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Ecology & Evolution

Review

Species roles and key interactions in vertebrate scavenger communities

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In scavenging assemblages, the functional traits of scavengers that impact the structure and function of ecological communities are becoming clearer. However, there are multiple terms for influential scavenger species that lack established definitions. As such, we propose a standardized terminology encompassing five functional roles: frequent scavenger, main biomass consumer, and keystone scavenger, as well as apex scavenger and mesoscavenger (defined through ecological roles and hierarchical positions). Furthermore, we identify and describe five key behaviors, and its actors related to competitive and facilitative interactions among scavengers – signaling scavenger, carrion broker, dominant scavenger, carcass cacher, and carrion transporter – which drive species' roles. We unify concepts of scavenger roles to facilitate comparisons among studies on scavenging.

Highlights

Vertebrate scavenging plays a crucial role in ecosystem functions, such as food web dynamics, nutrient cycling, nutrient movement, and disease control, and certain scavenger species are key to determining community structure.

As the importance of scavenging processes for the effective functioning of ecosystems is becoming clearer, there is a growing need to establish a unified conceptual framework regarding the scavenger roles and the interactions that drive them.

Scavenging dynamics is driven by complex facilitative and competitive interactions that are still not fully understood, highlighting the need for species-level studies, supported by field-based evidence.

Standardizing and promoting the terminology regarding the roles and interactions of species within vertebrate scavenger assemblages is instrumental in assessing the functional roles of scavenger species for nutrient recycling and in deepening our ecological understanding of scavenger species internationally.

Scavengers contribute differently to carrion decomposition

All animals die. Yet death is not the end – but instead the beginning of ecological interactions around the **carcass** (see Glossary). **Carrion** is a high-quality pulse resource [1] which appears in ephemeral and heterogeneous spatial patches. Carrion is a resource used by a wide diversity of organisms which can be broadly categorized into **scavengers** (including both vertebrates and invertebrates) and **decomposers** (which consist of microorganisms). Previous studies on vertebrate scavenger assemblages (the group of species that consume carrion) have shown that 2–15% of all vertebrate species are scavengers [2,3]. Moreover, this percentage is likely an underestimate, as there is a general underestimation of the **scavenging** behavior in diet studies [4] – suggesting that vertebrate scavenging is a common foraging strategy. Vertebrate scavenging plays a crucial role in ecosystem maintenance by facilitating ecosystem functions (e.g., food web dynamics, nutrient cycling, nutrient movement, disease control; Box 1) which are driven by the vertebrate scavenger assemblages in response to the presence of carrion.

Biological communities are formed as assemblages of many different species, but the contribution of species to community structure and functioning is asymmetrical. Some species play important roles (e.g., keystone species and dominant species), and their loss may have significant effects on community structure than can compromise the conservation of the ecological community [5–7]. Some scavenger species may also impact community structure and ecosystem functions disproportionately [8,9]. In vertebrate scavenging assemblages, species with specific traits, such as dietary specialization (obligate or facultative), high olfactory senses, sociality, larger home ranges, and nocturnal and crepuscular activity patterns, play an important role in the community composition and function [10–12]. Species with these traits impact the scavenging process by consuming large proportions of carcasses or by disrupting the carrion consumption to other species. Nevertheless, our knowledge of scavenger species' roles and their effects on the scavenging process is limited, complicated by roles and interactions tending to be species-specific in each ecosystem (e.g., [13]). In addition, various terms are used for important species within the scavenger community but without unified

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Box 1. Ecosystem functions by vertebrate scavenging

Food web dynamics

Scavenging forms food web links that connect the classical green food web (primary producers–consumers–predators) and the brown food web (detritus–decomposers) [98]. There are only 23 obligate scavengers in the world (i.e., vulture species primarily eating carrion). Most vertebrate scavengers are facultative scavengers that tend to have uncertain and weak connections, promoting food web heterogeneity and stability [99]. In addition, some scavengers are also predators [10], and the attraction of scavengers near carcasses may concentrate the function of predation spatiotemporally [100,101], thereby changing the dynamics of the relationships of predator–prey and even prey–secondary prey (e.g., plants) around the carcass [102–104].

