Opinion

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Scavenging: how carnivores and carrion structure communities

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Recent advances in the ecology of food webs underscore the importance of detritus and indirect predator–prey effects. However, most research considers detritus as an invariable pool and predation as the only interaction between carnivores and prey. Carrion consumption, scavenging, is a type of detrital feeding that should have widespread consequences for the structure and stability of food webs. Providing access to high-quality resources, facultative scavenging is a ubiquitous and phylogenetically widespread strategy. In this review, we argue that scavenging is underestimated by 16-fold in food-web research, producing inflated predation rates and underestimated indirect effects. Furthermore, more energy is generally transferred per link via scavenging than predation. Thus, future food-web research should consider scavenging, especially in light of how major global changes can affect scavengers.

The importance of detritus and detrital quality in the ecology of food webs

In community ecology, the importance of detritus and detrital linkages in food webs has recently gained broad recognition [1] alongside the more classically studied grazer world [2]. Research has deconstructed the simple food chains [3] of grazer systems to demonstrate that detritus is a widely used and crucial resource across ecosystems [4–6]. In particular, including detritus in food-web theory has resolved apparent paradoxes [7] and highlighted its role as a critical stabilizing force [8] controlling trophic dynamics in many systems [4,9].

Despite increased recognition, detritus is, in general, treated as single resource pool [10], an assumption that ignores extreme variation in detrital quality. The importance of detrital quality is evident, however, at the community and ecosystem levels. Within communities, dead plant material can affect trophic structure and cascading interactions between species [11], whereas detritus is tied to key services such as decomposition and nutrient cycling within ecosystems [12]. Treating detritus as multiple resource pools would be more appropriate because detritus spans the full range of quality present in a food web, from low-quality dead plant matter to high-quality carrion, or dead animal tissue [1].

Because of the high quality of carrion, its consumption, scavenging, is generally rapid [13] and widespread; multispecies scavenger guilds dominate the carnivore trophic level in many ecosystems. We use the term ‘scavenger’ to represent obligate and facultative scavengers with the acknowledgement that most scavengers are also predators and hence facultative [14–17]. Food-web ecology has yet to consistently recognize this type of detrital feeding as an important and distinct component of food webs. Uniquely, scavenging allows access to excellent food resources with no additional prey death and without the consumer

Glossary

Apparent competition: a food-web event in which two or more co-occurring prey populations share a common predator and thus experience linked population dynamics via greater predation pressure than they would if the predator fed on only one of the prey.
Assimilation efficiency: the proportion of a prey item ingested by a consumer that is not lost to sloppy feeding or egestion (values range from 0 to 1).
Autotrophs: the basal trophic level of the ‘green’ or grazing world composed of organisms that can make their own food (usually using sunlight).
Carrion: a high-quality form of detritus that is composed entirely of dead animal matter.
Connectance: a description of how many of all possible links in a food web are present. This usually involves the number of links present in a web divided by some metric of the number of taxa present in a web.
Detritus: the basal trophic level of the decomposer world. This is composed of debris or dead organic material. The quality of detritus covers a very large range: from the very low quality (i.e. high ratio of carbon:nitrogen or carbon:phosphorous) of dead and decaying plant materials to the high quality of carrion.
Donor-control: regulation of consumers by the abundance of their food resource.
Food web link: a feeding relationship through which energy and nutrients are transferred from one species to another.
Interaction strength: the *per-capita* effect of one species in a trophic relationship on another species.
Multi-channel feeding: consuming food items from the detrital and grazing (living autotroph-based) webs [26].
Predation: killing and subsequently consuming animal matter.
Production efficiency: the proportion of an assimilated prey item that is ultimately incorporated into new tissue via growth or reproduction (values range from 0 to 1).
Scavenger: organism that consumes carrion exclusively (obligate scavenger) or opportunistically (facultative scavenger); facultative scavengers are also predators and are more common.
Sloppy feeding: prey contents released into the environment during consumption.
Top–down control: dynamic regulation of prey populations via feeding by their predators.

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exerting energy to chase or subdue its prey. Thus, scavenging represents a significant form of energy transfer between trophic levels distinct from the predation, parasitism and disease that are more commonly considered in theoretical and empirical studies. Here, we propose a new framework for improving food-web analyses by including scavenging. We outline how scavenging fits into food-web theory, assess its prevalence across ecosystems and taxa, and suggest how the ecological importance of scavenging might shift with the current trajectory of major global changes.

