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Review

The Role of Carrion in the Landscapes of Fear and Disgust: A Review and Prospects

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Abstract: Animal behavior is greatly shaped by the 'landscape of fear', induced by predation risk, and the equivalent 'landscape of disgust', induced by parasitism or infection risk. However, the role that carrion may play in these landscapes of peril has been largely overlooked. Here, we aim to emphasize that animal carcasses likely represent ubiquitous hotspots for both predation and infection risk, thus being an outstanding paradigm of how predation and parasitism pressures can concur in space and time. By conducting a literature review, we highlight the manifold inter- and intra-specific interactions linked to carrion via predation and parasitism risks, which may affect not only scavengers, but also non-scavengers. However, we identified major knowledge gaps, as reviewed articles were highly biased towards fear, terrestrial environments, vertebrates, and behavioral responses. Based on the reviewed literature, we provide a conceptual framework on the main fear- and disgust-based interaction pathways associated with carrion resources. This framework may be used to formulate predictions about how the landscape of fear and disgust around carcasses might influence animals' individual behavior and ecological processes, from population to ecosystem functioning. We encourage ecologists, evolutionary biologists, epidemiologists, forensic scientists, and conservation biologists to explore the promising research avenues associated with the scary and disgusting facets of carrion. Acknowledging the multiple trophic and non-trophic interactions among dead and live animals, including both herbivores and carnivores, will notably improve our understanding of the overlapping pressures that shape the landscape of fear and disgust.

Keywords: carcass; confrontational scavenging; disease risk; facultative scavenger; landscape of peril; marine ecosystems; parasite risk; predator risk; terrestrial ecosystems

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1. Introduction

Recently, Buck et al. [1] and Weinstein et al. [2] formalized a correspondence between predator and parasite avoidance behaviors. They argued how infection risk must determine a three-dimensional 'landscape of disgust' equivalent to the 'landscape of fear' induced by predation risk (defined by [1] as "the relative levels of predation risk experienced by a prey individual, represented as peaks and valleys on the landscape"). In this way, animal behavior is largely shaped by perceived risk (from either predators or parasites), leading to high-risk sites avoidance and preference for low-risk patches [1,2]. Either jointly or independently, these natural enemies may lead to fitness costs in their victims through physiological (e.g., chronic stress [3]) and behavioral (e.g., changes in habitat preferences [4]) effects. Strikingly, these physiological responses and behavioral decisions not only result from direct encounters with enemies, but frequently rely on indirect cues linked to risk situations or resources, regardless of actual presence of predators or parasites (e.g., [5]). Thus, through inducing fear and disgust, predators and parasites lead to a pervasive 'landscape of peril' [6] that may indirectly affect individuals and populations, as well as communities and ecosystems via cascading effects [1,2,6].

If we delve into this integrative, general view, many scary (i.e., related to the landscape of fear) and disgusting (i.e., related to the landscape of disgust) facets of animal carcasses can be inferred. In doing so, it rapidly comes to light that carrion probably represents ubiquitous—as it is produced in all biomes—hotspots for both predation and infection risk. On one hand, predators of different trophic levels are usually attracted to carcasses worldwide [7], which may lead to predation risk to not only herbivores (e.g., [8]), but also subordinate predators (e.g., [9]). On the other hand, carrion has long been considered a prominent source of pathogens that can put scavenging animals (e.g., [10]) and other species that may be present at carcass sites (e.g., [11]) at risk. For instance, the behavioral and cognitive repertoire of modern humans are probably shaped in part by the exposure of earliest hominins to the risks of being killed or injured while scavenging large herbivore carcasses and acquiring parasites when consuming a decaying piece of meat [12–14]. Pressures associated with predation and parasitism risk at carrion resources seem to be so pervasive that even some plants have taken advantage of them. In particular, species of genera *Rafflesia*, *Aristolochia*, and *Helicodiceros*, among others, could use thanatosis (i.e., olfactory feigning of carrion) to not only attract pollinators, but also deter herbivores, especially during the flowering period [15].

