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Species loss on spatial patterns and composition of zoonotic parasites

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Species loss can result in the subsequent loss of affiliate species. Though largely ignored to date, these coextinctions can pose threats to human health by altering the composition, quantity and distribution of zoonotic parasites. We simulated host extinctions from more than 1300 host–parasite associations for 29 North American carnivores to investigate changes in parasite composition and species richness. We also explored the geography of zoonotic parasite richness under three carnivore composition scenarios and examined corresponding levels of human exposure. We found that changes in parasite assemblages differed among parasite groups. Because viruses tend to be generalists, the proportion of parasites that are viruses increased as more carnivores went extinct. Coextinction of carnivore parasites is unlikely to be common, given that few specialist parasites exploit hosts of conservation concern. However, local extirpations of widespread carnivore hosts can reduce overall zoonotic richness and shift distributions of parasite-rich areas. How biodiversity influences disease risks remains the subject of debate. Our results make clear that hosts vary in their contribution to human health risks. As a consequence, so too does the loss (or gain) of particular hosts. Anticipating changes in host composition in future environments may help inform parasite conservation and disease mitigation efforts.

1. Introduction

Extinction rarely occurs in isolation. Instead, because of the connections among strongly interacting species, the loss of one species can lead to the loss of affiliate species, a phenomenon referred to as extinction cascades or coextinction [1–4]. Parasites, by virtue of their dependence on one or more hosts, are affected by changes in the abundance, diversity and geography of those hosts [5–9]. As a consequence, changes in host populations will be likely to alter the relative commonness and distribution of parasites (including zoonotic parasites) able to colonize and infect humans [10,11]. Zoonotic parasites capable of infecting humans comprise nearly 60% of all human parasites [12] and are arguably the most prevalent human–natural coupled system. It is becoming clear that regional and global change can directly alter the composition and prevalence of zoonotic diseases [13–18]. What remains unclear is the extent to which changes in host faunas might also affect zoonotic parasites, whether in terms of their diversity, composition or geographical distribution.

The parasites of mammalian carnivores (Order Carnivora) comprise a diverse fauna that includes species that can pose risks for the health of humans and domesticates, and species that warrant conservation in their own right. On the one hand, extant carnivores—which include some of the most charismatic, vulnerable and influential species on the Earth [19]—can be threatened by their parasites (e.g. rabies, canine distemper). On the other hand, colonized carnivores can threaten other species in as much as they serve as reservoirs of zoonoses such as plague, toxoplasmosis, trichinosis and echinococcus [20]. Therefore, carnivores not only succumb to the consequences of parasites, but also serve to spread them. Over half of the 125 emerging zoonotic diseases are associated with carnivores [21]. While many carnivores are under threat and changes in carnivore populations will be likely to affect assemblages of parasites in any particular region, no studies have considered the broad-scale effects of carnivore extinctions on zoonotic

parasites of importance for human health. *A priori*, we predict local or regional extinctions of wide-ranging carnivore species to pose the greatest influence on health risks because wide-ranging hosts have been shown to host more parasite species in carnivores [22] and other mammals [23,24].

Ultimately, the fate of zoonotic parasites in light of host extinctions is dependent upon attributes of both hosts and their parasites, particularly parasite specificity and the threat status of hosts. Previous theoretical research showed that the extinction of carnivores could lead to the extinction of specialist parasites and simultaneously cause generalist parasites to become proportionally more widespread [25]. We build on these findings to consider the implications of carnivore extinctions on the distribution of zoonotic parasites and associated human exposure. First, we quantified the diversity of zoonotic parasites in 29 terrestrial North American carnivore species. Next, we evaluated the proportional change in the composition of parasites as a function of modelled host extinctions. It is unlikely that many carnivore species will go extinct in the near future from North America, but extirpations occur frequently. In this light, we assessed how the loss of carnivores under different composition scenarios would affect the spatial distribution of zoonotic parasite richness. Given the increased pressures on many carnivore populations and the continued emergence of zoonotic diseases, our study is both timely and pertinent to illuminate potential changes in the geographical patterns of parasite richness and human health exposure in a changing environment.

