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Opinion

Global change influences scavenging and carrion decomposition

Savannah L. Bartel [1,2,*] Torrey Stephenson,[3] David W. Crowder,[1] Menna E. Jones,[4] Andrew Storfer,[2] Michael S. Strickland,[3] and Laurel Lynch[3]

Carrion decomposition is fundamental to nutrient cycling in terrestrial ecosystems because it provides a high-quality resource to diverse organisms. A conceptual framework incorporating all phases of carrion decomposition with the full community of scavengers is needed to predict the effects of global change on core ecosystem processes. Because global change can differentially impact scavenger guilds and rates of carrion decomposition, our framework explicitly incorporates complex interactions among microbial, invertebrate, and vertebrate scavenger communities across three distinct phases of carcass decomposition. We hypothesize that carrion decomposition rates will be the most impacted when global change affects carcass discovery rates and the foraging behavior of competing scavenger guilds.

Highlights

Carrion decomposition is critical for the cycling of nutrients within ecosystems.

Carrion is a high-quality resource for a broad diversity of organisms and can be a central arena for competition and facilitation among microbial, invertebrate, and vertebrate consumers. Hence, understanding the factors that affect the trajectory of carrion decomposition enhances broader knowledge of how interkingdom and interspecies interactions shape both communities and ecosystems.

Human activities are drastically modifying carrion availability, scavenger communities, and the environmental context in which decomposition takes place. This necessitates a new framework to capture complex decomposition processes.

We propose an interdisciplinary framework to guide predictions of how global change will affect carrion decomposition, nutrient cycling, and ecosystem function in the Anthropocene.

An integrative perspective for carrion decomposition

An animal's death activates **carrion decomposition** (see Glossary), providing energy and nutrient resources to a broad diversity of scavengers [1–4]. By creating localized biodiversity hotspots, carrion drives interkingdom competition and facilitation and mediates nutrient cycling [1,3–5]. The speed of carrion decomposition is variable, ranging from 2 h to 82 days (see the supplemental information online). Scavenger communities are affected by global change factors, especially climate and land-use change, and species introductions, that alter carrion availability [6–9], scavenger community diversity [10–13], and the context in which decomposition occurs [14–18]. Decomposition involves action by microbes, invertebrates, and vertebrates (i.e., the **necrobiome** [1]), and the occurrence and foraging efficiency of these organisms are affected by the environment. Understanding how global change affects decomposition therefore requires an interdisciplinary perspective that scales from microbes to vertebrates and integrates animal behavior with population, community, and ecosystem ecology. While distinct carrion decomposition stages have been described for invertebrates and microbes [19–21], the participation of vertebrate scavengers is not integrated into these frameworks. Similarly, while the necrobiome framework describes how microbes, invertebrates, and vertebrates shape decomposition [1], it lacks detail on **scavenging** behavior and global change factors.

Here we present a framework that captures alternate pathways of terrestrial carrion decomposition and accounts for scavenger behavior across three phases of decomposition (i.e., discovery, consumption, and nutrient delivery). We outline environmental factors, and their sensitivity to human-induced change, that govern carrion decomposition across each phase. Finally, we suggest how our framework can generate testable predictions of how global change and scavenger behavior alter carrion decomposition and nutrient cycling in the Anthropocene.

Effects of global change across phases of carrion decomposition

Phase 0: carcass production

Recent estimates indicate that the total biomass of domestic mammals [630 metric tons (Mt)] far outweighs that of wild mammals (20 Mt) [22]. Within wild populations, large carcasses account for

[1]Department of Entomology, Washington State University, 166 FSHN, 100 Dairy Road, Pullman, WA 99164, USA
[2]School of Biological Sciences, Washington State University, 301 Abelson Hall, Pullman, WA 99164, USA
[3]Department of Soil and Water Systems, University of Idaho, 875 Perimeter Drive, Moscow, ID 83844, USA
[4]School of Natural Sciences, University of Tasmania, Life Sciences Building, Hobart, TAS 7001, Australia

*Correspondence:
savannah.bartel@wsu.edu (S.L. Bartel).

most vertebrate carrion (globally, seven of the top ten contributors are even-hoofed mammals) [22]. While carrion production (Figure 1) is unpredictable in populations where most animals die randomly of individual causes such as predation, it may be predictably pulsed where many animals die during a specific season or mass mortality event [6,23,24]. While most mass mortality events are associated with disease, human perturbation, or biotoxicity [8], their effects can ripple through ecosystems [7,25]. For example, when 2700 kg of feral pig (*Sus scrofa*) carcasses were used to simulate a mass mortality event, increases in consumer diversity altered the food web structure [7]. Extreme weather is also predicted to increase the frequency of mass mortality events in populations ranging from insects and fish to large vertebrates, making the functional role of scavengers increasingly important [26].

Other global change factors may alter spatiotemporal patterns in carrion production, particularly for large carcasses (Table 1). For example, ungulate carrions produced by livestock, roadkill, and hunting are more spatially concentrated than carrion produced by natural sources (e.g., predation, disease) [27]. The global decline of apex predator populations may also affect spatiotemporal patterns of carrion production because predation is a key source of mortality for many animals [11,28–30]. We expect predator declines will reduce spatial and diel concentrations of carrion because predators mediate when and where carrion is produced [29,31]. For example, in systems where carrion production peaks during winter, warmer winters may reduce the production of this resource to scavengers, but apex predators could buffer these effects by producing carrions throughout the winter that subsidizes scavenger communities [16]. We expect predator declines will increase the pulsed nature of carrion availability, particularly when prey are vulnerable to disease or resource limitation [32].

