

Review

The ecology of zoonotic parasites in the Carnivora

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The order Carnivora includes over 300 species that vary many orders of magnitude in size and inhabit all major biomes, from tropical rainforests to polar seas. The high diversity of carnivore parasites represents a source of potential emerging diseases of humans. Zoonotic risk from this group may be driven in part by exceptionally high functional diversity of host species in behavioral, physiological, and ecological traits. We review global macroecological patterns of zoonotic parasites within carnivores, and explore the traits of species that serve as hosts of zoonotic parasites. We synthesize theoretical and empirical research and suggest future work on the roles of carnivores as biotic multipliers, regulators, and sentinels of zoonotic disease as timely research frontiers.

Zoonotic and functional diversity in the Carnivora

In ecology, 'functional diversity' refers to the many ways that organisms contribute to the overall functioning of communities and ecosystems [1]. With 302 extant species¹, the order Carnivora is not the most species-rich among mammals (that distinction belongs to the orders Rodentia, the rodents, and Chiroptera, the bats), but it is among the most functionally diverse [2]. This functional diversity is manifested in exceptional dietary diversity [2,3], which influences all aspects of carnivore biology, ecology, and life history, including their suitability as hosts of parasites and pathogens.

Curiously, carnivores collectively carry a larger number of known zoonotic pathogens and parasites than any other mammal group (hereafter, **zoonotic parasites**; see [Glossary](#)) [4], despite having an order of magnitude fewer species than rodents (2590 extant species) or bats (1430 extant species). We posit that this zoonotic diversity is the outcome of high functional diversity observed in the Carnivora, in which ecological adaptations to support high dietary diversity have exposed this order to a parasite diversity that is disproportionate to their species diversity. Here we review recent literature and reanalyze relevant published data to explore the occurrence of zoonotic parasites and their hosts within the order Carnivora, and to identify research gaps that preclude a better understanding of current and future zoonotic risks in this order.

Transmission of zoonotic parasites in the Carnivora

Carnivorans (members of the order Carnivora, hereafter carnivores) host 182 known zoonotic parasite species causing 46 unique zoonoses [4] (see Table S1 in the supplemental information online). The majority of these parasites are of four major types (56 bacteria, 25 viruses, 66 helminths, and 28 protozoa; [Table 1](#)).

Zoonotic parasites can also be categorized into four transmission modes (defined as per [5]):

1. Close-contact transmission requires proximity, and transmission occurs through behaviors such as grooming, scratching, or biting (rabies, SARS-CoV-2).

Highlights

Despite nearly half of the Carnivora being zoonotic hosts, and their ubiquity across all major biomes globally, there remain surprising gaps in basic biological and ecological knowledge in this group that preclude deeper assessments of their zoonotic diversity and risk.

Functional traits related to dietary diversity suggest that zoonotic hosts in this group reflect an omnivorous life history strategy with potentially profound implications for infection tolerance.

The Carnivora will experience widespread changes to their global range distributions with unpredictable and significant impacts on biotic interactions, with cascading effects on zoonotic disease risk from carnivore hosts as well as their prey species.

Filling research gaps in the functional ecology of the Carnivora will improve our understanding of their roles as sentinels, regulators, sinks, or sources of zoonotic parasites.

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Table 1. The majority of known zoonotic parasites in carnivores are of four major parasite types and are found in 15 host families

Family ^a		Common names and species counts	Zoonotic parasites
Ailuridae		Red pandas Species: 2 Hosts: 1	8 Bacteria: 0 Helminths: 4 Protozoa: 4 Viruses: 0
Canidae		Dogs, foxes Species: 39 Hosts: 15	91 Bacteria: 28 Helminths: 37 Protozoa: 15 Viruses: 10
Eupleridae		Fossas Species: 7 Hosts: 1	1 Bacteria: 0 Helminths: 0 Protozoa: 1 Viruses: 0
Felidae		Cats Species: 46 Hosts: 16	47 Bacteria: 15 Helminths: 18 Protozoa: 8 Viruses: 4
Herpestidae		Mongoose, meerkats Species: 35 Hosts: 7	12 Bacteria: 5 Helminths: 2 Protozoa: 2 Viruses: 3
Hyaenidae		Hyenas Species: 4 Hosts: 2	7 Bacteria: 0 Helminths: 5 Protozoa: 1 Viruses: 1
Mephitidae		Skunks Species: 11 Hosts: 3	12 Bacteria: 5 Helminths: 1 Protozoa: 2 Viruses: 4
Mustelidae		Weasels, badgers, otters Species: 64 Hosts: 21	52 Bacteria: 15 Helminths: 16 Protozoa: 11 Viruses: 5

Glossary

Bridge host: an animal host that transmits a zoonotic pathogen from a reservoir host population to humans; it can often be a companion species or livestock.

Definitive host: in parasites with complex life cycles, the host in which sexual reproduction takes place.

Intermediate host: in parasites with complex life cycles, the host which supports one stage of a reproductive cycle, typically an intermediate stage in which sexual reproduction does not take place. It is often associated with trophic transmission, in which the parasite is consumed by the definitive host.

Reservoir host: an animal host in which a zoonotic parasite persists in a sylvatic cycle, and from which spillover transmission (sometimes through a bridge host) can lead to zoonotic infection in humans or other host species.

Secondary spillover: secondary spillover infection occurs after a human infected by a zoonotic pathogen (via spillover transmission) transmits the infection back to another animal (spillover transmission), which then transmits infection in a second spillover event to a human (secondary spillover); a timely example is human SARS-CoV-2 infection from American mink.

Sentinel host: an animal species that is not involved in parasite transmission but serves as a reliable indicator of parasite presence in a system.

Spillover transmission: the transmission of a zoonotic parasite from a human host back to an animal host.

Tolerance: refers to a species propensity to allow persistence of an infection by minimizing its negative effects rather than eliminating or preventing infection through immune activity

Top-down disease control: the regulation of host populations (e.g., through consumptive effects such as predation, or nonconsumptive effects, such as modifying host behaviors or distributions) leading to a reduction in disease incidence.

Trophic transmission: a form of parasite transmission that is completed when the infected prey host is consumed by a predator host.

