprehensive understanding of their ecosystem roles.

(3) The large number of species (invertebrates and vertebrates) recorded consuming carrion in the reviewed studies emphasises the significance of scavengers in stabilising food webs and facilitating nutrient cycling within aquatic ecosystems.

(4) Most of the reviewed studies identified ecological functions performed by carrion and scavengers rather than ecosystem threats. If healthy scavenger populations are preserved, the threats caused by longer persistence of carcasses in ecosystems could be largely avoided.

(5) The effects of carrion on aquatic ecosystems involve the entire food web, from soil and vegetation to vertebrates, and from individual to community level, highlighting the key role of carrion in these ecosystems. Studies on the carrion biomass produced in aquatic ecosystems, as well as biomass consumed by different scavenger groups (vertebrates, invertebrates and microbes) are key to understanding food webs and energy flows, and ultimately the roles they play in the functioning of these threatened ecosystems.

(6) It will be important to increase our knowledge on scavengers in aquatic ecosystems to understand their current roles, and the roles they may play in the future under global change. This could be most relevant in water–land nutrient transport due to the changes in the amounts and speed of nutrient movements, especially regarding phosphorus, and in disease control and impact mitigation due to the increased occurrence and magnitude of mass-mortality events in aquatic ecosystems.

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VII. DATA AVAILABILITY STATEMENT

Data used in the systematic review are available online in Database S1.

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IX. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Data S1. Database containing all the variables extracted for this review. The 'Dataset' sheet shows the main information used for the review. The 'Vertebrates' sheet lists the vertebrate species recorded in each article. The 'Invertebrate orders 'sheet lists the invertebrate orders recorded in each article. The sheet 'Invertebrate families 'lists the invertebrate families recorded in each article.

Appendix S1. PRISMA EcoEvo checklist (O'Dea *et al*., 2021).

Appendix S2. List of key words and search filters used in the systematic literature review.

Appendix S3. Flow diagram of the selection process for the articles used in the systematic literature review.

Appendix S4. Description of the inclusion criteria used in the two-stage review process.

Table S1. Complete list of variables used in the systematic literature review.

Table S2. Ecological functions performed by carrion and scavengers identified in the systematic literature review.

Table S3. Ecosystem threats associated with carrion and scavengers identified in the systematic literature review.

Table S4. Direction of ecosystem effects of carrion identified in the systematic literature review.
Table S5. List of invertebrate scavenger orders identified in the systematic literature review.
Table S6. List of invertebrate scavenger families identified in the systematic literature review.
Table S7. List of vertebrate scavengers identified in the systematic literature review.

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