Role of scavengers in food-web theory

Scavenging combines key facets of food webs that have been traditionally overlooked: the lack of a predation event [18], as well as the importance of detritus and its varying quality [1]. Classical food-web theory has focused on simple chains composed of plants, herbivores and predators [2], where carnivore feeding generally leads to prey death [19]. However, theory is beginning to recognize that feeding need not kill prey to have widespread effects on web dynamics [18,20,21]. Indeed, food webs are built upon and stabilized by most species being involved in multiple links, with recent evidence suggesting that ties to detritus could be acutely important to system stability [22].

Scavenging and the stability of food webs

Through detrital infusion to predators, facultative scavenging represents a type of multi-channel feeding [23], which recent theory suggests would make it an important stabilizing force in many food webs [8]. For maximum stability, multi-channel feeding should occur high in webs [8], as scavenging does. Furthermore, because scavengers feed on multiple prey species, they make webs more reticulate, which can stabilize food webs [20]. Thus, the type and number of feeding links involving scavengers should provide a stabilizing force in the complex webs of most ecosystems.

Additionally, scavenging provides predators with a dynamic connection to the detrital channel. Most models that include grazing and detrital webs only link predators with the detrital channel via nutrient cycling [3]. This dampens the ability of predators to strongly affect detrital webs and nutrient cycling. Models that include scavenging should incorporate nutrient cycling, acknowledging the effects of scavengers on available nutrient and detrital pools through excretion and sloppy feeding, respectively (the two additional components of predation generally included in nutrient cycling models [3]), and the ability of scavengers to affect the detrital pool by feeding upon it. Such models produce complex dynamics because nutrient cycling, which is dependent upon the size and quality of the detrital pool, will be tied to plant uptake by the grazing channel and to feeding on the detrital channel. This allows facultative scavengers to engage in a distinctive form of apparent competition [24] in which their living prey might be affected by the size of the detrital pool and *vice versa*. Apparent competition is generally considered to destabilize food webs [24], but we know of no studies that have examined its effect when feeding is tied to nutrient cycling, which conversely can stabilize webs [3].

Carrion and detrital quality

Modeling approaches can provide insight into how the high quality of carrion as a detrital resource affects the role of scavenging in the structure and stability of food webs. Community ecologists generally conceptualize detritus as a invariable low-quality pool because standing detrital stocks in most ecosystems are composed primarily of dead plant matter, relatively low-quality detrital material that is the slowest to decay [25,26]. Carrion, however, is generally consumed rapidly with competition for the resource high among microbes [27], scavengers, and often (in systems with speciose scavenger and predator guilds) the original predator of the carrion [28].

Although the high quality of carrion could affect the stability of food webs in several ways, one important effect could be via consumption efficiency. The stoichiometric quality of carrion is similar to that of tissue of scavengers, so carrion should be assimilated and processed efficiently by consumers. In contrast to modeling approaches that conceptualize detritus as a single, primarily plant-based pool, production and especially assimilation efficiencies should be much higher on carrion (0.30 vs 0.38, and 0.30 vs 0.83, respectively, see supplementary material online and [29] for further details). Such high assimilation efficiencies would: (1) retain more carrion-derived nutrients in the consumer versus detrital pool; and (2) increase consumers' population growth rates, accelerating the numerical response of the consumers and thus their ability to control prey populations, which should in turn stabilize food webs. Thus, models including scavengers should incorporate the high quality of carrion by considering how varying assimilation efficiencies affect the structure, stability and nutrient cycling of food webs.

Temporal and spatial patchiness of carrion

In many systems, carrion is available episodically as a pulsed resource [5]. For example, in the Serengeti, wildebeest carcasses, a major food resource for scavengers, are highly variable on intra- and inter-annual scales: 64% of deaths (and hence carcasses) occur in the 4-month dry season, whereas longer-term shifts in wildebeest forage also lead to changes in carcass number by up to 50% [30]. Such temporal variation could lead to carrion playing a dynamic part in the stability of food webs [31] in these systems. Additionally, carrion varies across space, and thus could be a structuring force underlying the movement and spatial distribution of scavengers [17,32,33].