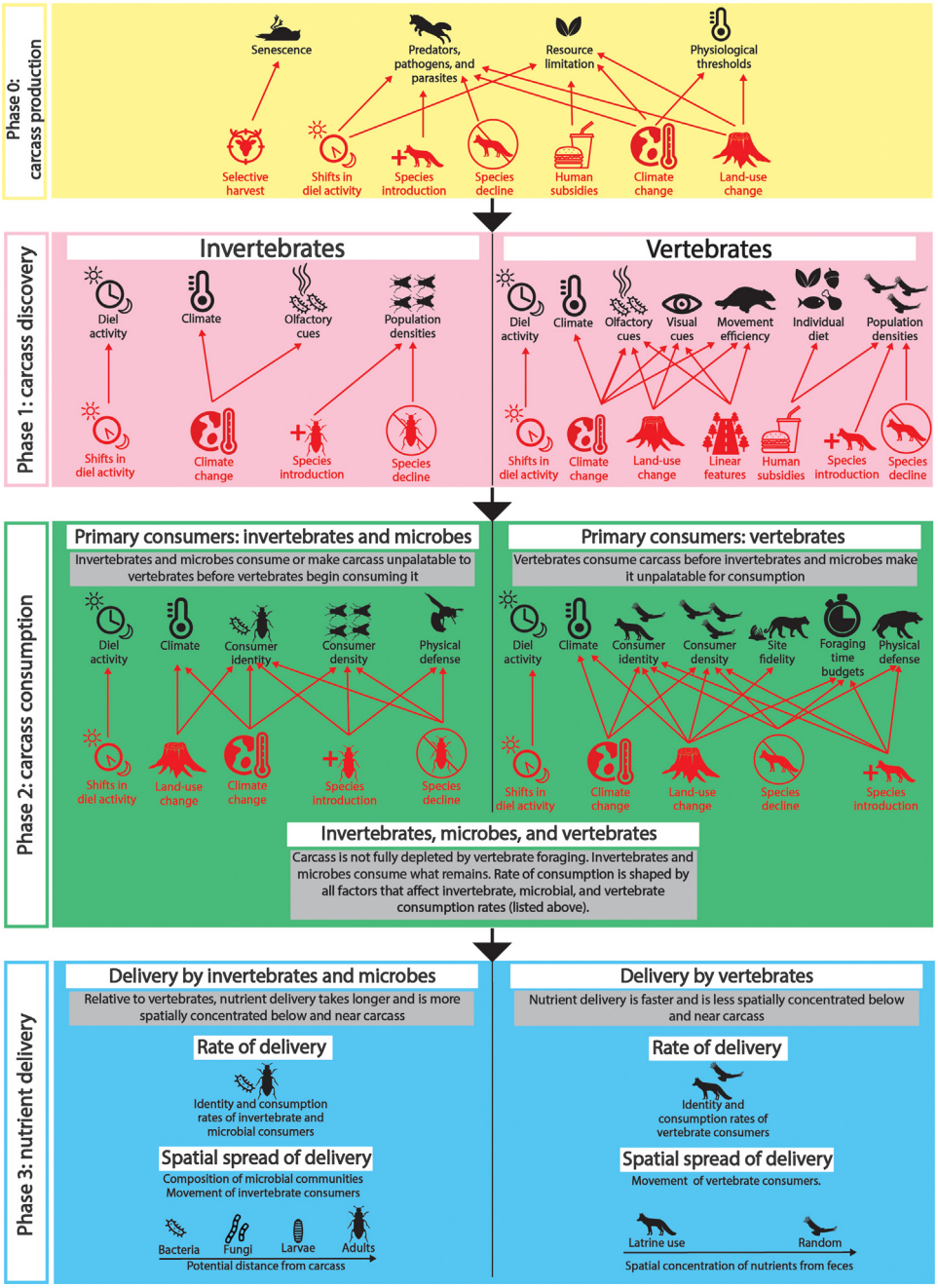
Phase 1: carcass discovery

Changes in carrion availability alter scavenger–resource encounter rates, the ability of scavengers to track carrion [7,23,32,33], and species pools [21]. These factors, along with environmental conditions [11,19], determine how quickly carrion is discovered (Figure 1). For instance, priority effects shape competition among scavengers [11,34–36] (e.g., carcasses that are rapidly discovered by vertebrates may be consumed before invertebrates initiate feeding). Similarly, some species defend carcasses against other scavengers – such as European wasps (*Vespula germanica*) that aggressively exclude flies and dingoes (*Canis lupus dingo*) (Box 1 and Table 1) – while microbial decomposers chemically modify carcasses in ways that may make them unpalatable for animal consumption [37,38]. As a result, environmental conditions that increase microbial activity [39,40] could promote carcass monopolization by microbes [38] (Table 1). While global change factors (e.g., land-use and climate change, species introductions [12–14,41,42]) directly affect scavenging species pools and carcass discovery rates (Figure 1 and Table 1), shifts in the diel activity periods of scavengers in response to humans [39,40] could also alter carcass discovery (Table 1). Human disturbance increases the nocturnality of large vertebrates [39], which may reduce the likelihood that vertebrates monopolize carrion produced in the daytime. Within vertebrate scavenging communities, apex predator declines can lengthen diel activity windows, increasing the probability of discovery by mesopredators [11].