However, we are just starting to uncover the manifold ecological and evolutionary ramifications of carrion within the context of predation and parasitism risks. Research on this topic is especially needed given the ongoing global environmental change. Understanding how animals thrive in the changing landscape of peril associated with carrion could provide important insights for the conservation of threatened scavengers. Moreover, studying how animals behave around carcass sites could reveal key findings of veterinary and epidemiological interest, which is particularly relevant in the current context of zoonotic diseases [16].

Our general aim is to examine the role that carrion plays in the landscapes of fear and disgust, which has been largely overlooked in the scientific literature despite its crucial eco-evolutionary, epidemiological, and management implications. Through a bibliographic review, we will identify the main ways in which carrion may be scary and disgusting, namely the principal interaction pathways between carcasses and their visitors (both carnivores and herbivores) that expose the former to predators and parasites at carcass sites. Here, predators and scavengers are defined as gatherers and miners, respectively, of live animals [17], with parasites including macroparasites, protists, fungi, bacteria, and viruses [18]. Then, we will determine the main knowledge gaps and provide ideas for future investigation on this emerging and highly promising research topic.

2. Material and Methods

Following guidelines provided by Haddaway et al. [19], we used the Web of Science to conduct a systematic review of the scientific literature on the landscapes of fear and disgust associated with carrion. Specifically, using the "Topic search" (i.e., title, abstract, and keywords), we searched for "articles" appearing prior to November 2020 that included the following combinations of terms: "landscape of fear" OR "fear" OR "predat* risk" AND "carrion" OR "carcass" OR "scaveng*"; and "landscape of disgust" OR "disgust" OR "parasit* risk" OR "parasit* avoidance" OR "disease risk" OR "disease avoidance" OR "infection risk" OR "infection avoidance" AND "carrion" OR "carcass" OR "scaveng*" (Appendix A). We further restricted our search in a two-steps process (e.g., [20]). First, title and abstract were screened to ensure we only included empirical studies dealing with the general topic of this review. Second, we read the full content of the selected articles, excluding articles mentioning only superficially in the introduction and discussion the searched terms, e.g., to motivate the study or suggest future research needs. Through this procedure, we obtained 26 articles. Then, we used Google Scholar to identify additional papers, restricting the search to the first 30 papers for each combination of terms. This complementary search provided 26 articles not identified previously in the Web of Science. In total, we obtained a final set of 52 articles for in-depth review (see References A1 for a complete list of reviewed references), which we consider sufficient to infer global patterns of research effort and relative differences among distinct interaction pathways.

We divided the selected articles in two main groups, depending on whether they were concerned with fear or disgust. Then, from each article, we obtained the following information. First, we extracted general data: year of publication; ecosystem under study (*terrestrial*, *coastal*, *marine*, *freshwater*); geographic location (i.e., the country where the study was conducted); period under study (*prehistorical*, *historical*); animals involved in the study (i.e., scavengers and non-scavengers that may feed or inspect around carcasses; *vertebrates*, *invertebrates*); the type of effects—studied, detected, or presumed—that the fear or disgust exerted on such species (*behavioral*, *physiological*, *demographic*, *non-specified*), and study design (*field study, observational*; *field study, experimental*; *field study, quasi-experimental*; *mesocosm experiment*; *other*). "Quasi-experimental" studies refer to those in which carcasses or artificial nests were placed in locations selected by the researchers, but no other condition was manipulated. For each field and mesocosm study, we also recorded the observation method (*direct observation*, *camera-trap*, *other*). Second, we identified the ways in which carrion and visitors to carrion sites could lead to predation or parasitism risk to these or other visitors. This, along with other key reviews on the topic (e.g., [21–27]), was the basis to elaborate a conceptual framework on the main interaction pathways around carrion resources that are related to fear and disgust. In the latter case, we distinguished consumptive (trophic) and non-consumptive (non-trophic) processes. We represented the framework separately for herbivore and carnivore carcasses, given that their decomposition process, persistence time in the environment, and associated risks are neatly different [28]. Third, we recorded the number of articles selected in the review that were related to each pathway, with the aim of identifying major knowledge gaps that could be key targets for future research.