Interaction strengths: predation versus scavenging

Scavenging has important consequences for interaction strengths in food webs because it does not directly cause demographic changes in populations of consumed taxa (Figure 1). Carrion is a donor-controlled resource and thus scavenging results in qualitatively different effects on the consumed taxa than predation [34]. Obligate scavengers do not cause tissue death, so they have no direct demographic impact on carrion species (although they could have indirect effects) [28]. Furthermore, facultative scavengers have no direct effect on taxa they consume as carrion, although they will have a direct negative impact on prey taxa that they consume via predation (Figure 1). In food-web

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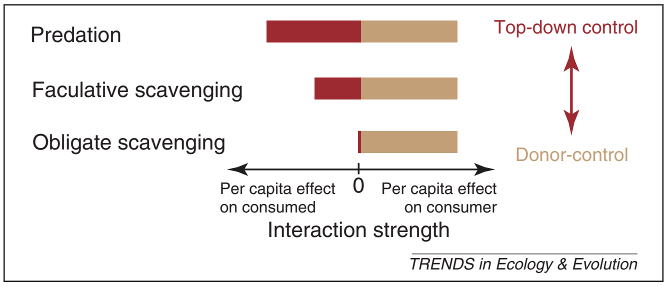

Figure 1. Conceptual diagram depicting potential differences in relative interaction strengths among forms of predation and scavenging. All predators and scavengers benefit from consumption. However, scavenging does not result in dynamic top–down control of prey populations as predation does. Thus, the *per-capita* effects on consumed taxa are highest when preyed upon and lowest when scavenged as carcasses. Facultative scavengers, which act as predators and scavengers, have an intermediate effect on consumed taxa.

analyses, grouping scavengers with predators would lead to an overestimation of interaction strengths [16].

Prevalence of scavenging in empirical webs

The risks associated with ignoring or underestimating scavenging are dependent upon its prevalence in real food webs. Scavenging is a phylogenetically widespread foraging strategy of invertebrates and vertebrates (Table S1), including such well-studied groups as ants, birds, crabs, fish and wolves. Despite this, representation of scavenging in empirical webs might be low because most scavengers are facultative and often only their predation links are represented [15–17]. Connections in food webs are most often derived from inferences of consumption because of the logistical difficulty of observing actual predation events. Thus, ecologists often utilize indirect approaches (such as molecular analyses or isotopic analyses) which identify only that a prey has been eaten but not whether it was killed or scavenged [35]. If most food webs underappreciate scavenging, they might inaccurately assess predator–prey interactions [35], energy flow [15], and important food-web metrics.

Scavenging is underestimated across ecosystems

To quantify scavenging prevalence across systems and how it affects food webs, we examined 23 food webs (Table S2) which have been commonly used in food-web studies over the past decade [36]. We identified all scavenging and predatory links as well as potential scavenging links, defined generally as a carnivory link by a taxa known to scavenge (full details of link assignment are given in the supplementary material online).

We found that most webs classified 83–100% of carnivory as predation; seven of the 23 food webs analyzed (spanning all ecosystem types) originally lacked scavenging links, despite the fact that all webs contained taxa known to opportunistically scavenge. Such high prevalence of predacious carnivory results from the absence of obligate scavengers or no explicit mention of carrion in the original datasets. However, the lack of scavengers could ultimately be owing to the historical omission of detrital channels in food-web ecology and lumping of all detritus into a single pool [1]. Of the 23 well-studied webs in our sample, three webs did not contain a detrital pool, 12 had a single detrital