Nutrient cycling

Vertebrate scavenging can suppress carrion **decomposition** and consumption by invertebrates, promoting nutrient cycling at higher trophic levels [105]. Even small amounts of carrion create landscape heterogeneity by altering nutrient composition in the soil, microbial biomass and diversity in the soil, and productivity of plants during the process of decomposition [106,107]. If scavenging does not occur and the majority of carcasses are incorporated into the decomposition process, the high nutrient loads can lead to an explosion of invertebrates and microorganisms, resulting in local eutrophication and having a significant impact on disease dynamics [108].

Nutrient movement

Vertebrate scavengers contribute to nutrient transport in/out of ecosystems by dispersing carrion-derived nutrients (e.g., carrion or feces) over longer distances [109] as they are more mobile than invertebrates and decomposers. The nutrient transport of carrion as a seasonal pulse resource is a widely known function of ecotones in river and coastal ecosystems (e.g., anadromous salmon carcasses [110–113], seal colonies [114], and mass drowning of wildebeests [115]). Scavenging is a dispersal pathway that transports nutrients (e.g., C, N, and P) and energy across ecosystems, with impacts that can persist for years to decades or longer [109,115,116].

Disease control

Regardless of the cause of death, carcasses can be disease hotspots in the landscape via pathogens and parasites [117]. Scavenging provides two opposing ecosystem functions related to disease dynamics: suppression and promotion, through contact with and ingestion of carrion associated with the risk of various diseases [105,118]. When pathogens are eliminated during the digestion process, it contributes to disease suppression. In contrast, some pathogens can pass through the digestive tract of scavengers [119,120], suggesting that the activities of scavengers on or around carcasses may facilitate the spread of disease. Moreover, several scavengers may concentrate around carcasses over short distances, permitting the direct transfer of pathogens among con- and heterospecifics.

definitions (e.g., main scavenger, frequent scavenger, and dominant scavenger; Table 1), contributing to confusion in understanding the roles of scavenger species.

In this article, we (i) propose a unified description of the different roles that scavenger species may take, thereby promoting the standardization of terminology, and (ii) describe the main behaviors and the group of the specific species (i.e., actors) which drive the facilitative and competitive interactions among scavenger species, which are key in determining the species role. While we focus on study cases from the most well-studied terrestrial ecosystems [14], our concepts and definitions can also be applied to marine and freshwater ecosystems.

Defining species' roles of scavengers

We define the roles of scavenger species in an assemblage into three categories based on their ecological role (Figure 1). **Frequent scavengers** appear at the largest number of carcasses in a system, and usually the most frequent scavenger would be the species that visits and feeds on most carcass types. The species composition of scavenger communities varies depending on environmental factors (spatial and temporal elements) and on the carcass types [15–18]. The frequent scavenger has the highest proportion of carcass consumption links from the scavenger assemblage, so that its loss can have a substantial impact on the food web structure (carrion–scavenger links) and stability of the scavenger assemblage [10,19].

Glossary

Apex scavenger: a scavenger species whose species role is exceptionally prominent compared to others in the scavenger assemblage.
Carcass: the corpse of a dead animal (invertebrate or vertebrate), either intact or partially consumed.
Carcass cacher: a species which stores and/or secures the remains of large kills or carcasses.
Carrion: ephemeral and unpredictable, but nutrient-rich, dead animal tissue.
Carrion broker: a species which facilitates the acquisition of carrion by other species by puncturing the thick skin or tearing apart the carcass.
Carrion transporter: a species which relocates and disperses carrion during their consumption process.
Decomposers: microorganisms that decompose carrion with saprozoic nutrition.
Decomposition: the fundamental process of dead organic matter being broken down into smaller parts by decomposers, and through which nutrients and energy are cycled in the environment.
Dominant scavenger: a species which can restrict the nutrition gained by other scavengers through monopolizing carrion and/or consuming the majority of the carrion.
Frequent scavenger: scavenger species which make use of the largest proportion of carcasses.
Keystone scavenger: a scavenger species whose effect on scavenger diversity, interaction, and scavenging functioning is large relative to its abundance.
Kleptoparasitism: the appropriation and use of prey killed by another species or individual.
Main biomass consumer: scavenger species which consume the largest proportion of carrion biomass.
Mesoscavenger: a less efficient scavenger species relative to the apex scavenger in the scavenger assemblage.
Scavenger: a carrion-consuming organism (vertebrate or invertebrate), often split into species which consume only carrion (obligate scavengers) and those which consume carrion opportunistically (facultative scavengers).
Scavenging: the process of carrion consumption (direct feeding) by animals (vertebrates or invertebrates).