3. Results and Discussion

3.1. General Results

We obtained more articles concerned with fear (75%, n = 39) than with disgust (25%, n = 13). No article empirically explored simultaneously both types of risk. Moreover, scientists became interested later on disgust than on fear, according to the year of publication of these articles (Figure 1A). Most articles on fear, and all articles on disgust, involved terrestrial ecosystems or mesocosms. Thus, representation of articles dealing with aquatic environments was scarce (Figure 1B). Most articles focused on present-day assemblages, while all studies concerned with prehistorical times were related to the predation (mainly) and infection risk faced at carcass sites by early hominins (Figure 1C). There were more articles studying vertebrates than invertebrates (Figure 1D), with the latter being mainly associated with marine and freshwater systems. Effects on visitors to carrion sites, as recorded in the reviewed articles, were mostly behavioral; only a few articles involved demographic effects (in all cases, related to bird nest predation), and none explored physiological effects on visitor species (Figure 1E). Studies on predation risk were mostly observational and quasi-experimental, though experimental approaches (all in mesocosm systems) were frequently used to assess parasitism risk. In addition, the intentional deployment of carcasses (and artificial nests) was normally associated with the use of camera-traps for monitoring bait use by animals, especially in disgust-related studies (Figure 1F). Most present-day studies were conducted in Australia, USA, and Europe, while all studies on early hominins were done with material from eastern Africa (Figure 1G).