Environmental and anthropogenic factors that affect the ability of vertebrate and invertebrate scavengers to detect olfactory and visual cues will also modulate carcass discovery rates (Table 1). For example, **volatile organic compounds (VOCs)** produced during decomposition [41,42] can serve as olfactory cues for carcass detection by scavengers at long distances [1,41,43–45]. Increases in precipitation due to climate change could inhibit carcass detection by dampening olfactory cues and increasing the dissolution and microbial uptake of volatile compounds [46,47]. By contrast, elevated temperatures could promote carcass detection by

Glossary

Biogeochemical hotspots: regions within the soil matrix with disproportionately high reaction rates and biogeochemical transformations of energy and/or nutrients.
Biological process rates: the speed at which biological processes, such as respiration and photosynthesis, occur. Abiotic factors (climate, temperature, moisture availability) and ecological interactions (competition, predation) influence process rates. Important necrobiome process rates are growth and respiration, exoenzyme synthesis and kinetics (e.g., V_{max}, the maximum velocity of an enzymatic reaction, and K_m, enzymatic substrate affinity), and microbial carbon use efficiencies (the amount of carbon in microbial biomass vs. substrate). Biological process rates indirectly govern other biogeochemical processes, including N cycling (ammonification, nitrification, denitrification, immobilization, N_2O production, and consumption) and soil properties (redox, pH, Fe oxidation and reduction, and mineral weathering).
Carrion decomposition: the process by which dead animal organic matter is broken down into smaller constituent parts by microbial, invertebrate, and vertebrate consumers.
Exploitation competition: the use of a shared resource by one individual or group reduces the amount available for other individuals or groups. Competition therefore occurs indirectly rather than through aggressive, physical interactions.
Interference competition: individuals or groups compete directly for resources through aggressive, physical interactions.
Landscapes of fear: the spatial variation in prey perception of predation risk.
Necrobiome: refers to the community of species associated with carcass decomposition (bacteria, fungi, nematodes, invertebrates, and vertebrates) and their interactions with the necromass, each other, and their ecosystem.
Scavenging: consumption of dead animal organic matter by animals (kingdom Animalia).
Volatile organic compounds (VOCs): a broad group of compounds that have high vapor pressure and evaporate at ambient temperature. VOCs are released during carcass decomposition, and a significant proportion of these



VOCs are byproducts of microbial metabolism. VOCs often produce odors and create olfactory cues for both invertebrates and vertebrate scavengers. While VOC profiles vary across the decomposition stage and necrobiome succession, common molecules include dimethyl disulfide, acetic acid, phenol, and indole.

Figure 1. Conceptual model synthesizing the phases of carrion decomposition and the most important factors (black icons) that shape carcass production (top yellow panel), discovery (pink panel), and consumption (green panel) rates by microbial, invertebrate, and vertebrate consumers. Icons in red represent common global change factors that can alter carcass production, discovery, or consumption rates. Red arrows describe which operating factors at each phase are affected by each global change factor. Carcass production (Phase 0) shapes the availability and predictability of carcasses for scavengers. Global change factors that affect spatiotemporal patterns in mortality will affect carcass production. Carcass discovery rates (Phase 1) can determine whether carcasses are primarily consumed by invertebrates or vertebrates. Global change factors that alter discovery rates can consequently alter consumer identity and

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increasing the emission of volatile compounds [42]. Visual cues are impacted by habitat structure (vegetative ground cover and canopy cover [14,44,48]), which shapes carcass visibility and may be affected by global change (Table 1). For example, carcass discovery by birds could be reduced by the spread of introduced shrubs that conceal carcasses [49], but reductions in canopy cover caused by deforestation or wildfire may increase carcass discovery (Table 1) [14]. Predicted declines in snow cover may have contrasting impacts on carcass discovery depending on the primary sensory modalities of scavengers (see Outstanding questions). As a result, environmental changes that modify the efficacy of different scavenging sensory modalities could shape species evolution in olfactory, visual, or auditory acuity.