2. Material and methods

(a) Zoonotic parasite species richness in carnivores

We used a list of parasites recently compiled for North American carnivores (see electronic supplementary material, table S1) to explore consequences of coextinction for human health and spatial patterns of zoonotic species richness [22]. We applied a broad definition of parasite by including both microorganisms such as viruses, bacteria and protozoa as well as macroorganisms such as cestodes, nematodes, trematodes and acanthocephale worms. We excluded arthropods (e.g. ticks, lice) from our analyses because, although vectors of many problematic parasites, they are infrequently the causative agent for zoonotic diseases. We categorized each parasite as being zoonotic if it had been reported as a natural case in humans relying primarily on the host–parasite database from the Natural History Museum (www.nhm.ac.uk/research-curation/scientific-resources/taxonomy-systematics/host-parasites/database) and a review on human diseases [12]. With these data, we explored zoonotic richness and patterns of specificity among parasite groups. We did not correct for sampling effort (i.e. number of published studies per host) because there was a weak relationship between parasite species richness and sampling effort after accounting for range size among carnivores ($r^2 = 0.002$, $p = 0.79$).

(b) Coextinction simulation and changes in parasite composition

We constructed presence–absence matrices of carnivore–parasite associations compiled from the literature and conducted simulations within the freeware program ESTIMATE5 following Koh *et al.* [1] and Dunn *et al.* [25]. By treating carnivore hosts as samples for the presence of parasite species, we could estimate parasite loss as a function of simulated random carnivore extinctions. We took

the inverse of sample accumulation from 100 randomizations, which traditionally measure species richness as more samples are added. Here, we evaluated the corresponding loss of parasites with the removal of each host sample. First, we partitioned the parasite data into zoonotic and non-zoonotic species, and determined whether the consequences of carnivore loss were comparable for the two groups. We expected parasites with more hosts to be less vulnerable to extinction, recognizing that zoonotic status already implies these parasites have at least two hosts: the carnivore and humans. We then repeated the simulation for each parasite group individually (e.g. protozoa and then, separately, trematodes) to determine how parasite composition was altered by host extinctions. Parasites differ in their risks to humans and other animals based on their ability to transmit and exploit new hosts, such that changes in the diversity of some groups are likely to have far greater consequences than changes in others [26]. Many viruses, in particular, are able to ‘jump’ the species barrier to new hosts owing to their high mutation and transmission rates [27–29] such that loss of hosts for viruses might have more negative consequences for human health than for other parasites that are less adaptable.

(c) Alterations to the spatial patterns in zoonotic species richness

We examined how the loss of carnivores could affect the spatial distribution of zoonotic parasites. The paucity of surveillance data, even for the most ubiquitous zoonoses, makes depicting the individual distributions of parasites at a management-relevant scale across the United States currently unattainable. Instead, we overlaid the distributions of hosts and assumed the entire parasite assemblage occurs throughout the distribution of a given host. Although this approach is unlikely to reflect the actual distribution of parasites, given additional abiotic and biotic requirements necessary for their presence, it is a reasonable first approximation. Harris & Dunn [22] showed that spatial patterns of parasite species richness were consistent, even if the distributions of host and parasites were not completely congruent. Additionally, we present uncorrected data because there was not a strong relationship between sampling effort on total ($r^2 = 0.07$; $p = 0.08$) and specialist ($r^2 = 0.07$; $p = 0.15$) parasite species richness across grid cells.

Because host extinctions are non-random and hosts pose varying levels of threat to humans based on their competency to be reservoirs, we evaluated changes in spatial patterns of zoonotic parasite species richness by comparing two host extinction scenarios to the original full model with all carnivores present. First, we removed widespread carnivore hosts that had distributions occurring in the highest quartile of species distributions in the entire dataset in North America. Widespread hosts may contribute more to spreading zoonotic disease because they have more parasites and have higher rates of encounter with other species, including humans. These hosts included: red fox (*Vulpes vulpes*), ermine (*Mustela ermine*), coyote (*Canis latrans*), grey wolf (*Canis lupus*), American mink (*Mustela vison*), least weasel (*Mustela nivalis*) and wolverine (*Gulo gulo*). Second, we removed carnivore hosts that are of conservation concern, representing the species most likely to be threatened with extinction. We defined species of conservation concern as those species listed as threatened, endangered or candidate in the US Endangered Species Act. These threatened and endangered host species (TES) included: grey wolf (*C. lupus*), red wolf (*Canis rufus*), island fox (*Urocyon littoralis*), Canada lynx (*Lynx canadensis*), fisher (*Martes pennanti*), black-footed ferret (*Mustela nigripes*) and brown bear (*Ursus arctos*).