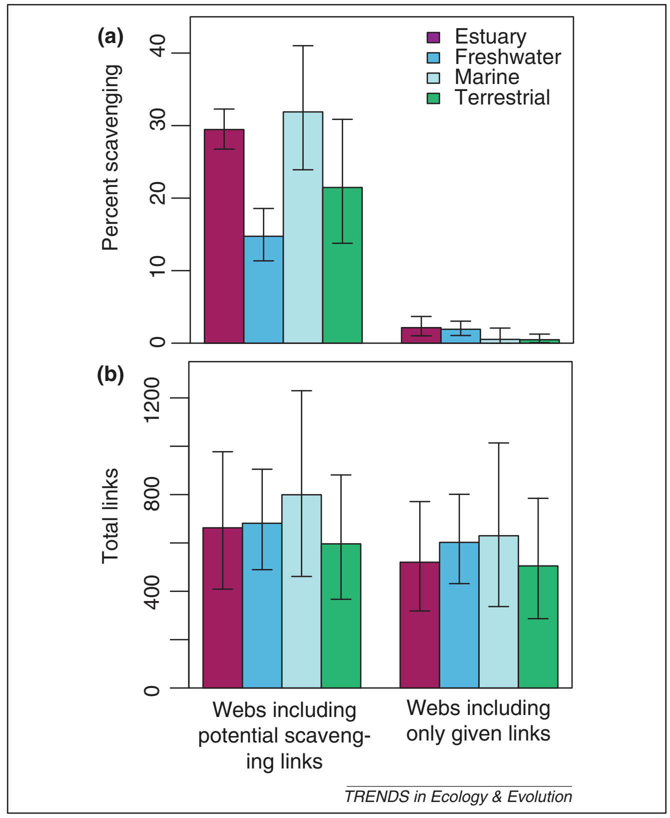

Figure 2. In an analysis of 23 commonly-studied food webs, including all potential scavenging links greatly increased the percent of all links that were scavenging links (**a**: $F_{1,\ 20} = 61.35$, $p < 0.0001$) consistently across systems (Table S3), but the increase was not driven by total links (**b**: $F_{1,\ 20} = 2.38$, $p = 0.14$).

pool, whereas only five distinguished carrion from other dead organic material.

Adjusting the webs to include scavenging links showed webs underestimated scavenging 16-fold (mean percentage of links that represented scavenging increased from 1.4% to 22%, Figure 2). The prevalence of estimated scavenging in webs was not affected by the total links of webs, suggesting webs of varying resolution were similar in their amount of estimated scavenging (Figure 2, Table S3). However, including scavenging also affected important food-web metrics; the mean number of links per species increased by 22% and web connectance increased by 26%, with no effect of system or original inclusion of detritus (Table S3). Overall, we found that scavenging can be involved in up to 45% of food-web links, suggesting that facultative scavengers exert strong influences on food webs.

Additionally, we found the strength of reported scavenging links to be strong. In the 10 webs that included estimates of energy flow (amount of carbon or other metric transferred from prey to consumer), we found that a minimum of 124-fold more energy was transferred per scavenging link than was transferred per predation link (see supplementary material online for details). These assessments correspond with species-specific estimates of scavenging flows, which demonstrate that locally important facultative scavengers such as sleeper sharks [37], coyotes [38] and arctic foxes [39] can derive more than half their diets from carrion. Unfortunately, system-wide (or even single trophic level) food-web estimates of carrion flows are absent from the literature. However, if the flow of energy via carrion is as large as our initial analyses suggest, incorrectly assuming that all carnivorous links represent predation could lead to underestimation of energy flow into the higher trophic levels and overestimation of the energy flow into the detrital food web. Including the links and strength of scavengers in webs in future research would advance how we understand the structure and stability of food webs in real ecosystems.

Scavenging responses to global change

Understanding how global change will affect food webs has been an important area of recent research that has focused distinctly on the grazer world. However, many predictions such as the mismatched timing of consumers and prey [40], and changing weather extremes, [41] including drought [42] – forecast pulses of animal death and thus carrion availability. Because scavengers are often generalists, they should be able to exploit such pulses and scavenging could become more prevalent [43].

However, such increases in carrion and scavengers might be only transient. Global changes such as the increasing harvest of animals could lead to simpler food webs. A future equilibrium for many systems could include fundamentally lower animal, and hence carrion, biomass, with equally reduced scavenger guilds. Here we briefly discuss how biological invasions, disease transmission and biodiversity decline, particularly of top predators, can affect carrion availability and the associated rates of scavenging in the short- and long-term.

Invasions influence scavenging rates and carrion availability

Species introductions can alter the prevalence of scavenging in an ecosystem in several ways. Scavenging by the invader can reduce carrion and cause native scavengers to shift their diets [43], or population crashes of invaders after initial booms can increase carrion availability for other species (at least temporarily) [44,45]. Opportunistic scavenging by invasive species can also contribute to the invasion success by supplementing the diet of the invader with carrion. For example, generalists make good invasive species [43]: of the 56 animals on the 100 Worst Invasive Species list, 64% are predatory generalists and 75% of these opportunistically scavenge [44]. Scavenging could have promoted the invasion of the western yellowjacket in Hawaii (Box 1); similarly, the prolific scavenging habits of rats can make them especially successful island invaders [45]. Furthermore, synergistic interactions of multiple invaders can result from high population densities of one invader providing carrion to promote the success of another. Such knock-on effects have been suspected on islands upon which rabbits and rats have been introduced [45]. Moreover, as climate change alters species ranges, generalists such as scavengers might respond most successfully to community changes after the range expansions of other species and to subsequent disruptions in trophic interactions [46]. Alternatively, scavengers might themselves be most likely to extend their ranges and become 'native invaders'.