Phase 2: carcass consumption

The identity and behavior of scavengers that consume carrion impact decomposition rates [45,50]. In general, large vertebrates consume carcasses more rapidly than invertebrates and microbes [51–53], whereas carcasses consumed by invertebrates and microbes decompose faster than those consumed by microbes alone [9,54,55] (Figure 1). Variation in body and group size among scavengers influences ecological interactions [1,11,45,56,57] and the probability that carcasses are monopolized by dominant scavengers (Table 1). Complex interactions among scavenger guilds are shaped by carcass size [58], how well scavengers track carcass availability [59], and the degree of temporal overlap among competitors [60]. Dominant scavengers can outcompete subordinate ones via two primary mechanisms. In **exploitation competition**, monopolization by dominant scavengers should yield the highest decomposition rates [11,61,62]. For example, Tasmanian devils (*Sarcophilus harrisii*) outcompete mesoscavengers through rapid carcass discovery and consumption. In Tasmania, the spread of a highly transmissible and lethal cancer has resulted in Tasmanian devil population crashes, leading to substantial decreases in carrion decomposition rates (Box 1, [11]). Elevated rates of decomposition could benefit wildlife conservation efforts, for example, by limiting the prevalence of disease-causing bacteria (e.g., *Mycobacterium bovis*) [2,63]. By contrast, with **interference competition**, monopolization could reduce carrion decomposition rates. For example, the physical defense of carcasses by European wasps reduces consumption by other scavengers, slowing overall decomposition (Box 1, [13]). In this case, carcass monopolization could reduce carrion availability for other scavengers [2,3,64] via competitive exclusion, potentially leading to population decline and a reduction in biodiversity. We hypothesize that the decline [11] or introduction [13,65] of competitively dominant scavengers will predictably alter carrion decomposition (Box 1) depending on the behaviors used to outcompete subordinates. Our framework predicts that global declines in dominant scavengers may increase carrion availability for mesoscavengers [11] and decrease natal dispersal, while relaxed interspecific competition could increase intraspecific competition and natal dispersal. In either case, altering dispersal patterns can affect gene flow, population genetic structure, and the evolutionary potential of scavenging subpopulations.

Scavengers can also facilitate carcass consumption by other species [66,67]. Carcass degradation by microbes often follows a successional trajectory whereby bacterial communities resemble the host microbiome during the initial stages of carrion decomposition, but increasingly resemble soil microbiomes as decay progresses [41]. During this ecological succession, the concentration and chemical diversity of VOCs increase, facilitating carrion detection by invertebrates and vertebrates. Ground-dwelling invertebrates, such as beetles and ants, can also facilitate microbial

carcass consumption rates. Carcass consumption rates (Phase 2) and the identity of carcass consumers determine the rate and spatial spread of nutrient delivery (blue panel). Hence, global change factors that alter rates of carcass discovery and consumption, and the identity of consumers can have cascading effects on spatiotemporal patterns in nutrient delivery (Phase 3).

Table 1. Predictions for how different global change factors will affect environmental variables operating at different phases of carrion decomposition

		Aspects of global change that affect environmental variables						
Operating factors	Environmental variables	Climate change	Shifts in diel activity	Species introduction or decline	Land-use change	Linear landscape features	Human subsidies	Selective harvest
Carcass production								
Senescence	Demographic structure							Selective harvest of age/stage groups alters demography
Predators, pathogens, and parasites	Presence/absence and population cycle of predators, pathogens, and parasites	Range expansion of predators, pathogens, and parasites	Temporal overlap with predators, pathogens, and parasites	Gain/loss of predators, pathogens, or parasites	Gain/loss of spatial refugia		Alternative resources for predators may reduce predation pressure	
Resource limitation	Availability of resources	Extreme weather events (e.g., drought) or changes in climate alter resource availability	Temporal overlap with resources/prey	Gain/loss of competitors or prey	Reduction or increase in land cover of habitat		Increased availability of resources	
Physiological thresholds	Daily and annual temperature and precipitation	Extreme weather events or seasonal shifts in temperature and/or precipitation						
Carcass discovery								
Temporal overlap of competing scavengers and carcass production	Climate, daily weather, and predation risk	Shifts in species phenology and length of daily activity windows	Shifts in temporal overlap with competitors and carcass production					
Olfactory cues from volatile organic compounds	Microbial activity, precipitation, and wind speed through the landscape	Microbial activity increases with temperature and precipitation			Increased airflow and wind speed in human-modified habitats, such as agricultural fields and tree plantations	Increased air flow and wind speed through linear features increase the spatial spread of volatile cues		
Scavenger population densities	Scavenger population cycles and spatiotemporal patterns in habitat use	Scavenger range expansions/ contractions due to climate		Gain/loss of scavenger population			Scavenger populations increase due to human subsidies	
Visual cues	Characteristics of habitat structure that shape carcass visibility: canopy cover and ground cover	Extreme weather events alter habitat structure (e.g., fire)		Introduced shrubs increase ground cover and decrease carcass visibility	Deforestation increases the visibility of carrion by decreasing canopy cover. Fire suppression decreases visibility by increasing canopy cover	Carcasses are more visible when located along linear features		

Table 1. (continued)