We evaluated the total and proportional change in zoonotic parasite species richness based on the various host composition scenarios: all hosts present, widespread hosts removed and TES hosts removed. Because the absence of certain species may alter spatial patterns of zoonotic species richness, changes in zoonotic risk for humans may also be observed. We defined risk based on exposure

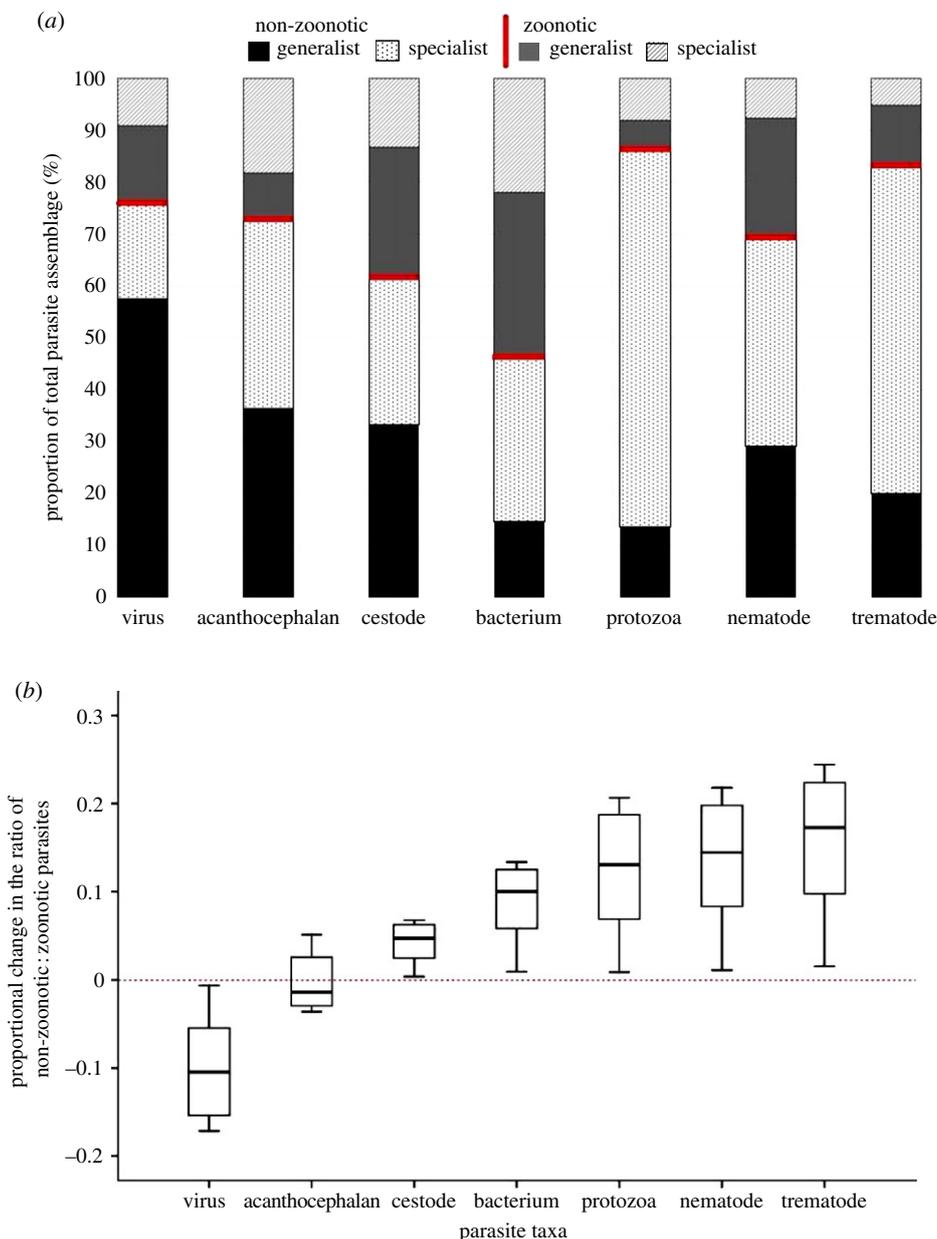


Figure 1 (a) Data summary of parasite composition: proportion zoonotic, non-zoonotic and specialist among taxa from host–parasite records reported in 29 North American carnivores. (b) Proportional change in the ratio of non-zoonotic to zoonotic parasites when all carnivores go extinct one by one. Parasite taxa below the no-change reference line (dashed line) indicate fewer non-zoonotic than zoonotic parasites (i.e. more zoonotic parasites within the community) and those above have more non-zoonotic parasites. (Online version in colour.)

and assumed that risk was higher when more humans resided in parasite-rich areas. We identified the 90th percentile of parasite species richness (i.e. highest 10%) for each scenario and mapped their locations to evaluate the geographical extent of human exposure. We calculated the number of people inhabiting these parasite-rich grid cells in North America according to population abundance estimates. Human population size for 2010 was extracted from the Gridded Population of the World dataset at a 1° latitude/longitude resolution (<http://sedac.ciesin.columbia.edu/gpw/>).