Indirect effects of climate change on rates of scavenging: implications for top–down controls

Climate change might have cascading consequences for scavengers via alterations in the patterns and prevalence of disease [47–49]. In many ecosystems, diseases provide major top–down control of animal populations [18]. Death from disease, especially epidemics [50], can produce large short-term pulses of carrion into systems [51], providing a crucial resource base for diverse populations of scavengers [52].

Furthermore, climate change, disease and predator abundance often interact strongly to influence the spatial and temporal patterning of carrion resources in ecosystems [52,53]. Because predators can regulate their prey populations, predator declines can shift systems from top–down to bottom–up control [53]. Such predator release can lead to rapid growth of prey populations, which are then at risk of disease epidemics and associated mass mortality. For example, populations of sea urchins off the California coast in the USA exponentially increased after the over-harvesting of their main predator – spiny lobsters [50]. Sea urchins then experienced widespread die-off after an epidemic in high-density populations and provided mass inputs of urchin carrion [50]. This suggests that predators might be important in buffering prey populations from rapid changes in population size. Thus, long-term maintenance of carrion and scavengers could be dependent upon maintaining healthy populations of predators.

Evidence that predators also mitigate the effects of climate change on scavengers further supports this hypothesis. In a well-studied case, re-introduction of the gray wolf to Yellowstone National Park (USA) [54] altered the supply and availability of carrion [55] with cascading effects on the scavenger community (Box 1). Re-introduction of top predators can also increase scavenging by causing a diet switch of established predators. For example, after a wolf re-colonization event in Norway, resident wolverines shifted their diet to rely more heavily upon scavenged wolf kills, and reduced their consumption of wolverine-predated prey by up to half [56].

Anthropogenic effects on carrion supply and lag effects

In addition to how disease, decline of top predators and invasions regulate natural sources of carrion, numerous direct anthropogenic forces affect carrion influxes [8]. Many types of commercial harvesting of top predators produce carrion as a byproduct that is generally left in the ecosystem. For example, marine fisheries have extremely high bycatch [57], resulting in millions of metric tons of carrion added to ocean ecosystems annually [58]. Additionally, harvests that collect only part of animals, such as shark-fin fisheries and elk hunting, leave the remaining biomass for scavengers [32,59]. In such ways, human activities could directly increase carrion supply and hence the prevalence of scavenging.

Indirect anthropogenic effects, however, could ultimately reduce carrion and scavenging guilds. Carrion associated with harvesting healthy individuals initially benefits

Box 1. The role and prevalence of scavenging could shift dramatically with global change

Here we review two well-documented cases demonstrating how scavenging can influence invasion and the community-level effects of climate change.

Case study: yellowjacket invasion in Hawaii, USA

The invasion of non-native *Vespula pensylvanica* yellowjackets in the Hawaiian Islands provides one example of how scavenging can play a part in 'invasional meltdown', in which interactions between two non-native species (yellowjackets and honey bees) facilitate invasion success and increase their impacts. Honey bees, introduced for their pollination services, produce tens of thousands of kilograms of dead biomass annually in Hawaii – providing an abundant supply of insect carrion. A generalist predator and scavenger, *V. pensylvanica* [62], feeds heavily on honey bees, which it depredates (60% of the time) and scavenges (40%) [63]. Diet subsidies in the form of carrion could facilitate growth of the yellowjacket population, thus increasing their ability to suppress prey and competitor species and magnifying the effects on native species, such as solitary *Hylaeus* bees (Figure Ia). Given the role of *Hylaeus* as native pollinators [64], strong predation could have cascading effects on native plant pollination regimes (Figure Ia).

Case study: wolves return to Yellowstone National Park (USA)

In Yellowstone National Park, the interaction between predators and climate can be important for buffering diverse scavenger populations from the effects of climate change. In the decades before wolf re-introduction, a suite of 13 (mostly facultative) scavenger species, including eagles, coyotes, and grizzly bears, relied upon the winter-induced mortality of elk and other vertebrates for crucial carrion resources (Figure Ib) [65]. However, as climate change produced milder winters, carrion resources declined in the late-winter months (Figure Ib) [55] because winter mortality in elk was largely dependent upon snow depth, a variable that decreases with warmer winter temperatures [66]. After re-introduction, wolves increased carrion by preying upon large ungulates throughout the year [65], producing a consistent influx of carrion in winter months regardless of winter severity (Figure 1b). The largest increases (35–66%) in carrion influx due to wolf predation, however, occurred during mild winters [65].