		Aspects of global change that affect environmental variables						
Operating factors	Environmental variables	Climate change	Shifts in diel activity	Species introduction or decline	Land-use change	Linear landscape features	Human subsidies	Selective harvest
Scavenger movement efficiency	Characteristics of habitat structure that impede movement: habitat complexity, vegetation cover, slope, snow depth, and woody debris. Landscape features that facilitate or impede movement: habitat edges, corridors, or impervious surfaces	Extreme weather events alter habitat structure and landscape composition. Increased temperatures and changes in precipitation alter snow depth			Scavengers may move more efficiently in habitats with less vegetative ground cover (e.g., fire-prone habitats and agricultural land)	Scavenger movement efficiency is higher along linear features		
Inclusion of carrion in individual diet	Availability of carrion versus alternative resources, competition, and degree of individual diet specialization in population	Shifting phenology of alternative resources					Scavengers include less carrion in their diets due to the availability of human subsidies	
Carcass consumption								
Temporal overlap of competing scavengers and carcass production	Climate, daily weather, and predation risk	Shifts in daily activity windows due to changes in daily temperature	Contraction or expansion of activity windows due to shifts in diel activity periods. Shifts in temporal overlap with competitors and carcass production		Human-modified habitats may have different microclimates than original habitat, thus altering the temporal niche of scavengers			
Consumer identity	Rate of discovery and competitive/facilitative interactions among scavengers	Climate-induced shifts in carcass discovery rates. Climate-induced shifts in microbial scavenger activity		Gain/loss of scavenger population	Changes in discovery rates caused by land-use change			
Consumer density	Scavenger population density and intraspecific competition or facilitation	Climate-induced shifts in scavenger population densities and microbial scavenger activity		Gain/loss of scavenger population	Scavengers may be more (or less) active in human-modified habitats			
Site fidelity	Predation risk, resource availability, and competitive interactions			Introduced predators may lead to subordinate scavengers abandoning carcasses sooner	Apex predators are more likely to abandon carcasses near human activity		Scavengers with alternative human-subsidized resources may be less likely to abandon carcasses sooner	

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Table 1. (continued)

		Aspects of global change that affect environmental variables						
Operating factors	Environmental variables	Climate change	Shifts in diel activity	Species introduction or decline	Land-use change	Linear landscape features	Human subsidies	Selective harvest
Foraging time budgets	Predation risk, resource availability, competitive interactions, and physiological thresholds			The decline of apex predators may lead to increased foraging time for subordinate scavengers. Predator introduction may have an inverse effect	Scavengers may spend less time foraging in habitats near human activity. Human-modified habitats may be perceived as more or less risky to attack by predators		Scavengers with alternative human-subsidized resources may spend less time foraging at carcasses	
Physical defense	The ability for individuals or groups to defend carcass against competitors			Gain/loss of scavenger population with physical-defense abilities				

decomposition by removing hide [43], while aerial invertebrates can influence carrion decomposition both directly (flesh consumption) and indirectly (flies laying eggs). While fly larvae rapidly convert carcass flesh into biomass, they also release organic matter and nutrients to the soil and increase internal carcass temperatures [68,69], which could simultaneously facilitate bacterial decomposition and deter vertebrate consumers by putrefying flesh [43]. Declines in the abundance and diversity of scavengers that facilitate carrion discovery could slow decomposition by constraining invertebrate and vertebrate consumers [50]. More work is needed to understand how shifts in microbial activity modulate competition among scavenger guilds (see Outstanding questions).

Scavenger foraging behavior, including the duration of foraging bouts and site fidelity, shapes carcass consumption and is directly affected by global change. Anthropogenic disturbance can generate **landscapes of fear** that alter the foraging behavior of large vertebrates [70,71]. For example, pumas (*Puma concolor*) forage less and are less likely to return to kill sites, near areas of high human activity [70,71], which may increase carcass consumption by subordinate scavengers. Furthermore, fear of apex predators increases the time mesoscavengers allocate to vigilance while foraging, reducing carrion consumption [11,72]. Predator declines may thus increase carrion consumption by mesoscavengers (Box 1), although it remains unclear whether these shifts in behavior alter rates of carrion decomposition and nutrient delivery.

Phase 3: nutrient delivery

Scavenger behavior determines rates of nutrient delivery from carrion to the ecosystem. In the absence of hide disruption, microbially mediated decomposition occurs within the carcass until the bloat and seepage stage, when nutrients are released belowground [73]. The influx of soluble organic matter into the soil could relieve nutrient constraints on microbial metabolism and plant growth. Production of nutrient-rich plant litter near carrion sites can also promote microbial growth and decomposition, enhancing carbon storage aboveground through greater net primary productivity and belowground via soil organic matter formation [29,74]. By contrast, vertebrate scavengers rapidly and diffusely deliver carrion-derived nutrients to ecosystems via the excretion

of waste [28], which could dampen localized **biogeochemical hotspots** under carcasses but support greater ecosystem function by increasing net primary productivity overall (Figure 1).

Preferential feeding by vertebrate versus invertebrate scavengers may also alter the delivery of key nutrients (see Outstanding questions). Animal bones contain minerals such as calcium and phosphorus that broadly constrain ecosystem productivity. In the absence of direct bone consumption, which requires behavioral and/or digestive specialization [75–77], large bones can persist from decades to millennia [78,79]. The decline of scavengers that can consume and digest large bones (e.g., Tasmanian devils; Box 1) could reduce the delivery of these nutrients to soils, with implications for plant productivity [80] and soil carbon sequestration [81].