Zoonotic capacity: encompasses both species susceptibility and the ability to transmit infection to humans. This term distinguishes reservoir and bridge

Table 1. (continued)

Family ^a		Common names and species counts	Zoonotic parasites
Nandiniidae		African palm civet Species: 1 Hosts: 1	1 Bacteria: 0 Helminths: 0 Protozoa: 1 Viruses: 0
Odobenidae		Walrus Species: 1 Hosts: 1	3 Bacteria: 1 Helminths: 1 Protozoa: 0 Viruses: 0
Otariidae		Eared seals Species: 15 Hosts: 7	15 Bacteria: 6 Helminths: 4 Protozoa: 4 Viruses: 0
Phocidae		Earless seals Species: 18 Hosts: 8	19 Bacteria: 4 Helminths: 3 Protozoa: 3 Viruses: 7
Procyonidae		Raccoons, coatis, kinkajous Species: 13 Hosts: 6	40 Bacteria: 19 Helminths: 4 Protozoa: 5 Viruses: 10
Ursidae		Bears Species: 8 Hosts: 5	32 Bacteria: 13 Helminths: 6 Protozoa: 4 Viruses: 6
Viverridae		Genets, civets, binturongs Species: 36 Hosts: 7	17 Bacteria: 5 Helminths: 2 Protozoa: 6 Viruses: 3

hosts from hosts acquiring dead-end infections that do not transmit onward.

Zoonotic parasite: a parasite or pathogen that originates and largely persists in nonhuman animal host populations that can infect and cause disease in humans.

Zoonotic risk: the risk posed by a host related to the transmission of a zoonotic parasite, or the risk posed by a zoonotic parasite to cause disease in a human host.

2. Non-close-contact transmission occurs through contact with infectious particles that persist in the environment, such as through contaminated food or water (*Leptospira*, [6]).
3. Zoonotic parasites that are vector-borne are transmitted by biting arthropods, including ticks (*Borrelia burgdorferi*, Lyme disease, [7,8]), mosquitoes (*Francisella tularensis*, tularemia, [9]), and fleas (*Yersinia pestis*, plague, [10]).
4. The most numerous zoonotic parasites in carnivores have complex life cycles that require both **intermediate hosts** and **definitive hosts**, and often use **trophic transmission**, where transmission requires the consumption of intermediate stages. We refer to this mode as 'intermediate transmission' to maintain previous naming conventions (as in [5]).

The transmission modes used by zoonotic parasites directly determine the roles that carnivore hosts play in both maintaining and transmitting these parasites. For instance, zoonotic parasites use carnivore species as **bridge hosts** (SARS-CoV-2, Box 1) or as **reservoir hosts** [4,11,12]. While both bridge and reservoir hosts can transmit zoonotic parasites to humans, only reservoir hosts are involved in maintaining zoonotic parasite populations in the wild. For example, in northern Kenya, serological patterns of rabies virus suggest that domestic dogs serve as important reservoirs that repeatedly seed spillover transmission to other wild carnivore hosts, such as African wild dogs, black-backed jackals, spotted and striped hyenas, and African lions [12]. In sub-Saharan Africa, domesticated dogs also serve as an important reservoir host for guinea worm (*Dracunculus medinensis*) [13]. Guinea worm is a zoonotic helminth parasite that has a complex life cycle in which copepods (aquatic crustaceans) are infected by guinea worm larvae. These larvae develop into adult worms when they are trophically transmitted to suitable definitive hosts including humans, nonhuman primates, dogs, and cats [14]. While dogs do not directly transmit guinea worms to humans, they become infected by consuming infected water, or by scavenging the remains of infected fish or frogs (prepared by humans), maintaining guinea worm infection in this system and complicating ongoing efforts at global eradication [13].

While all mammal species encounter parasites with these major transmission modes, one intuitive prediction for carnivores that is exemplified by the guinea worm system is that trophic transmission modes will predominate given that carnivory is a distinguishing feature of this order. This idea gives rise to ancillary hypotheses. One hypothesis is that predators in this group bioaccumulate the parasites of their prey [15], leading to a positive relationship between the diversity of prey items and parasite richness. A related hypothesis is that the number of zoonotic parasites observed in carnivores will scale with the degree of carnivory, measured as either prey diversity or the percentage of diet composed of meat. An absence of this pattern (no relationship between zoonotic parasite richness and carnivory) could suggest that carnivores possess adaptations protecting them from the higher diversity of parasites encountered via prey (e.g., [16,17]). Similarly, confirmation of a positive carnivory–parasite richness relationship without corresponding increases in disease would also suggest tolerance adaptations in carnivore hosts. These may include, for instance, immune strategies or behavioral strategies to minimize infection risk [16], or the sequestration of gut flora that enable some species to harbor pathogens without physiological damage [18].

Transmission modes of zoonotic parasites strongly underlie **zoonotic risk**, or the risk that the parasite could infect and cause disease in humans [19]. Despite this human-centric perspective,

Notes to Table 1:

^aThere are 66 helminths, 56 bacteria, 25 viruses, and 28 protozoa causing 46 unique zoonoses across carnivore hosts from 15 families (photos are an example of species from each family). We exclude Prionodontidae, as species from this family are not known to carry zoonoses. Less common parasite types (e.g., prions) are not represented. Data and image attributions are reported in Table S2. Zoonotic parasites found for each species in the families detailed here can be found in Table S1.

other mammals are also at risk from diseases that are shared in common with humans [20–22]. **Spillback transmission** from humans to wild carnivores is a topic of ongoing research in the wake of the COVID-19 pandemic in which human-adapted variants of the SARS-CoV-2 coronavirus have infected numerous suitable carnivore hosts and caused lethal disease in at least one species, the American mink (Box 1). Thus, SARS-CoV-2 infection may also be categorized as an anthroponosis, a disease in animals that is caused by a predominantly human pathogen, which may pose particular risk to carnivore species with distributions that overlap human-dominated landscapes, or species that occur in zoos.