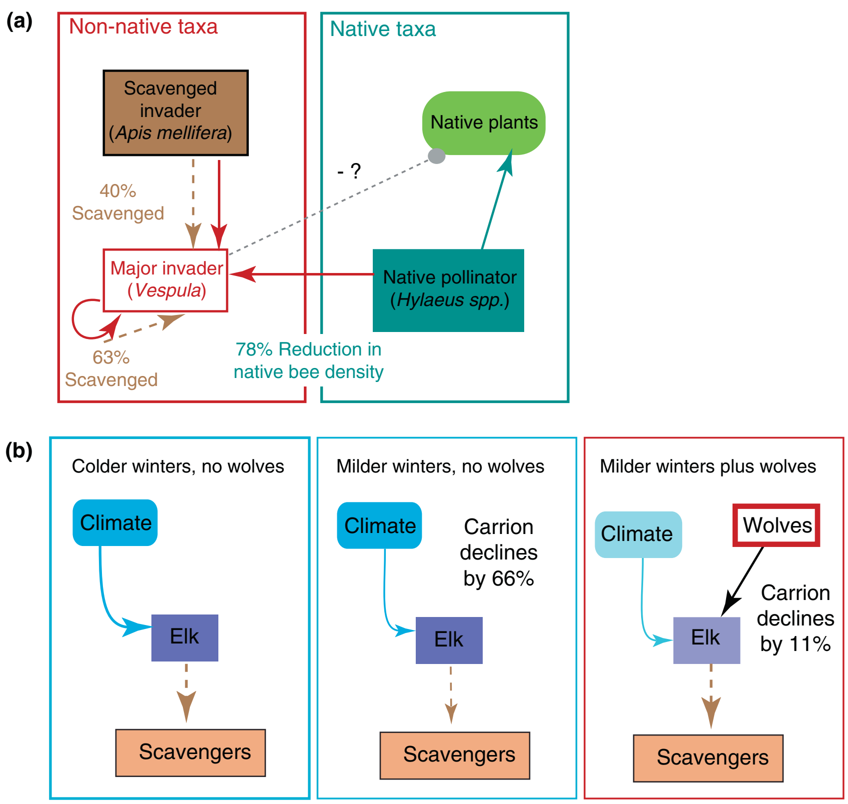

Figure I. Scavenging can modify the effects of invasion and climate change. Arrows indicate the direction of effects, and line thickness shows the relative effect size. Solid lines indicate predation and dashed lines scavenging. Indirect effects are represented by dashed-lines ending in circles. Blue lines represent climate effects in **(b)**.

scavengers, but it comes at a lagged cost to scavengers. Because harvesting removes biomass and nutrients from the system, it reduces the number of reproducing prey, thus fundamentally changing systems. As humans 'fish down the food web' [60], they create harvested webs that are simpler, less stable and which provide fewer resources [61]. Moreover, harvesting continually removes the highest-quality biomass, decreasing the quality of naturally occurring carrion in systems. Such food-web effects, combined with evidence from the indirect effects of top predators on disease spread and consistency of carrion, suggests that the long-term effects of human-associated global changes should reduce scavenger populations.

Conclusions

By uniting advances in the evolving paradigm of food webs, combining the roles of non-classical consumer–prey interactions, detritus, and multi-channel feeding, scavenging should be an important component of modern food-web ecology. Greater inclusion of scavenging in theoretical and empirical studies would foster a more integrated understanding of how complex web dynamics interact. Future theoretical studies that incorporate the roles of carrion as a high-quality detrital resource for scavengers and a path for nutrient cycling could then tease apart how such interactions collectively alter the structure of food webs. In empirical studies, more reticulate, complex webs that better estimate the prevalence of scavenging across and within ecosystems can be achieved by including feeding links in webs resulting from scavenging and all non-classical predation events (e.g. disease and parasitism). Because of important effects on trophic pathways within food webs and cascading effects on system stability, the role and prevalence of scavenging in real and modeled webs could become increasingly important for predicting future community structure and dynamics.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.tree.2010.12.011.

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