Table 1. List of various scavengers' terms and their meanings from previous studies[a]

Term	Meaning	Refs
Main scavenger	The species that scavenged (fed on) the largest proportion of carcasses	[74–76]
	The species that first detects carcasses and feeds on most of the carcasses visited	[77]
	The species that visited more than 10% of the monitored carcasses	[78]
	The species selected according to the feeding rate	[79]
	Unclear meaning	[80,81]
Frequent scavenger	The species that visit (detect) the largest proportion of carcasses	[54,82–84]
	The species that scavenged (fed on) the largest proportion of carcasses	[18,81,85,86]
	Unclear meaning	[87]
Common scavenger	The species that scavenged (fed on) the largest proportion of carcasses	[88]
	The species that visit (detect) the largest proportion of carcasses	[80]
	Unclear meaning	[86]
Dominant scavenger	The species that outcompete many other species for carrion	[53,54,89]
	The species that enhance the carcass decomposition speed	[90]
	The species that is numerically dominant	[91]
	Not clearly defined	[75,92–94]
Keystone scavenger	The species with a more central location in the scavenger assemblage network	[95]
	Unclear meaning	[96,97]

[a]The references focus on vertebrate scavengers in terrestrial ecosystems. The table shows that identical terms are sometimes used to convey different meanings or are employed without precise meanings, and conversely, that distinct terms are sometimes used to refer to the same meaning.

Signaling scavenger: a species disseminating information related to the presence of carcasses to other scavengers.

Main biomass consumers consume the most carrion biomass per carcass. They can limit access to carrion resources for other scavengers, thereby influencing scavenging function. Studies investigating structural characteristics of scavenger communities often use the scavenging frequency to identify the frequent scavengers, but few quantify the proportion of carrion consumed per carcass [20,21]. This is due primarily to the challenges of measuring carcass weight in the field and estimating species' consumption rates through still images or videos. However, determining consumption rates for each species is essential for identifying the main biomass consumers. For example, Mateo-Tomás *et al.* [22] calculated the carrion consumption rate (i.e., g/day: the carrion weight is divided by the number of days that it took the vertebrate scavenger community to deplete that carcass) and estimated carrion consumption rate per species in different ecosystems. But this method has challenges, such as estimating the amount of the carrion consumed by an individual on a visit to the carcass and accurately accounting for invertebrate consumption during carcass depletion. However, Inger *et al.* [23] estimated and compared the proportion of carcass biomass consumed among species based on total biomass loss of carrion, foraging time of each species, and body mass of each species. Methods for calculating species' carrion consumption rates in terms of carrion mass should be further developed. Mateo-Tomás *et al.* [22] suggested that just one or two scavenger species may account for more than 50% of the carrion consumed per day in several ecosystems. Therefore, examining the effects of the main biomass consumers on the scavenging assemblage represents an important research avenue for the role of carrion consumption.

Keystone scavengers establish strong interactions with other scavengers, affecting ecosystem functioning more than would be expected by their abundance [24]. For example, regardless of the