The identity and behavior of scavengers determine the spatial spread of carrion-derived nutrients (Box 2), but few studies capture interactions among scavenging guilds [1,43]. When carrion is primarily decomposed by microbes and invertebrates, nutrients will be delivered directly below the carcass, creating biogeochemical hotspots [82,83]. Fungal decomposition may increase the spread of carcass-derived nutrients and bacterial communities via extensive hyphal networks [84]. By contrast, carrion consumption by invertebrates induces variable spatial patterns in nutrient delivery. During consumption, dipteran larvae excrete large amounts of ammonia as waste and deliver soluble nitrogen to the soil under a carcass [85], but after consumption, dispersing larvae carry large quantities of nutrients several meters from the carcass [86]. Adult flies and carrion beetles (Silphidae) can fly multiple kilometers from a carcass after consumption, dispersing nutrients across the landscape as frass and dead biomass [9,86], or concentrating nutrient delivery along wind and storm pathways [87]. Vertebrate scavenging could result in random nutrient dispersal up to several kilometers from the carcass, or induce biogeochemical hotspots if species concentrate their urine and feces in latrines. The extent of mammal movement is reduced in human-modified landscapes [88], so the delivery of nutrients by mammals may be spatially restricted in areas with a high human footprint. It thus remains an open question whether the activity of vertebrate or aerial invertebrate scavengers maximizes the spatial diffusion of

Box 1. Case studies of carcass decomposition in the Anthropocene

Apex predator and scavenger decline: Tasmanian devil (*S. harrisii*)

Within vertebrate scavenging communities, top predators can also be competitively dominant scavengers [12]. Top predator declines may therefore induce trophic cascades that alter the nature and rate of carrion decomposition. For example, the rapid decline of Tasmanian devil populations due to the emergence of a highly transmissible cancer is predicted to alter the nature and rate of carrion decomposition. A recent study found that carcasses persist three times longer in regions where devil populations have declined relative to regions with intact populations [11]. The activation of compensatory scavenging pathways following devil declines increased consumption by less efficient mesoscavengers [e.g., native quolls (*Dasyurus maculatus*) and ravens (*Corvus tasmanicus*)], invertebrates, and microbial communities [12]. We therefore predict that Tasmanian devil declines will reduce the rate and spatial spread of nutrient delivery across the landscape (Figure I). As devils are among the few carnivore species morphologically adapted to completely consume larger bones, their decline should also directly reduce the delivery of nutrients concentrated within bone material (i.e., calcium and phosphorus).

Species introduction: European wasp (*V. germanica*)

The European wasp is a generalist opportunistic insect that is native to Europe, northern Africa, and Asia and has been introduced to Australia, New Zealand, North America, and South America [14]. Recent experiments in the European wasp's introduced range in Australia suggest that they can detect fresh carcasses within minutes of deployment and may monopolize carrion by physically excluding native scavengers [13]. European wasps were reported to kill native adult blowflies (Calliphoridae) [13], eliminating fly larvae at carcasses monopolized by European wasps [13]. European wasps also reduced carcass consumption by native dingoes (*Canis dingo*) [13]. By preventing the establishment of larval masses on carcasses and consumption by large vertebrates, European wasps may thus reduce the rate of carrion consumption and nutrient delivery in their introduced ranges (Figure I), but the magnitude of these effects will depend on how they impact native scavenging communities.