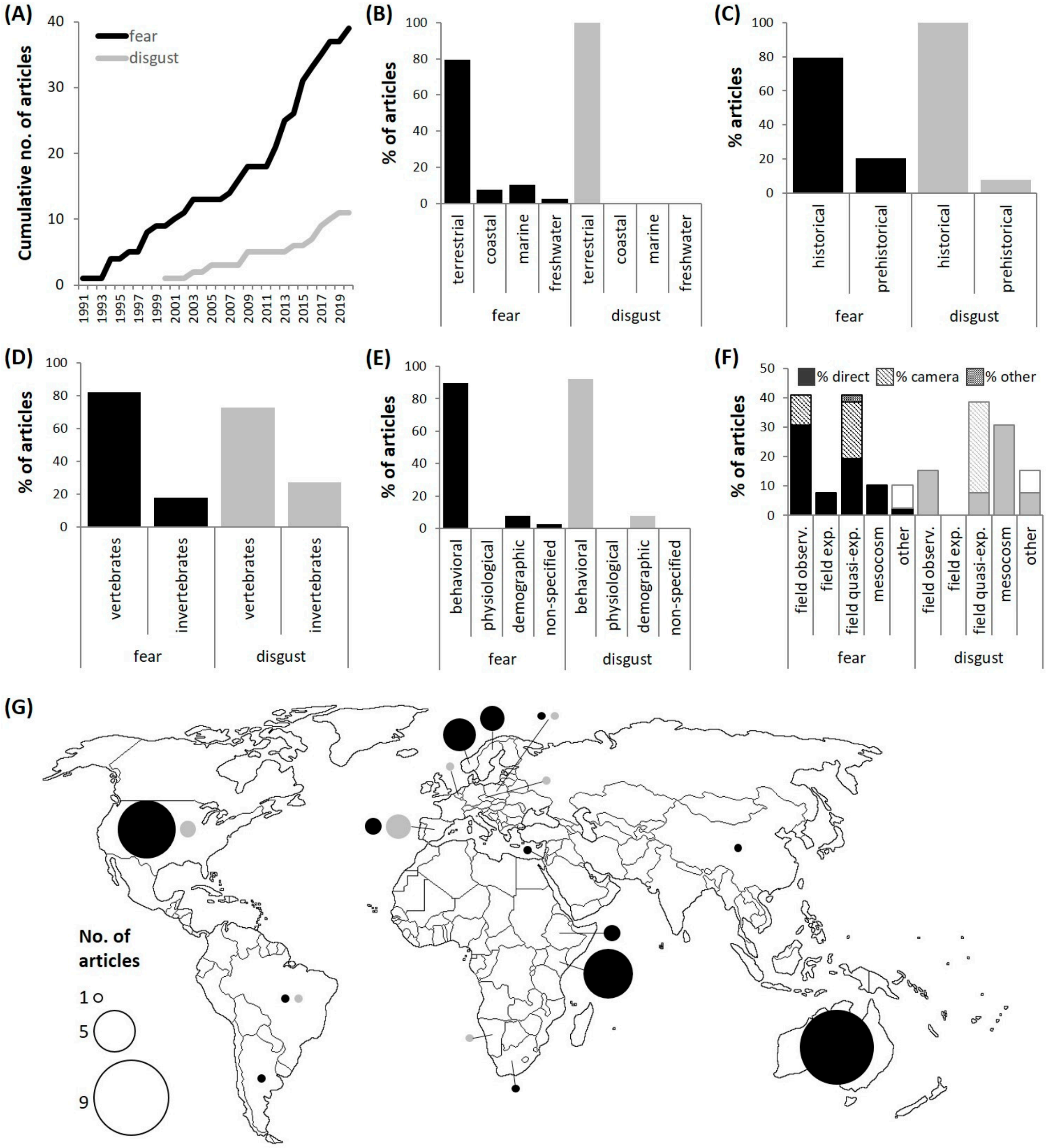

Figure 1. Distribution of reviewed articles according to publication year (**A**), ecosystem (**B**), period (**C**), type of animals at (potential) risk (**D**), effects of the risks on such animals (**E**), study design (different bars) and observation method (within bars) (**F**), and geographic location (**G**). See main text for details.

3.2. Interaction Pathways and Research Effort

Figure 2 shows our conceptual model for the main fear- and disgust-based interaction pathways associated with carcasses of carnivore and herbivore species. In general, while animals may be mainly disgusted by carcasses themselves, scare is genuinely related to other animals that may be attracted to the carcass for any reason or present by chance in its vicinities.