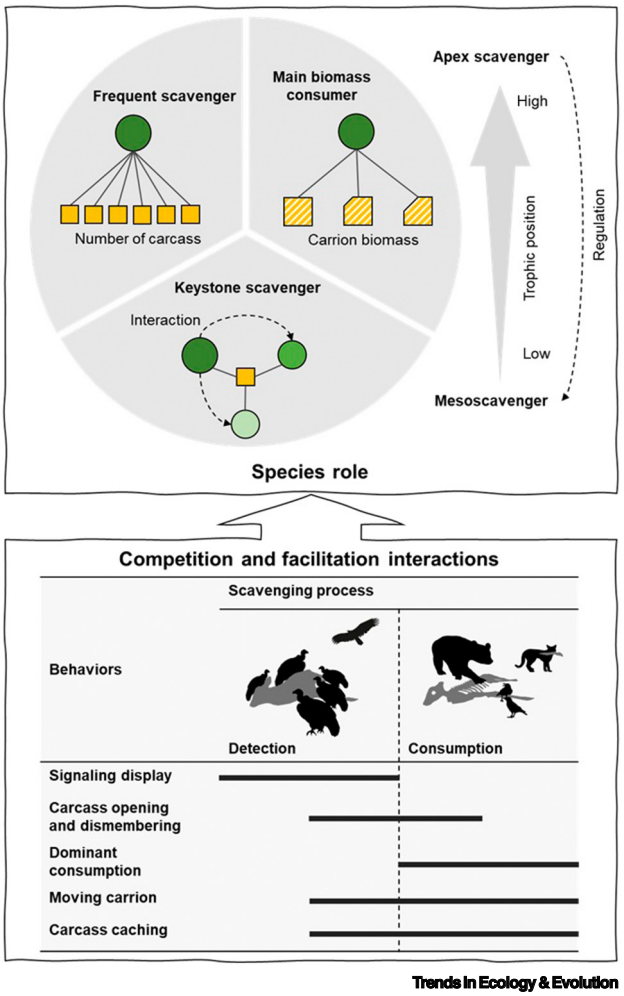

Figure 1. The five species roles of scavengers (top) and the main potential behaviors related to the facilitative and competitive interactions driving the role of scavengers (bottom). At the top, the green circles represent scavenger species, with varying shades indicating different species. The species with the darkest color shows those which fulfill each role. The yellow squares represent carcasses. The solid lines indicate the consumption of carcasses. At the bottom are the mechanisms of competition and facilitation interactions that drive the species' roles. These interactions are determined by five potential behaviors which are interconnected during different phases of the scavenging process (detection and consumption).

scavenging frequency or the amount of carrion consumed, species locating carcasses, or opening their thick skin, provide other species access to the soft tissues, and can therefore be keystone scavengers. Keystone scavengers influence the behavior of other scavenger species through interactions, affecting scavenging (i.e., the process of carrion consumption by vertebrates and invertebrates) and its functioning. Therefore, it is important to identify what interactions exist within the scavenger assemblage and which species provide these interactions to understand the coexistence mechanisms of different species in scavenger communities.

Apex scavengers are species that occupy the highest trophic position in the scavenger assemblage, often functioning as the most influential agents in scavenging processes and dynamics [25] (Figure 1). For example, Méndez *et al*. [25] identified the Andean condor (*Vultur gryphus*), and Cunningham *et al.* [26] identified the Tasmanian devil (*Sarcophilus harrisii*) as apex scavengers from the perspective of their role as main biomass consumers, due to their high carrion consumption rates. Thus, apex scavengers may also be frequent scavengers, main biomass consumers, and/or keystone scavengers, thereby being functionally dominant at scavenging efficiency (e.g., obligate, high olfaction, and social foraging [10]) [27]. This classification is based on the hierarchical position of the species in the scavenger assemblage. Thus, species which exhibit lower

scavenging efficiency, compared with apex scavengers, are categorized as **mesoscavengers**. The distinction between apex scavengers and mesoscavengers is related to the ability of the populations of the species to self-regulate their densities. Apex scavengers are not influenced by other scavengers in terms of scavenging efficiency or their population size; instead, these factors are determined by the availability of carrion or other food resources, as well as environmental factors (e.g., [28,29]). In contrast, mesoscavengers are affected by the presence or absence of apex scavengers in terms of their scavenging efficiency and population size [30]. Therefore, the terms apex scavenger and mesoscavenger are useful when examining relative interactions among scavenger species and the resulting consequences – such as changes in mesoscavenger population sizes or carrion persistence. However, when evaluating the ecological roles of a scavenger itself, it is more appropriate to use terms such as 'frequent scavenger', 'main biomass consumer', or 'keystone scavenger'.