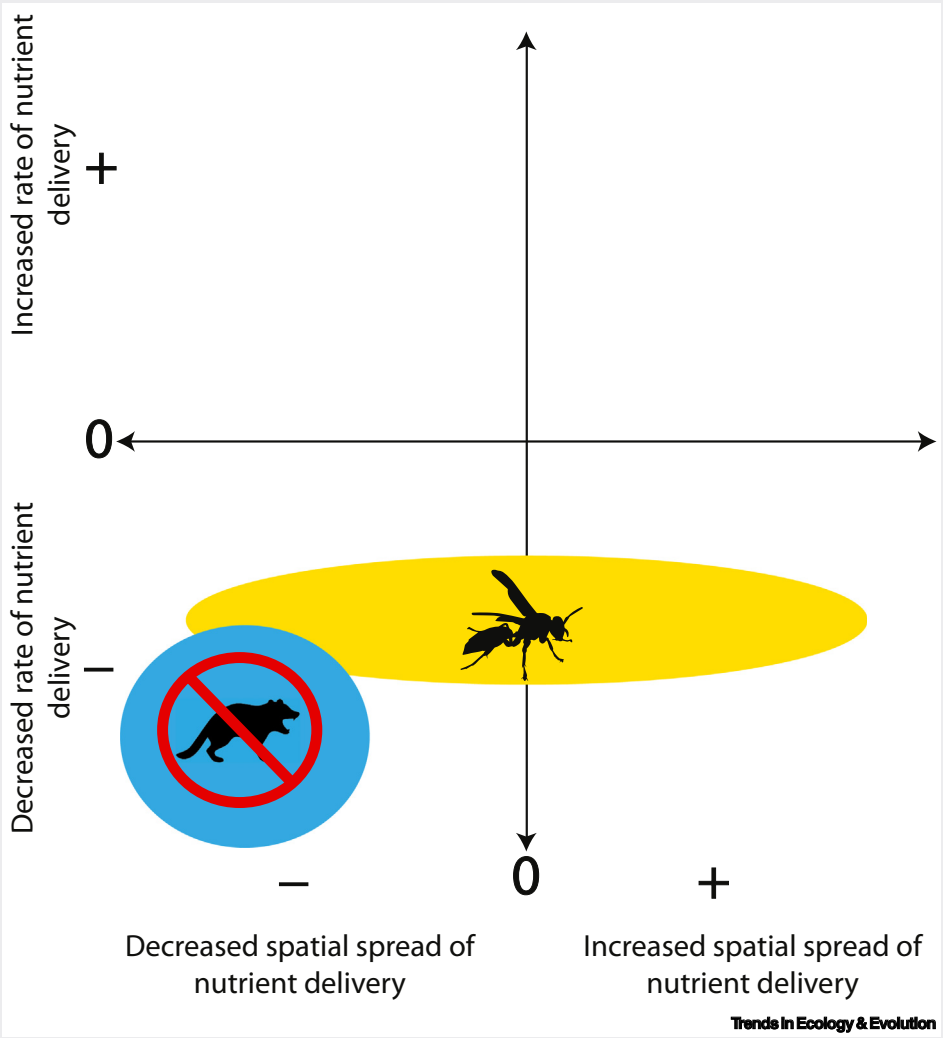

Figure I. Aspects of global change, including the decline or introduction of scavenging species can alter the rate and spatial spread of nutrient delivery within ecosystems. Each axis represents a dimension of nutrient delivery. The intersection of the axes represents baseline conditions in a system, in the absence of a given global change factor. Positive values (+) indicate that a global change factor leads to an increase in the rate (*y*-axis) or spatial spread (*x*-axis) of nutrient delivery. Ellipses illustrate the range of potential outcomes, which may be context dependent (e.g., broad ellipses represent more variability). We predict that the decline of Tasmanian devils (*Sarcophilus harrisii*; blue ellipsis) will lead to decreased decomposition rates and spatial delivery of nutrients. We predict the introduction of European wasps (*Vespula germanica*) will lead to decreased rates of nutrient delivery, but their effect on the spatial spread of nutrient delivery remains uncertain.

Outstanding questions

Microbial consumers can facilitate carcass discovery by invertebrates and vertebrates by producing VOCs, but they can also chemically modify flesh to make it unpalatable or unsafe. Will increased microbial consumption rates due to increases in temperature and precipitation enhance or impede consumption by invertebrates and vertebrates?

Since snow cover simultaneously affects visual and olfactory cues, will reduced snow cover favor carcass discovery by scavengers with strong visual acuity? How will such changes in cue strength mediate competition among scavengers, and will scavengers be able to adapt to these changing conditions through behavior or evolution?

Does preferential feeding depend on competition (i.e., do species only preferentially feed when in competitive environments)? What are the consequences for shifts in competitive interactions (e.g., the introduction of a new competitor) for preferential feeding and nutrient delivery belowground?

Biogeochemical hotspots under carcasses are typically rich in nitrogen, and nitrogen limitation is predicted to increasingly limit ecosystem productivity under global change. Will nitrogen limitation be alleviated in systems with high carcass inputs, and will this translate to substantial increases in ecosystem productivity?

How will global change affect aquatic carrion decomposition and the delivery of carrion-derived nutrients to both aquatic and terrestrial ecosystems?

nutrients (see Outstanding questions). Global change factors that alter which scavenging taxon dominates consumption and the rate at which carrion is consumed will dramatically alter the spatiotemporal dynamics of nutrient delivery (Figure 1).

Concluding remarks

Our framework illustrates how global change will differentially affect carcass discovery by competing scavenging guilds, alter carcass decomposition rates, and generate cascading effects on nutrient

Box 2. Spatiotemporal patterns in nutrient delivery by different scavengers

The temporal rate and spatial spread of nutrient delivery from carrion decomposition broadly depend on which taxonomic groups are the dominant consumers (Figure IA). The flush of carcass-derived nutrients belowground can stimulate the microbial necrobiome by inducing a biogeochemical hotspot. Based on ecological stoichiometry theory, opportunistic bacteria should capitalize on this pulsed resource because carrion-derived organic matter has a lower carbon-to-nitrogen ratio than plant litter and more closely reflects bacterial demand (Figure IB). Microbial use of carcass-derived nutrients could stimulate organic matter turnover (via 'priming' effects) or increase soil organic matter formation by stabilizing microbial-derived materials (e.g., metabolites, necromass) on the mineral matrix (Figure IB). Invertebrate communities may consume carcass-derived material more rapidly than microbial communities, reducing the depth of nutrient delivery belowground, but increasing the spatial delivery of nutrients via frass deposition and dispersal (Figure IC). Vertebrate consumers broadly disperse carcass-derived organic matter via excrement and urine deposition (Figure ID). Sloppy feeders that break up and leave behind small pieces of carrion (e.g., avian and mammalian scavengers) could increase the delivery of nutrients belowground relative to efficient feeders that rapidly ingest and translocate carrion-derived organics.