Zoonotic hosts among the Carnivora

Previous work has reported that approximately 46% of carnivores harbor zoonotic pathogens (140/302 species) [4]. Zoonotic hosts are currently found in 15 out of 16 families, with Mustelidae (weasels, badgers, otters and their relatives) and Felidae (cats) harboring the most zoonotic host species, and Canidae (dogs) harboring the greatest diversity of zoonotic parasites (the rare and understudied family, Prionodontidae, harbors none) (Table 1). In general, species with terrestrial foraging strategies have more zoonotic parasites than marine foraging species despite more study effort devoted to marine species on average (as measured by Web of Science topic search hits; data available in Table S3). The parasites found across these host groups may be expected to cluster among phylogenetically related species since successful transmission depends on host behaviors and rates of infectious contact that vary with functional ecology [23–26]. For instance, foraging behaviors vary widely from strict endotherm predators (e.g., cheetah, family Felidae) to nearly strict herbivores (e.g., giant panda, family Ursidae), which may influence the sources from which zoonotic pathogens are acquired (prey vs. plants). Sociality or group living will also affect the successful transmission and dynamics of parasites that are spread through close contact (e.g., wolves, [24,27]). In contrast, most ursids (bears) and mustelids are asocial and relatively solitary except during mating and courtship [28]. Interestingly, however, both zoonotic parasites and zoonotic hosts appear evenly distributed across the carnivore phylogeny. Furthermore, parasite transmission modes, which might be expected to track host functional traits (e.g., [16,29]), also do not cluster across host phylogeny, and instead are relatively evenly distributed (Figure 1). A clustering analysis performed on previously published carnivore parasite data [2] showed no significant phylogenetic

Box 1. Potential reservoirs of SARS-CoV-2 among carnivores

Following initial spillover transmission, likely from a bat to a human, SARS-CoV-2 has spilled back from humans into other animals. Nearly all confirmed spillback hosts are carnivores [85], and some have the capacity to transmit SARS-CoV-2 onward to other hosts, including humans (**zoonotic capacity**). For example, SARS-CoV-2 spilled back from humans to farmed mink in 11 countries across North America and Europeⁱⁱ, leading to widespread mink mortality from lethal disease and culling of 17 million mink in Denmark [86,87]. SARS-CoV-2 has also spilled over a second time from farmed mink to humans [88], and has been confirmed in a wild mink in the USA (presumed to have become infected through an escaped farmed mink)^{iii,iv} [89].

A recent analysis predicted the zoonotic capacity for SARS-CoV-2 across all 5400 mammals by integrating structural models of three-dimensional virus–host protein–protein interactions with machine-learning models of species' traits [52]. This analysis identified several likely carnivore hosts, including several with large geographic ranges: red fox (*Vulpes*, ~50 countries), European polecat (*Mustela putorius*), raccoon dog (*Nyctereutes procyonoides*), stoat (*Mustela erminea*), and wolf (*Canis lupus*). Notably, numerous prey species have also been predicted and confirmed with zoonotic capacity for SARS-CoV-2, including in common laboratory mice [90], and deer mice (*P. maniculatus*), with onward transmission experimentally confirmed in this species [91,92].

Carnivores with the highest likelihood of SARS-CoV-2 exposure will occur in close proximity to humans, and in countries with many human COVID-19 cases (Figure 1). The inset map (adapted from [52]) shows particularly high richness for these species in Southeast Asia and Eastern Europe, and includes several carnivores in close contact with people because they are both farmed and wild (red fox, *V. vulpes*; Asiatic black bears, *Ursus thibetanus*; raccoon dogs, *N. procyonoides*) or live traded (grey wolf, *Canis lupus*; jaguar, *Panthera onca*) [93].

Ongoing spillback infection increases the likelihood of a wild sylvatic cycle for SARS-CoV-2, which may perpetuate **secondary spillovers** of virus variants from novel hosts to people [52,91,94]. Spillback infection may also further threaten declining or endangered carnivore species^v, such as grizzly bear (*Ursus arctos*, listed as threatened), polar bear (*Ursus maritimus*, vulnerable), wolf (*Canis lupus*, endangered), giant panda (*Ailuropoda melanoleuca*, vulnerable) and red panda (*Ailurus fulgens*, endangered), which are predicted to be susceptible to SARS-CoV-2 infection and are regularly handled by biologists or wildlife managers.