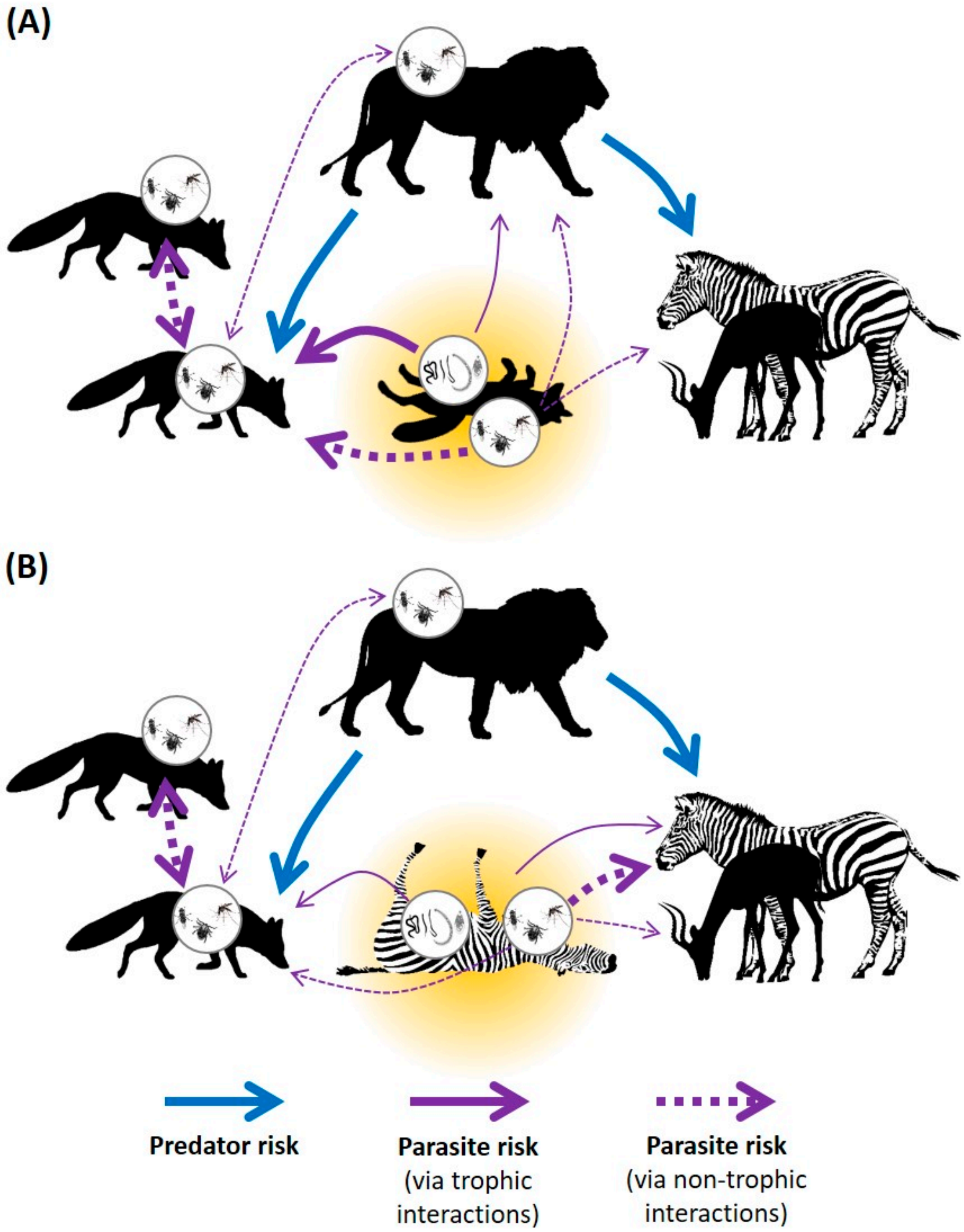

Figure 2. Animal carcasses may be both disgusting and scary. However, the parasite and predator risks vary widely according to the species identity of the carcass and its visitors. (**A**) Carnivores visiting carnivore carcasses may face both predation and infection risk. Parasites may be transmitted to carnivores by either the carcass or other carnivore visitors, with the probability of transmission being proportional to their phylogenetic relationship [29,30]. (**B**) Herbivore carcasses are relatively safe for carnivores in terms of direct parasite transmission (at least, regarding direct life cycle parasites), but these carnivores may still be subject of parasite and predation risk from other carnivores. Herbivores may be at predation and parasitism risk at both carnivore and herbivore carcass sites, with the latter representing comparatively higher risk of acquiring parasites. Interactions among carnivores are more frequent at large carcasses [31] and in the absence of vultures [32], which are highly efficient scavengers [33,34]. Arrow width is roughly proportional to the intensity of risk.

Among the different pathways associated with carnivore carrion, only the risk of acquiring parasites through intra-guild and, especially, intra-specific scavenging received some scientific interest within the reviewed articles (e.g., [35–37]; Figure 3A).