3. Results

(a) High specificity and diversity in zoonotic parasites of North American carnivores

The dataset comprised more than 1300 host–parasite records. Of the 394 unique parasite species roughly a third were zoonotic ($n = 114$); 32% of those were nematodes. Over half of all

bacteria species included in our study from North American carnivores were zoonotic (figure 1a). Some of the most frequently reported (largest number of host species) zoonotic parasites included: *Yersinia pestis* (causative agent for plague, found in $n = 15$ carnivore hosts), *Trichinella nativa* ($n = 16$); *Toxoplasma gondii* (a leading cause of food-borne illness in the US, in $n = 15$) and *Leptospira interrogans* ($n = 10$). Conversely, 35% of zoonotic species were found only in a single carnivore species (i.e. carnivore specialist parasites), though some of these are also present in other non-carnivore animal species.

Carnivore hosts varied in zoonotic parasite species richness ($n = 29$, mean = 14, s.e. = 2.5). The raccoon (*Procyon lotor*) and coyote (*C. latrans*) had the greatest number of zoonotic parasites, with 42 and 45 species, respectively. At the opposite extreme, only one zoonotic parasite has been reported from the least weasel (*M. nivalis*). Zoonotic parasite species richness did not differ as a function of the conservation status of host species (Wilcoxon $W = 67$, $p = 0.627$) or their

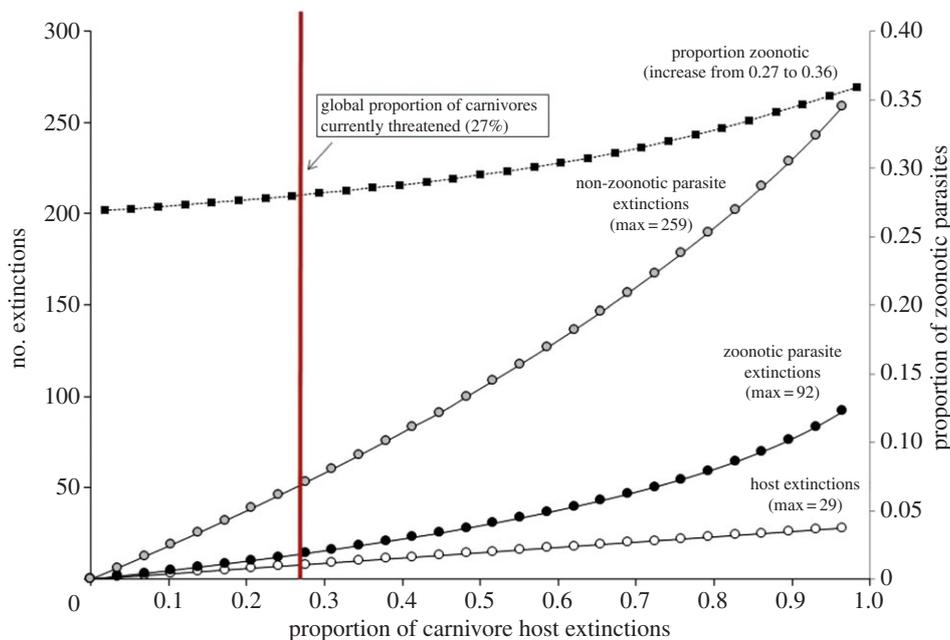


Figure 2 The number of non-zoonotic parasite extinctions (grey circles), zoonotic parasite extinctions (black circles), the proportion of the total parasite assemblage that is zoonotic (black squares) and the number of extinct carnivores (white circles). Values represent means from 100 simulations. (Online version in colour.)

geographical range sizes (Wilcoxon $W = 70.5$, $p = 0.759$). However, host rarity influenced the number of specialist zoonotic parasites among hosts; specialists tended to be confined to common hosts, whereas hosts of conservation concern hosted generalists. The fisher (*M. pennanti*) was the only TES that hosted a zoonotic specialist parasite not reported on any other carnivore host in our database.