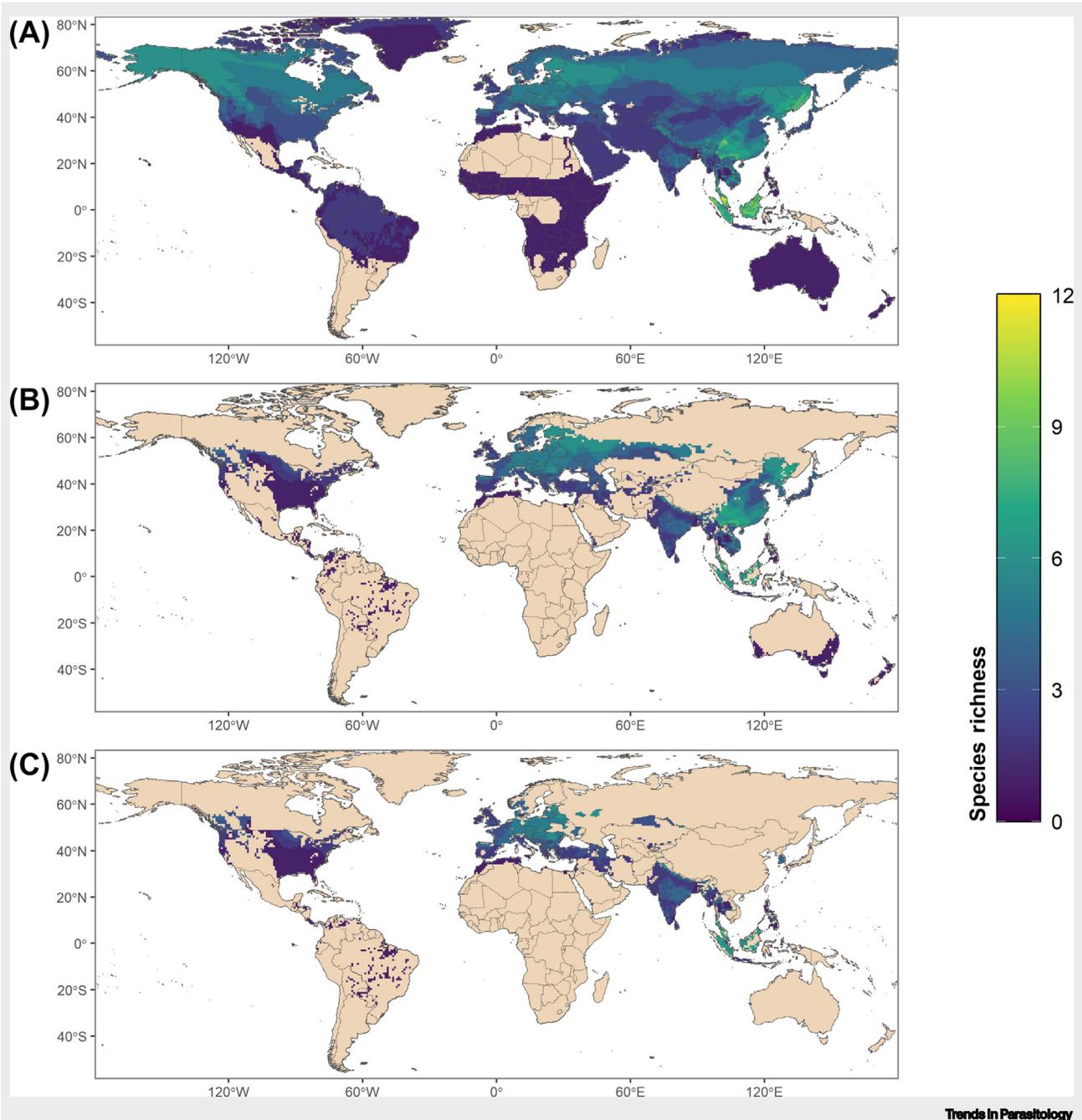


Figure 1. Predicted carnivore hosts of severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2) are widely distributed and vary in their risk of spillback infection from humans. Many terrestrial carnivores within the top 10% of predicted zoonotic capacity for SARS-CoV-2 (A) do not overlap in geographic range with human-altered landscapes (B), but many species that do persist in these landscapes also overlap areas of high COVID-19 prevalence in humans (C) and may therefore be at greater risk of becoming infected by humans, and contributing to secondary spillover following successful establishment of sylvatic transmission. This figure presents the carnivore subset of mammal species presented in [52].

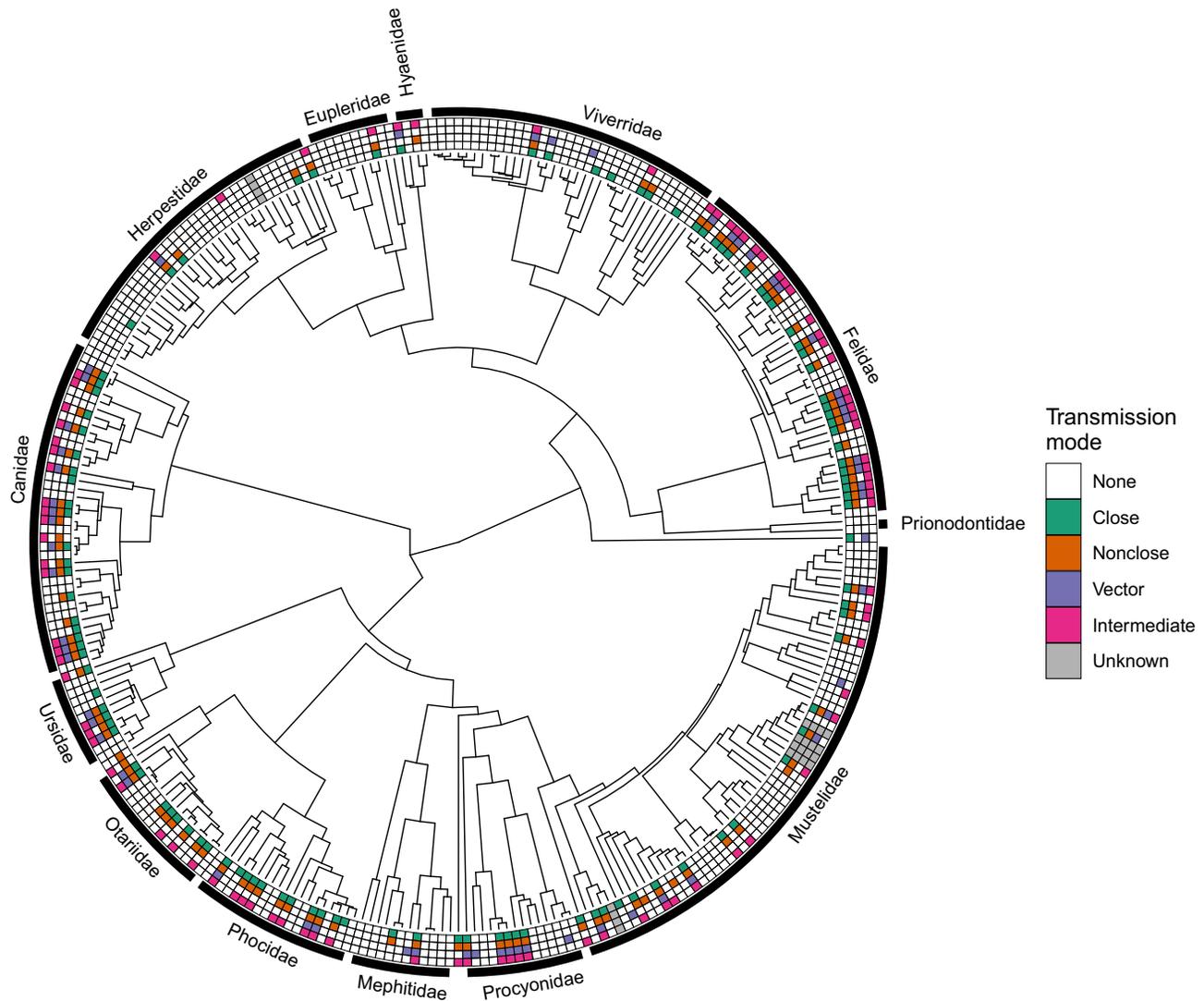
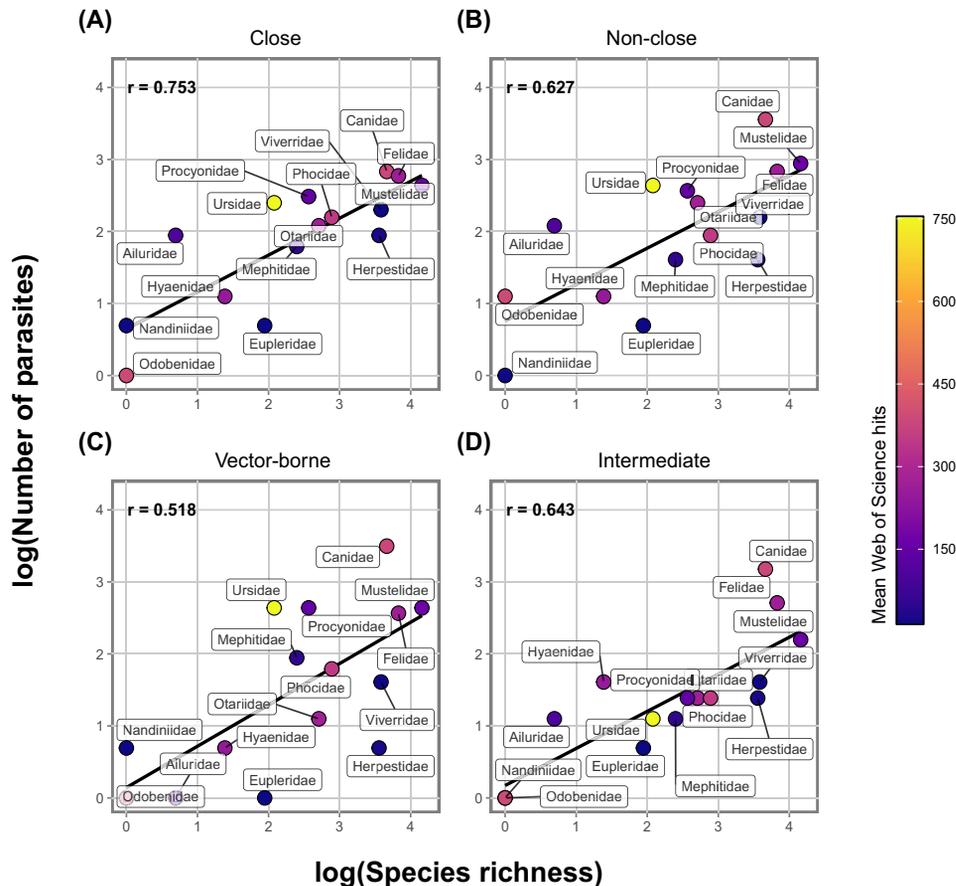