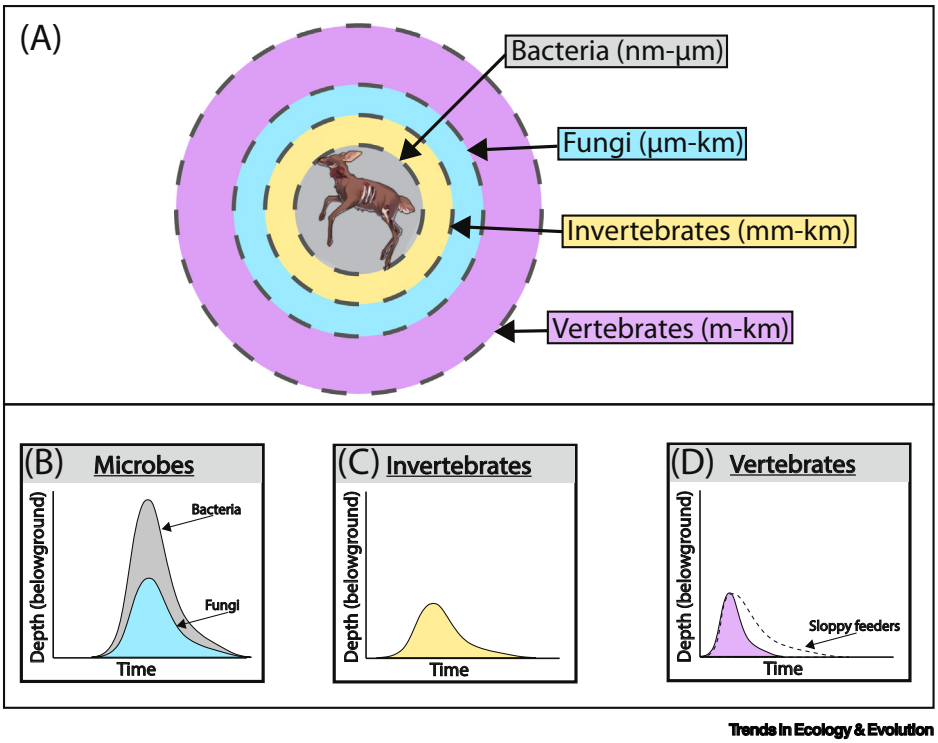

Figure I. Conceptual diagram depicting the spatial (upper panel) and temporal (lower panel) delivery of carcass-derived nutrients across different taxonomic groups of scavengers. The distance away from the carcass (A) and distance below the carcass (i.e., belowground depth; B–D) that carcass-derived nutrients are delivered depend on scavenger identity.

cycling (Figure 1). We hypothesize that carrion decomposition rates will be most impacted in systems where global change affects both carcass production and discovery rates by different scavenger guilds (Table 1), generating substantial shifts in the identity of carcass consumers. Even in cases where scavenger communities remain unchanged, global change that alters scavenger behavior will affect rates of carrion decomposition.

Understanding the effects of global change on carrion decomposition requires research that tracks the community of scavenging taxa, as well as the trajectory of carrion across all

phases of decomposition. Newsome *et al.* [3] provide details on experimental methods that could test key hypotheses that emerge from our perspective. We suggest experimental carcasses be deployed across various environmental contexts (e.g., human-modified vs. undisturbed habitats), at different densities (e.g., discrete vs. simulated mass mortality events), and/or under various, experimentally manipulated global change scenarios (see Table 1 for testable predictions). For example, to evaluate whether deforestation increases carcass discovery by visual scavengers, empiricists should manipulate carcass visibility in both logged and intact forests. They can then evaluate cascading effects on scavenger interactions by manipulating avian access to carcasses in both forest types and quantifying decomposition rates. Similarly, shifts in mean annual precipitation or temperature could be simulated in the field (e.g., via rain-out shelters or experimental warming) to measure how abiotic conditions impact scavenger behavior and carcass decomposition.

While our framework is focused on terrestrial ecosystems, global change also affects aquatic carrion decomposition [89,90], which can facilitate nutrient transport within and across aquatic and terrestrial ecosystems. For example, mass migration and mortality of salmon subsidize productivity in both aquatic and terrestrial systems [90]. We anticipate many of the general concepts within our framework can predict how aquatic carrion decomposition will change in the Anthropocene (see Outstanding questions). Finally, as **biological process rates** increase with rising temperatures, we suspect the delivery of carcass-derived nutrients will play a key role in alleviating plant and microbial nutrient limitations [91]. These effects will be most pronounced in systems with strong nutrient (e.g., tropical forests with depleted soils) or environmental (e.g., temperature in high-latitude systems or moisture in arid sites) constraints on biological productivity. Our framework can also be used to guide restoration or conservation interventions in these sensitive ecosystems. Management efforts must first be focused on restoring native scavenger communities either through species protection or reintroductions. We emphasize that ecosystems where multiple aspects of global change operate in tandem to shift carcass discovery and consumption should be prioritized for management (Table 1). For example, fire suppression can reduce the visibility of carcasses and the movement efficiency of scavengers (Table 1), which could result in declines in carrion decomposition rates (Figure 1). Prescribed fires may be used in such contexts to improve detection, and thereby decomposition, by both invertebrates and vertebrates (Table 1). Management efforts to improve the carcass discovery and consumption rates of scavengers will promote rapid nutrient delivery. Such efforts may include prohibiting human activity in sensitive habitats during periods when scavengers are active or prioritizing population control of introduced predators or competitors of native scavengers (Table 1). In summary, we suggest that sensitive ecosystems may benefit from management efforts that are focused on maintaining intact scavenging communities and efficient scavenging behavior.

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Declaration of interests

No interests are declared.

Supplemental information

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