Scavenger interactions and behaviors driving species role

Competitive and facilitative interactions may serve as important driving factors in determining the roles of species in each scavenger assemblage (Figure 1). Competition typically exerts negative effects, whereas facilitation benefits other species. For example, species with intrinsic abilities for carrion consumption can substantially reduce the amount of carrion available and negatively impact the potential nutritional gain for other species (i.e., exploitative competition; [31]). In addition, agonistic behaviors – such as fights and aggression towards other scavengers to defend carcasses and the creation of landscapes of fear around carcasses – reduce the opportunity of other species to exploit carrion (i.e., interference competition; [32–34]). In contrast, behaviors such sharing the location of a carcass or opening the thick skin of a carcass can increase opportunities for other species to access and utilize the carrion (i.e., facilitation). Competitive and facilitative interactions via scavenging process are related to key behaviors provided by specific scavenger species (Figure 1, Table 2). These behaviors may strongly contribute to either competition or facilitation, or in some cases, to both. In addition, these behaviors are dynamic in time as they are interconnected and often shift through the different successional stages of the carrion (i.e., carcass detection and consumption: Figure 1).

Signaling scavenger

Signaling scavengers are involved in disseminating information related to the presence of carcasses to other individuals or species (i.e., signaling display). Animals communicate with conspecifics and heterospecifics by sending and receiving information through visual, auditory, olfactory, chemical, or tactile cues [35], either intentionally or unintentionally. Unintentional information transfer includes local enhancement, where conspecifics are used to provide information about the position of food [13,36–38]. Within scavenger guilds, the assembly of individuals/species

Table 2. List of key behaviors and actors that drive the facilitative and competitive interactions among scavenger species

Actor	Description of behavior
Signaling scavenger	Transmitting information about carcass position to con- or heterospecifics
Carrion broker	Tearing apart the skin of a carcass and thus facilitating access for other species to the nutritious inside or splitting the carcass into smaller pieces that are easier to handle
Dominant scavenger	Consuming the majority of a carcass or carrion biomass and monopolizing a carcass, thereby precluding access to carrion resources for other species
Carrion transporter	The movement and dispersal of carrion from the space or system where the carcass originated to a different space or system
Carcass cacher	The storing and/or securing carrion, thereby altering the natural consumption process that the carcass would typically follow

around a carcass is itself a visual cue that tells other scavengers where the carcass is located [39]. Another unintentional aspect of foraging is being followed by other individuals/species. For example, Harel *et al.* [40] demonstrated that informed Eurasian griffon vultures (*Gyps fulvus*) returning to previously visited carcasses were followed by uninformed conspecifics, allowing them access to these resources. This following behavior has also been detected among individuals from different species. In a Neotropical assemblage, turkey vultures (*Cathartes aura*), which have keen olfactory abilities, are followed by other vulture species lacking the sense of smell to find carcasses [36]. Similarly, Kane and Kendal [13] observed such following behavior between mammals and vultures, indicating that mammalian scavengers may find carrion twice as fast when following vultures. Furthermore, species-specific cueing between vultures and mammals was evident, with black-backed jackals following mainly the lappet-faced vulture (*Torgos tracheliotos*), and spotted hyenas (*Crocuta Crocuta*) following the Rüppell's vulture (*Gyps rueppellii*). Informed species may also provide olfactory cues by opening the carcass and therefore releasing putrid gases [8] or by scent marking near carcasses.

A similar signaling display involves predators informing scavengers about the location of carcasses. For example, common ravens (*Corvus corax*) routinely follow gray wolves (*Canis lupus*) during winter, often finding ungulate carcasses within minutes of when they are killed by wolves [41]. Red foxes (*Vulpes vulpes*) also find carcasses by following snow tracks left by wolves [42]. Predators can also produce acoustic cues while hunting or competing over the kill that can be used by scavengers to locate leftovers of predation kills [43].

Carrion broker

When carcasses are too large for predators or scavengers to consume in a single visit, **carrion brokers** can facilitate the acquisition of carrion by other species by opening the thick skin, tearing apart the carcass or dismembering it into smaller pieces (i.e., carcass opening and dismembering) [32]. Opening carcasses with thick hides provides access to the nutrition-rich interior of carcasses (i.e., access to small meat pieces and organs) to all scavenger species, including the less robust ones [32,44]. This behavior may also provide resources for more specialist species like bearded vultures, which are bone-eaters [44,45]. Carcass opening and dismembering is often performed by species at higher trophic levels, benefitting species at lower trophic levels – referred to as a 'trophic advantage' [39].