Figure 1. Zoonotic hosts are distributed throughout the Carnivora phylogenetic tree. Hosts carry one or more zoonotic parasites with four major transmission modes (legend). The heatmap of parasite transmission modes indicates families that are well sampled for parasites (Canidae, Felidae, Phocidae) vs. those that are undersampled given their species richness relative to other clades (Viverridae, Herpestidae, Mustelidae). The phylogenetic tree is a consensus tree of mammal relationships trimmed to the order Carnivora from [95].

clustering for close contact transmission (mean P value = 0.46), non-close-contact (mean P value = 0.07), vector-borne (mean P value = 0.42), or intermediate transmission modes (mean P value = 0.07) (see Box S1 for full methods and code). This lack of clustering may be driven in part from behavioral adaptations that are hypothesized to reduce exposure to some parasites. For instance, allogrooming removes ectoparasites [30], and avoidance behaviors reduce the risk of close-contact pathogen transmission [31]. While these are not all examples of zoonotic pathogens, the influence of labile behaviors on parasite richness patterns is well documented in other taxa (e.g., [32–34]) and are likely contributing to observed patterns of zoonotic parasite richness in carnivores.

We observed a positive correlation between zoonotic parasite richness and carnivore host species richness across host families and across all major parasite transmission modes (Figure 2).



Trends in Parasitology

Figure 2. Carnivore hosts of zoonotic parasites or pathogens come from multiple families, in which parasite richness varies by transmission mode (close, non-close, intermediate, vector-borne). Families that harbor more zoonotic parasites than expected (from the observed positive correlation between parasites and (the natural log of) host species richness) appear above the regression line, while families below the line harbor fewer zoonotic parasites (Pearson correlation coefficients appear in the top left corner of each plot). While nonzoonotic parasite richness is known to increase with study effort (point color indicating Web of Science hits), for zoonotic parasite richness the relationship with study effort does not appear monotonic. Zoonotic pathogens transmitted by multiple modes appear in multiple panels. The points for Odobenidae and Ailuridae are obscured in panel C (neither family hosts vector-borne zoonotic parasites).

A similar pattern is well documented for mammal parasites in general [35,36]. However, there are notable departures from this positive correlation for zoonotic parasites in particular carnivore families. For instance, across all transmission modes, the canids and felids carry more zoonotic parasites than expected for their species richness (Figure 2A–D). Similarly, Ursidae (bears) and Procyonidae (raccoons, coatis, kinkajous, etc.) carry more zoonotic parasites than expected for close, non-close, and vector-transmitted parasites (Figure 2A–C). In contrast, the Hyaenidae (hyenas) showed fewer zoonotic parasites than expected for these three transmission modes (Figure 2A–C) despite similar levels of study effort compared to other groups (as measured by Web of Science topic search hits; Table S3).

Though a greater proportion of carnivores are hosts for zoonotic parasites compared to other mammal groups [4], whether this accurately reflects zoonotic risk remains unresolved. For instance, given their functional diversity, it is possible that carnivores are acting as **sentinel**

hosts [37] rather than true reservoir hosts for zoonoses that are maintained by other species, such as their prey. Dallas *et al.* showed that host traits related to ranging are among the most important for predicting patterns of parasite sharing networks across mammal clades [29]. Stephens *et al.* showed significant overlap in parasites found in carnivores and their ungulate prey [38]. These and other comparative studies of carnivore parasites [39,40] describe parasite sharing (the number of parasites in common between two species), which could be driven by range overlaps rather than directional transmission that would occur via infection from consuming ungulate prey, for example. Understanding the degree to which carnivore hosts actively transmit zoonotic parasites to other species, including humans, is fundamental to assessing the zoonotic risk posed by this group, but incomplete characterization of the natural cycles of many zoonotic parasites remains a barrier.