(b) Both the proportion and composition of zoonotic parasites were altered by carnivore host extinctions

Our random simulations predict that the extinction of a single host could lead to multiple parasite extinctions, with the caveat (which we will return to) that no switches to new hosts occur and host extinctions are random with respect to host identity. For example, we estimate that on average 67 parasites would go extinct if eight North American carnivores went extinct based on mean outputs from 100 simulations (figure 2). However, the proportion of zoonotic parasite extinctions owing to carnivore extinctions was lower than that of non-zoonotic parasites in part owing to the lower host-specificity in this group. On average, zoonotic parasites exploited twice the number of carnivore hosts compared with non-parasites ($T = -4.75$, $p < 0.001$). Additionally, the proportion of specialist parasites (which exploit only one carnivore host) was higher for non-zoonotic parasites across all taxa (figure 1a). As a result, the proportion of parasites that were zoonotic changed as carnivores went extinct. However, this ratio between zoonotic and non-zoonotic varied across parasite taxa. Carnivore extinctions led to increases in the proportions of parasite species that were zoonotic viruses and acanthocephales, but did not lead to increases for other parasite taxa (figure 1b).

(c) Importance of carnivore host composition on zoonotic parasite geography

Because carnivore hosts vary in the number of zoonotic parasites they harbour, changes in host distribution will alter spatial patterns of zoonotic parasite species richness. Removing carnivore

hosts of conservation concern resulted in estimates of zoonotic species richness per grid cell (range = 2–108) similar to those when no hosts went extinct (range = 2–109). Furthermore, there was spatial congruence in the patterns of diversity of zoonotic parasites when TES were removed and in the no-host extinction scenario. Conversely, removing widespread hosts reduced zoonotic parasite species richness (range = 2–89) and led to the extinction of 13 parasite species from carnivores, including *Giardia duodenalis*, canine rotavirus and *Dirofilaria repens*. Losing widespread carnivore hosts (as opposed to TES hosts) also altered the geographical pattern of zoonotic species richness; the geographical locations of zoonotic-rich areas shifted to mid-longitudes (figure 3).

Contrary to *a priori* predictions, locations with the most zoonotic parasites (i.e. 90th percentile) varied among the different host extinction scenarios. When all carnivore hosts were present, approximately 59 million people lived within the top zoonotic-rich grid cells. When TES hosts were removed, human exposure was reduced by 15 million people. By contrast, human exposure to zoonotic parasites increased by 21 million people when widespread hosts went extinct (figure 4). When considering the entire spatial extent (not just the most parasite-rich cells), nearly all 1° latitude/longitude grid cells (98%) experienced some change in carnivore diversity (and hence zoonotic parasite species richness) when widespread hosts went extinct. The proportional decrease in zoonotic species richness across space varied from 0 to 0.77 when widespread hosts were removed. Furthermore, the greatest change in zoonotic species richness occurred in northern latitudes where the human population is lower. Nevertheless, over 900 000 people reside in the 57 860 km² area that would experience a 75% or greater reduction in zoonotic parasite species richness with the extinction of widespread carnivores.

4. Discussion

Despite growing efforts to explore consequences of species loss, few studies have examined how extinction alters