Describing direct behavioral observations is crucial to understand carcass opening and dismembering, and their ecological effects [32]. For example, Selva *et al.* [46] documented gray wolves opening the thick skin of European bison (*Bison bonasus*) carcasses, making them more accessible to smaller scavengers, while Cortés-Avizanda *et al*. [39] found that small scavengers refrained from feeding until the larger griffon vultures had landed and opened the carcasses. Notably, species capable of opening and dismembering a carcass are often **dominant scavengers**, due to their high trophic levels and morphological features adapted to scavenging (e.g., beaks of vultures [47], jaws of the Tasmanian devil [48]). Consequently, even if the carcass is open and accessible, subordinate scavengers are less likely to benefit from the carcass if the carcass is monopolized. Conversely, there are cases in which multiple individuals cooperate to tear a carcass, without relying on large species to open it. For example, striated caracaras (*Phalcoboenus australis*) forage carcasses by having multiple mouths tearing at the carcass from different angles [49]. This group foraging behavior potentially increases the chance that one of them is able to obtain the reward more quickly than if each of them works alone [49]. Therefore, it is imperative to determine whether and in which situations the facilitating effect of carcass opening and dismembering is obscured by intra- and inter-specific competition when quantifying its effect on scavenger communities.

Dominant scavenger

Dominant scavengers restrict the nutrition gained by other scavengers through monopolizing carrion and/or consuming carrion entirely [33,39,50] (i.e., dominant consumption). The effect of dominant scavengers amplifies at large carcasses, as these carcasses tend to last longer and have the potential to attract more scavenger individuals and species, intensifying intra- and inter-specific competition. Competitive advantages among scavengers are often related to functional traits, including body size [50,51] and sociality [10,51]. But in direct confrontations due to carcasses traits (such as body size) and individual factors (such as hunger) can determine the outcome of competitive interactions [52]. Dominant scavengers may also force predators to abandon their killed prey [53–55]. Such direct limitations by dominant scavengers can cascade through populations and systems, driving some scavenger species to the use of alternative food resources [56].

However, scent marking, or rubbing on or around carcasses, has been observed across various taxa – for example, wolverine (*Gulo gulo*) [57], red fox [58], and Asiatic black bear (*Ursus thibetanus*) [59]. While the full implications of these behaviors remain unclear, scent marking (such as the spraying of feces or urine) is generally used to assert social status, maintain territories, and defend food resources [57,60]. Given that marked or rubbed carcasses are often avoided [61], carcass consumption by other species may be reduced. Also, predator carcasses may produce fear responses in scavengers that can be their prey [62]. Understanding the carcass marking and rubbing that contribute to the different aspects of landscape of fear may provide insights into the limiting effects of dominant consumption.

The extent of carcass consumption by dominant scavengers is often related to scavenging specialization (obligate and facultative), large body sizes associated with stomach capacity, and sociality such as whether they can consume large portions of carrion as a group [10,11]. Moreover, the intrinsic ability to detect carcasses and generalist traits (i.e., tolerance or preference for carrion and dietary flexibility) are likely relevant factors to identify dominant scavengers. For example, bears – for example, brown bears (*Ursus arctos*), American black bears (*Ursus americanus*), and Asiatic black bears – are dominant scavengers due to their large body size and preference for carrion [33,53,59,63], while *Corvus* spp. are also dominant scavengers due to their social behavior [64]. Dominant consumption influences scavenging patterns such as changing the time that other scavengers spend searching for carcasses and potentially intensifying interference competition over the limited available resources.

Carrion transporter

Carrion is often relocated and dispersed by **carrion transporters** (i.e., species moving carrion). For example, brown bears scavenge and selectively carry energy-rich body parts when salmon carcasses are abundant [65]. Also, some avian scavengers tend to carry carrion away from the feeding site [20]. These carcasses, which have been moved, can also be detected by other scavengers, providing scavenging opportunities to them. This effect becomes particularly important when the movement occurs across different spatial strata (e.g., from ground to canopy) or ecosystems (e.g., from grassland to forest). However, if carrion is brought to a nest or burrow, access for other scavengers is limited. Yet the effects of moving carrion have not been quantified due to the difficulty of tracking carcasses [38]. Investigating how much carrion is transported to different locations, and whether the distribution of this relocated carrion increases the overall diversity of the scavenger assemblage, would be useful in clarifying the role of carrion transporters. This is important to understand not only for species interactions but also because of the effect of nutrient movement (Box 1).