Carnivores may also serve as ecological sinks that reduce zoonotic risk to humans by regulating populations of prey species that pose transmission risks to humans [41–45]. One of the best studied examples of **top-down disease control** [43] is the regulation of white-footed mouse populations by red fox in the northeastern USA [46]. Functionally diverse communities with healthy populations of predators, such as foxes, reduce the incidence of Lyme disease by limiting the density of white-footed mice. Mice are highly competent hosts for *Borrelia burgdorferi*, and the preferred hosts for larval ticks that are most likely, as nymphs, to transmit the pathogen to humans [47]. Besides consumption, population regulation also results from the indirect effects of predators on the distribution or behaviors of prey [48], for example when elk shift their habitat selection in response to the presence of wolves [49]. When prey species are also reservoirs of zoonotic disease, such ‘remote control’ of prey by predators could influence disease dynamics (e.g., [50]) and zoonotic transmission from reservoir prey. Similar nonconsumptive interactions could influence the host-seeking behavior of vectors (remote control of tick vectors by spider predators, [51]), which may influence their local abundance or distributions. In general, these phenomena have yet to be widely investigated.

Traits related to omnivory distinguish zoonotic hosts from non-hosts

To determine whether particular traits are common among carnivores that tend to host zoonotic pathogens, we reanalyzed previously published data on zoonoses and carnivore host traits to examine the effect of species-level traits on zoonotic status in this group [4,52] (Box S2). The original data on host traits and zoonotic status were collated from multiple published sources [53–56] (Tables S3 and S4). We applied a binary classification analysis to these data to assess which features are most important for differentiating zoonotic hosts from nonhost species (code to reproduce this boosted regression analysis can be found in Box S2). We found that carnivore zoonotic hosts shared a set of common features that differentiated zoonotic hosts from nonhost species with 74% accuracy (according to the area under the receiver operator curve, AUC, a common metric for measuring the performance of classification models [57]; Figure 3). Zoonotic hosts generally reach sexual maturity later than nonhosts, which appears to be driven by males reaching sexual maturity later than females. Hosts tend to have relatively few, small litters of mid- to large-sized young that are more completely developed at birth (early eye opening) following longer gestation periods. Zoonotic hosts are also distinct from nonhosts in their diets, which are composed of >20% fruit (Figure 3). The dietary diversity of omnivorous carnivores (e.g., canids) is linked to longer gestation periods and larger neonates, who receive the benefits of diverse food resources over a long period of time [58]. Neonates of omnivorous carnivores also disperse at earlier ages and are capable of foraging independently sooner than endotherm specialists [58].

Across all mammals, home ranges tend to increase with adult body size and the percentage of dietary meat [59]. Within the Carnivora, zoonotic hosts were more likely to have small to medium