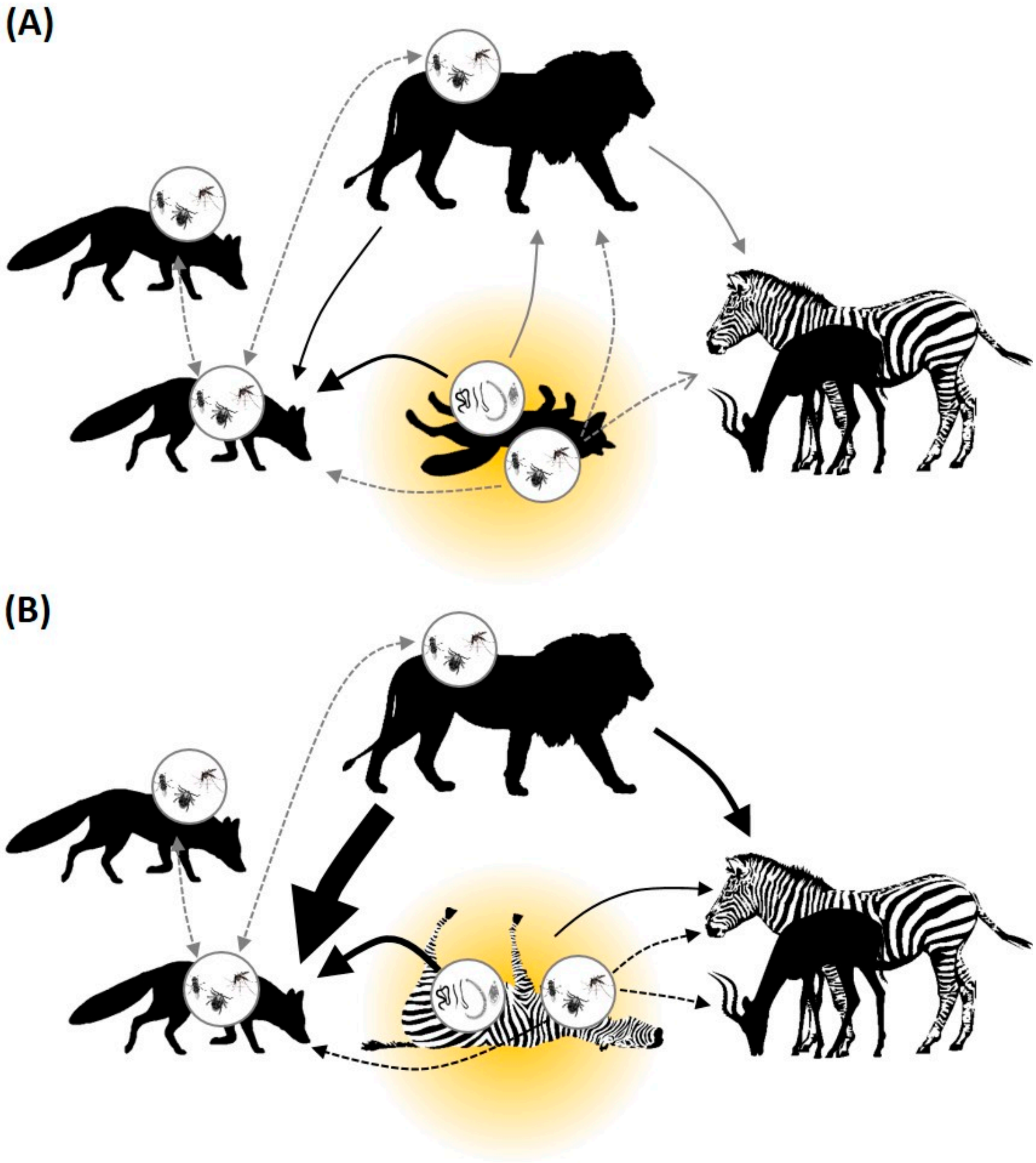

Figure 3. Research effort devoted to the main fear- and disgust-related interaction pathways around (**A**) carnivore and (**B**) herbivore carrion, according to our literature review. Those pathways for which we found at least one article are shown by black arrows (we use grey arrows otherwise). Arrow width is proportional to the number of articles.

Regarding herbivore carcasses (Figure 3B), most studies have focused on the predation risk affecting species that are present in the vicinities of carcass sites, both herbivores (e.g., [8,38–40]) and, mostly, carnivores (e.g., [9,41–47]). Within these articles, several studies explored how Plio/Pleistocene hominins were subject of predation risk while exploiting large carcasses (a process called confrontational/aggressive/active/power scavenging), according to paleontological evidences and behavioral, ecological, and energetics modelling (e.g., [13,48]), behavioral studies of modern human hunter-gatherer societies [49] or other primates [50], and other procedures [51]. Other studies have focused on several aspects of parasitism, especially the risk of acquiring parasites from meat consumption by carnivores (e.g., [52–54]).

3.3. Carrion Is Disgusting

Mammalian carnivores avoid feeding on other carnivore carcasses, especially of conspecifics, likely to reduce exposure to parasites [35–37]. These findings highlight that the risk of direct infection is higher among phylogenetically close organisms, which share more parasite species [1,29,30,37]. In turn, the carnivore carrion-avoidance behavior of carnivores enables a wide array of indirect ecological effects, both consumptive (e.g., scavenging of mammalian carnivore carcasses by a well-structured community of insects) and non-consumptive (e.g., hair collection by birds for nest construction), linked to carnivore carcasses [37,55]. This, together with the observation that grazers avoid foraging near herbivore carcasses to prevent infectious risk (e.g., [2,53,56]), indicates that dead animals may disgust both scavenging and non-scavenging species (Figure 3). However, effects of carrion on vegetation growth may lead to increased disease risk for herbivores that are attracted to carcass sites once carrion has been removed, in a sort of ecological trap that favors infection by highly resistant pathogens [11]. Regarding the mechanism by which scavengers may discriminate risky carcasses, some carnivores such as mammalian meso-carnivores seem to rely on carrion odor (e.g., to distinguish intra- from inter-specific carrion [37]), while others such as ants and beetles may detect the presence of certain pathogens by smelling or tasting their metabolites in the carcass [52].