Carcass cacher

The storing and/or securing of carrion (i.e., caching) can have both facilitating and limiting effects on detection and consumption of carcasses by other scavengers. Many carnivores are **carcass cachers**, and accumulate the remains of large carcass kills (i.e., those too large to be consumed in one feeding), including leopard (*Panthera pardus*) [66], puma (*Puma concolor*) [67], American black bear and Asiatic black bear [68], Eurasian lynx (*Lynx lynx*) [69], and European wildcat (*Felis silvestris*) [70]. Methods of caching carcasses are diverse, including burying, covering with plant litter, hoisting into trees, and submerging underwater [66]. Cached carcasses have been posited to reduce **kleptoparasitism** through lowering the probability of carcass detection by competing invertebrate and vertebrate scavengers [66,70]. In contrast, some scavengers which use carrion from cached locations (e.g., burrow nests or arboreal sites) are provided with opportunities to consume carrion that was not available where the carrion was originally found. However, reports on caching behavior are limited, and the extent of its negative and positive effects are not yet well understood.

Concluding remarks

We have identified the main roles of vertebrate scavengers and established terms and definitions for these roles. The promotion and widespread adoption of these terms is crucial for advancing the international understanding of scavenger species' ecology and contribute to their conservation. Scavenging research has been steadily increasing in recent years [14], and this standardization is likely to help overcome language barriers for research (e.g., [71]). Considering that scavenger communities are strongly influenced by anthropogenic factors on a global scale [72], conservation efforts based on international analyses and cooperation are indispensable. In this context, unified definitions will drive the global research forward – while expanding these definitions across multiple languages would likely be an effective next step.

Identifying the role of scavengers and the interactions that drive them at the species level is also important. Here, we have shown the main actors driving the facilitative and competitive interactions that play a crucial role in scavenging dynamics and scavenger communities. Given the dynamic nature of each interaction (with shifts and intertwining according to the status of the relationship among individuals/species in the process of detection and consumption of a given carcass), further investigation of interactions and scavenger roles across different environments and carcass types is needed (see Outstanding questions). Furthermore, the case studies revealed that competitive and facilitative interactions are closely related to the role of scavengers (i.e., some interactions cannot occur in the absence of specific actors fulfilling a particular role). Advancements in high-quality motion-triggered cameras, GPS devices, and the deep-learning techniques that analyze the large amounts of both photo and video data obtained from these devices will enable behavioral information to promote an understanding of the main consequences of species interactions for scavenging dynamics [32,73]. In addition, field enclosure experiments that manipulate the presence or density of potential key species (i.e., species that play roles in the scavenger assemblage) will elucidate the causal consequences of species interactions. These fundamental studies should continue to be accumulated in order to establish the ecological roles of scavengers within biological communities.

Outstanding questions

Are there any other interactions driving the role of scavengers?

To what extent do frequent scavengers, main biomass consumers, and keystone scavengers overlap in their roles?

How are the interactions and behaviors driving species' roles related to each other?

To what extent can biotic, abiotic, and anthropogenic factors influencing the composition of the scavenger community alter the role of scavengers?

How does the loss of the roles of scavengers affect scavenging dynamics and its ecosystem functioning?

What are the ecological and functional consequences of carcass caching and carrion moving?

Acknowledgments

A.I. was supported partly by the Japan Society for the Promotion of Science KAKENHI grants (no. JP24K23917). A.I. and S.K. were also supported by the Institute of Global Innovation Research and University Research Administration Center in Tokyo University of Agriculture and Technology. M.L.A. was supported by the Illinois Natural History Survey and University of Illinois. E.S.G. received the grants RYC2019-027216-I and CNS2023-144791 funded by the Spanish Ministry of Science, Innovation and Universities (MCIN/AEI/ 10.13039/501100011033) and by ESF Investing in your future.

Declaration of interests

The authors declare no competing interests.

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