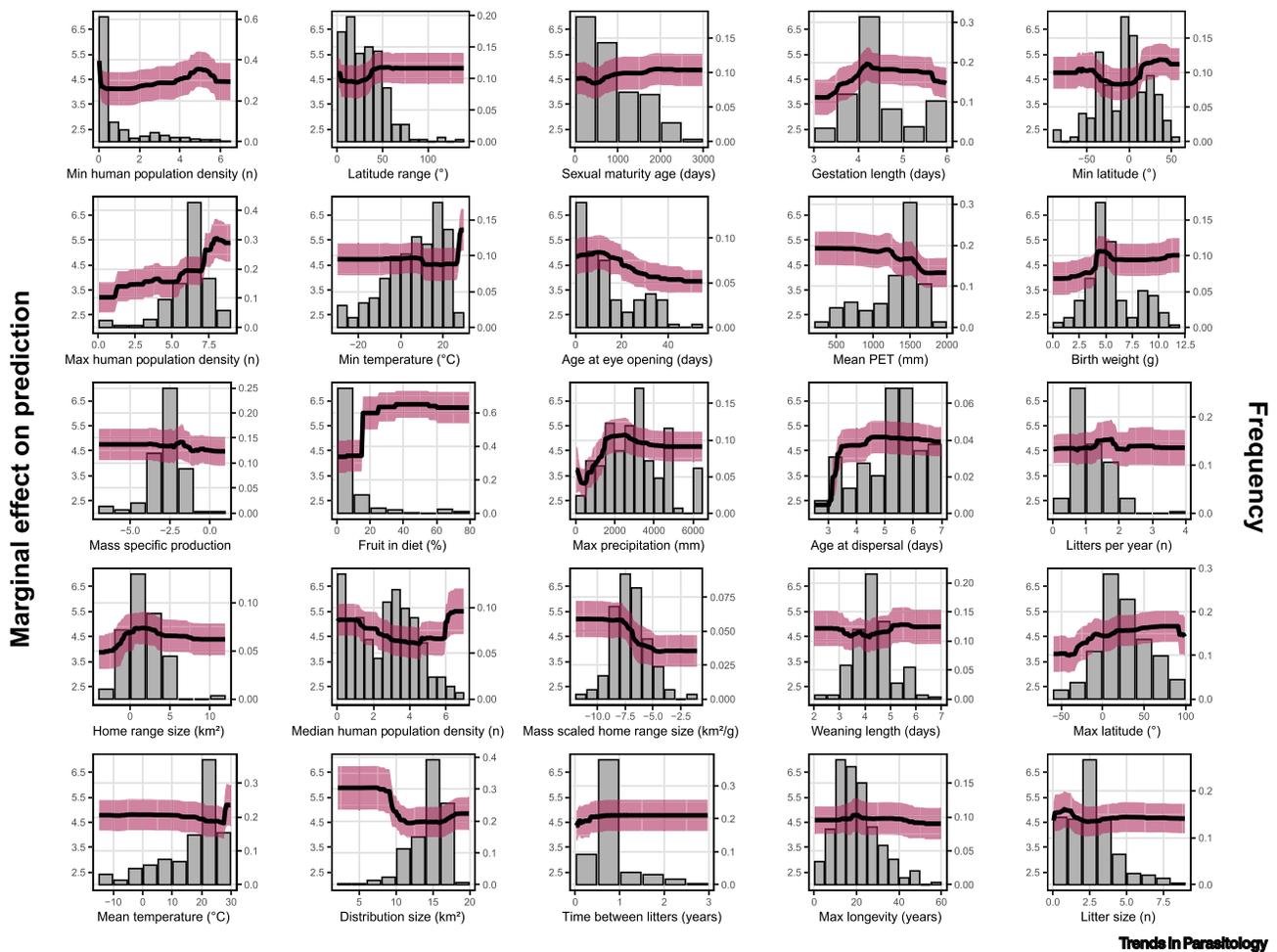


Figure 3. Zoonotic hosts in the Carnivora are characterized by a suite of correlated traits that distinguish them from non-hosts. Important traits were identified through a generalized boosted regression analysis using previously published species-level traits and zoonotic diseases reported for all extant carnivores ([4]; all data and code available in Box S2 and Table S3). Traits are listed in descending order of importance for classifying hosts from nonhosts from left to right, top to bottom (black lines), and frequency histograms depict trait values across all carnivore species. Bolded lines represent the mean of 10 bootstrap runs, while the shaded regions show the 95% confidence interval. Left y-axis is the marginal effect of a given variable (x-axis) on model prediction accuracy. The right y-axis represents the fraction of species with trait values in a given bar (bin). Due to heavily skewed distributions, the following variables are log-transformed: minimum human population density, maximum human population density, mass specific production, home range size, median human population density, mass scaled home range size, and distribution size. PET, potential evapotranspiration.

home ranges more typical of omnivores (Figure 3). Even after scaling for body size, zoonotic hosts tend to occupy relatively small home ranges that occur predominantly in northern latitudes where temperature minima and means are relatively low. Notably, neither taxonomy (family level variables) nor marine vs. terrestrial adaptations were important predictors of zoonotic reservoir status in carnivores. Thus, functional traits and geographic range captured important variation relevant to zoonotic potential in carnivores. A key outstanding question then is whether disease dynamics are similar in distantly related species with similar functional roles across ecological communities [60].

Taken together, diet and traits reflecting diverse foraging habits are particularly important indicators of the likelihood of harboring zoonotic parasites in carnivores (e.g., [61]). Foraging habits in many species vary with seasonality in food availability that may provide insight to variation in

host tolerance and infection recrudescence. Highly frugivorous carnivores, for instance, sample a diversity of food items that become available at different times during the year [62]. Notably, periods of intense frugivory lead to unexpectedly large increases in energy metabolism in bears comparable to the high metabolic rates typical of frugivorous bats (e.g., *Artibeus jamaicensis*, *Rousettus aegyptiacus*) [63], a feature that is thought to contribute to the unique **tolerance** of bats to virulent zoonotic viruses [64]. High metabolic rates are also characteristic of many fast-living species in which zoonotic risk is hypothesized to be high compared to slow-living species [65,66]. Thus, the capacity for extremely high metabolic rates (either seasonally or for sustained periods) may be a distinguishing feature of zoonotic reservoirs across mammalian orders.

Seasonally dynamic foraging behaviors balance protein:carbohydrate ratios and macronutrient intake with shifting food availability [67,68]. Carnivore species adapted to seasonal habitats that impose energy constraints (foraging for limited resources, thermoregulating in colder temperatures) may allocate energetic resources to maximize fitness. In omnivores, this strategy may be counterbalanced by greater functional diversity that relaxes resource constraints [69] and

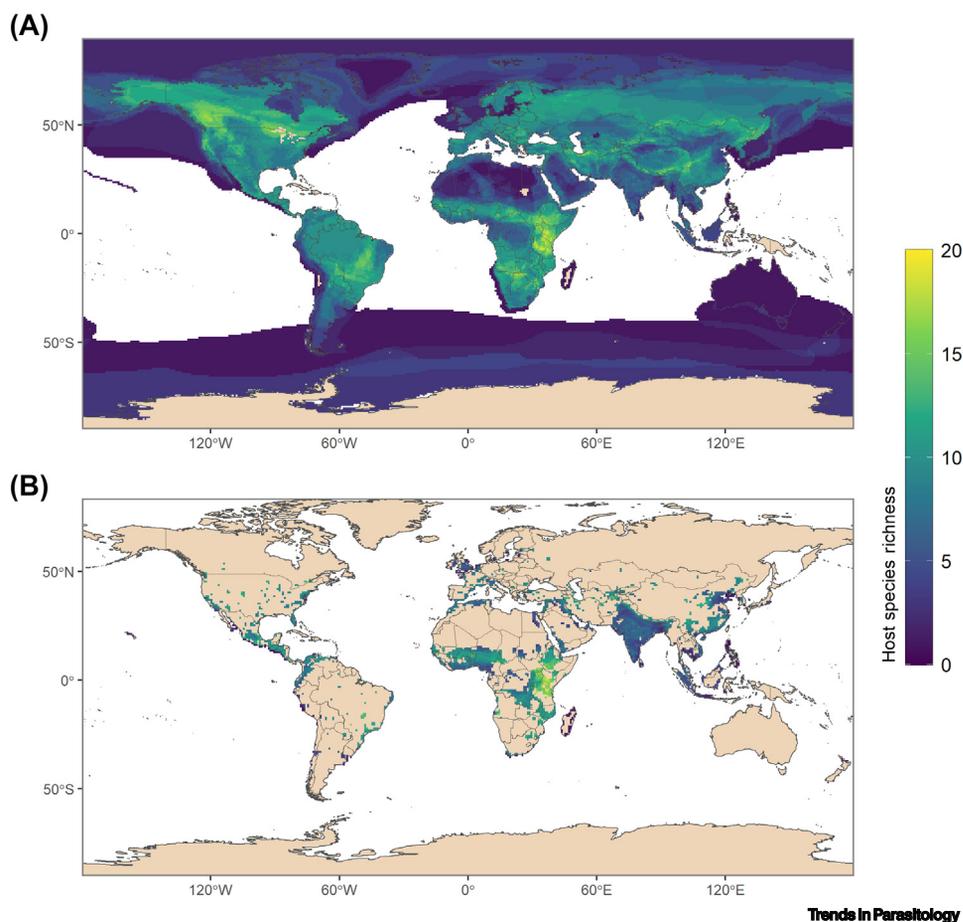


Figure 4. Aquatic and terrestrial carnivore hosts of zoonotic diseases have wide, global distribution with multiple hotspots on multiple continents. Geographic ranges of currently known carnivore hosts (A) overlap with regions of high human population density growth from 2000 to 2020 (B). Multiple zoonotic host species overlap with the areas representing the top 20% of global human population growth from 2000 to 2020 [96], such as cougar (*Puma concolor*), lion (*Panthera leo*), palm civet (*Paguma larvata*), and badger (*Meles meles*) (B). Spatial resolution is 100 km². A full species list is available in Table S5. Areas with no species of interest are colored light beige (land, e.g., Antarctica) or white (ocean, e.g., the Gulf of Mexico).