In addition to meat-borne parasites, other pathogens present at carcass sites could be transmitted to any animal that approaches at a sufficient distance [11,53,57]. In addition, carcasses may indirectly favor parasite transmission among the scavengers that come into contact while scavenging, a circumstance that would be especially plausible in the absence of vultures [32], which are specialized, obligate scavengers that quickly remove carcasses [33,34,58]. However, these and other mechanisms of carcass-mediated infection risk (Figure 3) remain largely speculative and need further empirical support.

Besides carcass type, carrion-related infection risk—and the duration of the infective period—may be dependent on many other factors, such as parasite identity, carcass origin, the degree of starvation shown by the scavenger, and climatic conditions (e.g., [35,41,59]). Given the important ecological, evolutionary, and sanitary implications of the management of wild [60] and domestic animal carcasses [61], these issues require urgent scientific attention.

3.4. Carrion Is Scary

Herbivore carcass sites may be avoided by other herbivores because of high probability of predator–prey encounters (e.g., [8,38,40]; Figure 3B). Indeed, the probability of predation of ground-nesting birds increases near both predictable and unpredictable carrion resources [39,62]. The increased predation risk around carcasses is mainly explained by the fact that most predators behave also as facultative scavengers that are, to a greater or lesser extent, attracted to carrion [63,64]. This predation risk is likely higher at large carcasses because they are visited by more and larger predator species than smaller carcasses [7,31]. In addition to herbivores, small and medium-sized carnivores also avoid carcasses to prevent the risk of confronting dominant predators (e.g., [5,9,43,45,47,65]). In fact, the risk of being attacked by a larger predator, such as lion (*Panthera leo*) and spotted hyaena (*Crocuta crocuta*), may be so high that certain sympatric mammalian carnivores, such as cheetahs (*Acinonyx jubatus*) and wild dogs (*Lycaon pictus*), very rarely scavenge [66]. Cheetahs, even leave their own kills once satiated, no matter how much meat may be left [67].

However, how carnivores and herbivores behave at carnivore carcasses in relation to predation risk is virtually unknown (but see [41,65]; Figure 3A). In these cases, carcasses of predators may also be scary by themselves, as other scavengers that are within the prey base of the dead predators might even avoid the risk of inspecting such carcasses.

The risk that a given animal, either scavenger or not, is willing to accept at a carcass site may depend on several factors, such as sociality. For instance, spotted hyaenas are able to even displace lions from a carcass provided that the former outnumber the latter by a factor of 4 and no male lions are present at the carcass [68]. Coyotes (*Canis latrans*) may also displace wolves (*C. lupus*) from their kills when the former are in numerical advantage [9]. In addition, both hyaenas and (alpha) coyotes may trade off greater risk for high-quality carrion, as dominant carnivores may also facilitate carrion supply and detection [9,68]. Finally, hungry, sick, unexperienced, or senescent scavengers are probably more prone to face risky situations (e.g., [44,65,69]), though this needs further empirical confirmation.

3.5. Conclusions and Directions for Further Research

Overall, this review highlights the manifold inter- and intra-specific interactions linked to carrion via predation and parasitism risks, which may affect not only carrion consumers, but also non-consumers. Animal carcasses are an outstanding paradigm of how predation and parasitism pressures can concur in space and time, which is a major gap in predator- and parasite-avoidance scientific knowledge [1]. Carcasses may represent hotspots of infection and predation risk to both carnivores and herbivores, although the risk is highly dependent on a number of factors, such as carcass identity (Figure 2) and the size of the animals visiting carcass sites. For instance, large herbivores and top predators will be more reactive to parasite than to predator risk [1]. Thus, the multiple predator and parasite risk pathways that may arise around carnivore (Figure 2A) and herbivore carrion (Figure 2B), which are far more diverse than previously recognized, may differ qualitatively and quantitatively.