underpins patterns of parasite tolerance vs. resistance [70]. Infection tolerance by hosts (their ability to limit the negative health effects of parasitism) and related differences in immune profiles have been observed for other seasonally dynamic populations, for example in rodents and birds (reviewed in [71]), though similar studies for carnivores are lacking [72]. Infection tolerance may also correspond to a more general ecological tolerance by some omnivorous carnivores (e.g., [73]) enabling persistence and potentially more successful adaptation to a diversity of habitats and altered climate regimes. The effects of resource availability/allocation and infection tolerance is a research frontier in disease ecology [74] with much to offer toward our understanding of host defenses and disease dynamics in the Carnivora.

Biogeography of zoonotic risk

Carnivores are among the most widely distributed zoonotic hosts globally [4]. Hotspots of carnivore host diversity occur on nearly every continent, in tropical, temperate, and arctic regions (Figure 4A). There are numerous carnivore hosts that geographically overlap with areas that have experienced human population growth over the past two decades (Figure 4B), with hotspots in Southeast Asia, parts of East and West Africa, and southern Mexico through Central America. While this view obscures important zoonotic transmission dynamics occurring in less populous areas (e.g., northern latitudes, particularly subarctic and arctic regions), the top quintile of locations where human population density has increased over the last 20 years maps on to locations where zoonotic hosts are increasingly in proximity to humans.

Of course, these maps only capture the distribution of carnivore hosts of zoonotic parasites very broadly and do not reflect the species interactions within communities [60], especially those taking place in human-altered landscapes. Changes in predator–prey dynamics, and movement behavior caused by urbanization (e.g., [75]), will be critical for understanding zoonotic disease risk [76,77] and anthroponotic risk to wildlife [52]. These alterations may be particularly important and understudied in northerly latitudes experiencing some of the most rapid climate warming compared to other regions [78]. In some habitats, the velocity of climate change is predicted to exceed the ability of species to keep pace [79]. Even in protected areas within northern biomes such as boreal forest and tundra, intact communities are predicted to persist less than 100 years under current warming scenarios [79]. For many carnivores, particularly those occupying higher trophic positions, the impacts of warming in combination with anthropogenic effects on biodiversity and environmental conditions are expected to lead to unpredictable trophic cascades affecting all lower trophic levels [76,77,80,81] with potentially profound effects on zoonotic parasite diversity and transmission risk.

Concluding remarks

Compared to more speciose mammal groups, our understanding of zoonoses among carnivores is poor, especially for marine species and species found at northern latitudes. Based on what is currently known about zoonotic parasites in carnivores, dietary diversity and diversity in foraging habits appear to be accurate indicators of zoonotic status in this group, but the mechanistic underpinnings of this relationship remain unclear (see [Outstanding questions](#)). In addition to preventing a clearer picture of zoonotic capacity and omnivory, gaps and biases in baseline knowledge about the life history and ecology of carnivore hosts and their parasites make more challenging the already difficult task of predicting how transmission from wild hosts may propagate through bridge hosts to humans. Data from expanded surveillance is needed to better characterize carnivores as sentinels, sinks, regulators, or bridges for the transmission of zoonotic parasites to humans, and to assess anthroponotic risks they face from increasing human populations. Many carnivores are declining globally [82], and all will be forced to adapt to a warming planet in which the effects of climate change will be greatest at northern latitudes where many

Outstanding questions

Is there a general relationship between omnivory and zoonotic capacity in mammals? What are the mechanistic underpinnings of this relationship in carnivores?

Does the richness of parasites with trophic transmission scale with omnivory across mammals?

Do predators bioaccumulate the parasites of their prey?

Are carnivores particularly tolerant to zoonotic parasites compared to other mammal groups?

How does infection tolerance in carnivores covary with ecological tolerance?

To what degree are carnivores serving as zoonotic sinks or sentinels vs. reservoirs of transmissible infection?

Are there distinct predictors of zoonotic capacity in carnivores? Do they differ from those of other mammal groups (e.g., bats and rodents)?

How does the zoonotic potential of marine carnivores compare to terrestrial carnivores? What traits of marine mammals influence their zoonotic potential?

How do human-altered environments influence zoonotic capacity in carnivores?

Does the zoonotic potential of a species vary within its range and, if so, what factors drive this?

Do the geographic patterns of carnivore zoonotic parasites vary according to parasite taxonomy or parasite traits?

zoonotic hosts in this group are currently distributed. Some carnivores will likely thrive as small mammal ranges and plant food resources expand to warmer climates [83], or in human-altered habitats favoring species with high ecological tolerance. However, predicting how such imminent changes will affect zoonotic transmission risk from this group is difficult [84], especially given the paucity of comparative studies of the relationship between functional diversity and infectious disease (see Outstanding questions), which have been held back by a lack of basic information about the ecology of carnivore species and the pathogens they carry.

Acknowledgments

This work was improved by previous discussions with John L. Gittleman, and was supported by the NSF Ecology and Evolution of Infectious Diseases program (DEB 1717282).

Declaration of interests

The authors declare no competing interests.

Supplemental information

Supplemental information associated with this article can be found online at <https://doi.org/10.1016/j.pt.2021.08.006>.

Resources

ⁱ<https://doi.org/10.5281/zenodo.4139818>

ⁱⁱwww.oie.int/en/scientific-expertise/specific-information-and-recommendations/questions-and-answers-on-2019-novel-coronavirus/events-in-animals/

ⁱⁱⁱ<https://promedmail.org/promed-post/?id=8015608>

^{iv}<https://bit.ly/3AdodZS>

^v<https://ecos.fws.gov/ecp/report/species-listings-by-tax-group?statusCategory=Listed&groupName=All%20Animals>

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