However, fully understanding of animal behavior around carrion resources requires exploring simultaneously different sources of risk [1], as avoiding one risk may increase [70] or decrease [71] another. Furthermore, Buck et al. [1] argue that "because predators are generally more mobile than parasites, the predator-induced landscape of fear might be more dynamic than the parasite-induced landscape of disgust". We highlight that, given the generally unpredictable and ephemeral nature of carrion [63,64,72], the very different life cycles of different parasite species [73], and the seasonality associated with their infective stages [74], carcass-induced landscape of disgust may be also highly dynamic.

The conceptual framework of the landscape of peril might also benefit from empirical evidence of aquatic ecosystems addressing key issues that differentiate them from terrestrial ones. For example, parasites in aquatic environments are more mobile than in terrestrial ecosystems, due to both active (i.e., locomotion and motility) and passive (e.g., currents and tides) transport through water [18]. Other relevant differences between terrestrial and aquatic systems relate to the cues to detect predators and parasites, which may differ qualitatively and quantitatively between air and water. In general, while visual, auditory and mechanosensory cues play a more prominent role in terrestrial environments, chemical cues are substantially more used by aquatic animals [18]. Comparative studies on how animals perceive and avoid predation and parasitism risk at carcass sites in terrestrial vs. aquatic environments are virtually absent, which opens exciting avenues for further research.

The conceptual model we present here (Figure 2) allows formulating predictions about how the landscape of fear and disgust around carcasses might influence animals' individual behavior and ecological processes, from population to ecosystem functioning. This could be especially useful in the current global change scenario, which includes high rates of species extinctions, invasions, and re-colonizations of both predators and parasites (e.g., [75]), as well as a growing evidence of the effect of human footprint on scavenger guilds [7]. In addition, our literature review has clearly shown that the research effort so far on predator and parasite risks associated with carrion has been highly unevenly distributed through the different interaction pathways, with most studies dealing with predation risk at vertebrate herbivore carcasses in terrestrial ecosystems (Figure 3). Thus, there is ample room and motivation for future investigation. Furthermore, most research has focused on behavioral responses (particularly, avoidance) of different species in relation to fear and disgust. However, to which extent are these behaviors innate or learned is an open question [36]. Moreover, other individual responses (e.g., physiological), as well as the effects at the population, community, and ecosystem levels remain largely unexplored and require further empirical evidence. While physiological responses have not been explored so far in a carrion context (to our knowledge), it is reasonable to think that the risks associated with carrion may exert different physiological costs (e.g., transitory and chronic stress) on animals visiting carcass sites, such as prey and subordinate predators. Future research might benefit from the application of novel (including experimental) methods in scavenging ecology and its interaction with different disciplines, as well as from the spatiotemporal quantification of carrion biomass [28,76] and the long-term monitoring of carcasses and scavenger guilds in different ecosystems [7]. Finally, besides freshwater and marine studies, terrestrial studies from tropical biomes would be especially welcome, as most research (for the historical period context) so far has focused on temperate, Mediterranean, and boreal systems.

In conclusion, future research should study the trade-offs and synergistic effects of both predator and parasite risk associated with carcasses of different nature and size in contrasting ecosystems and seasons, as well as the relative importance of these and other selective pressures. These ecological processes may have important consequences for animals facing predator and parasite risks, with individual costs ranging from diminished feeding rate to death, which may lead to wide ecological, evolutionary, epidemiological, forensic, and conservation implications. Acknowledging the multiple trophic (e.g., [64]) and non-trophic (e.g., [77]) ways in which dead animals directly and indirectly interact with living animals, including both herbivores and carnivores, will notably improve our understanding of the overlapping pressures that shape the landscape of fear and disgust.

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Conflicts of Interest: The authors declare no conflict of interest.

Appendix A References A1. Articles Reviewed. Articles Identified in the Google Scholar Search Only Are Marked with an Asterisk

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