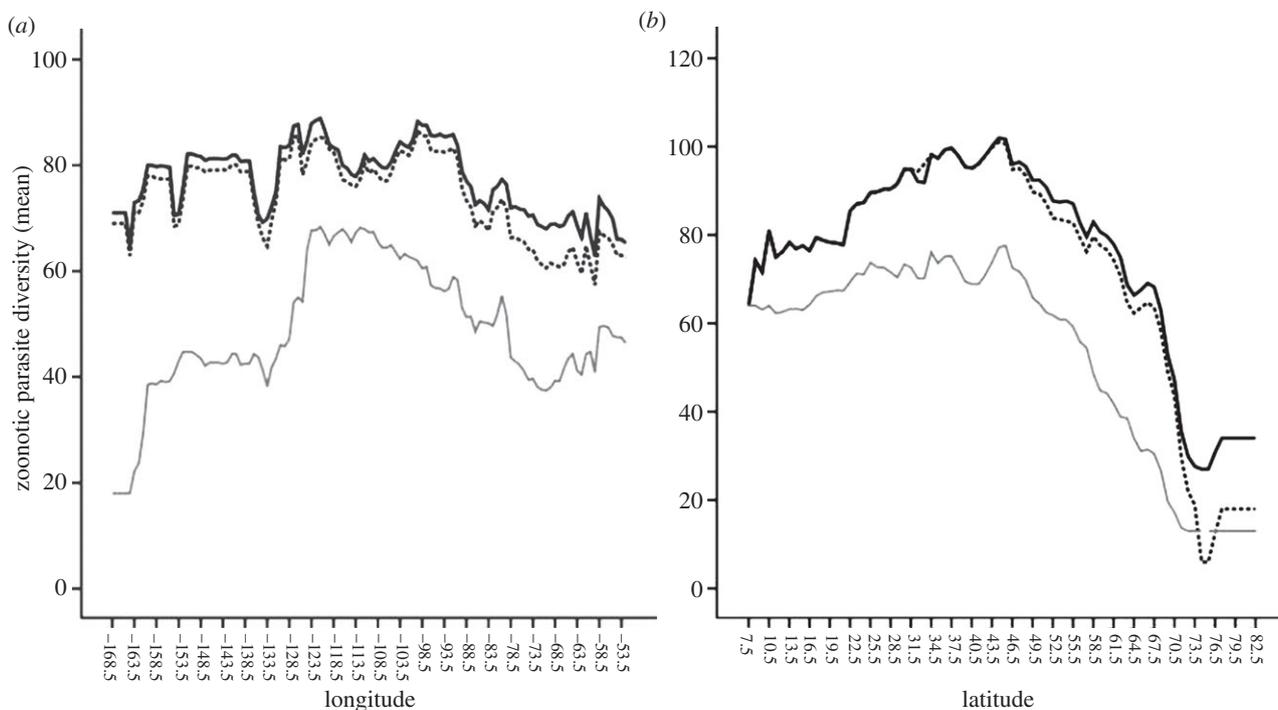


Figure 3. (a–b) Patterns of zoonotic parasite species richness resulting from three carnivore-extinction scenarios: all hosts present (black line), TES removed (black dotted line) and widespread hosts removed (grey line).

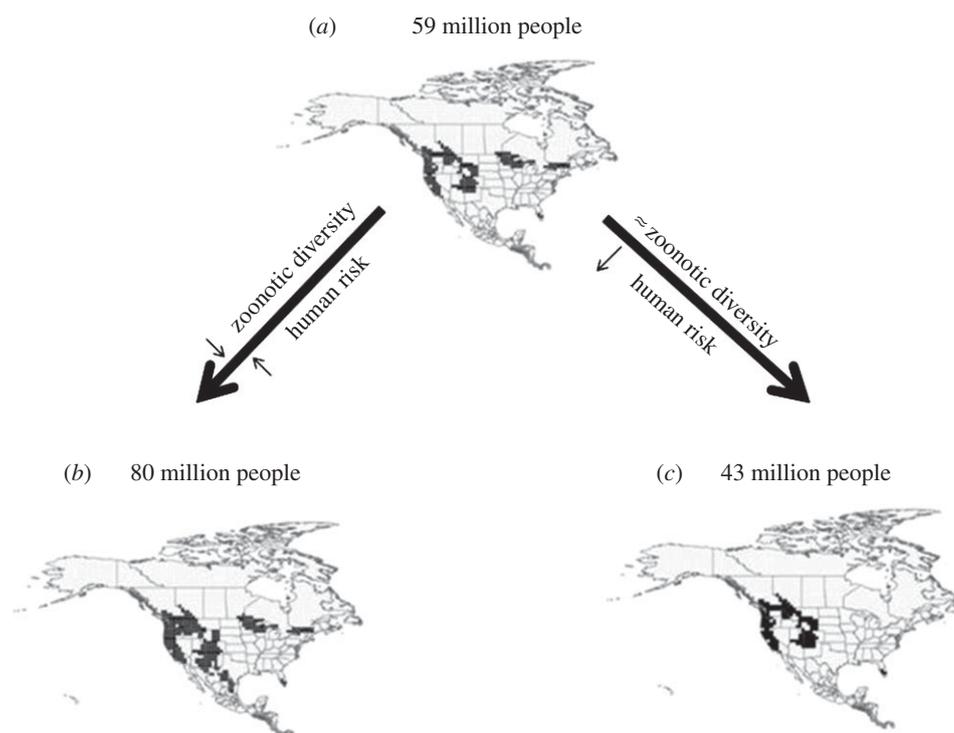


Figure 4. Overlap between zoonotic parasite hotspots (top 10% of grid cells) and human population size under different carnivore composition scenarios: (a) all hosts present, (b) widespread hosts removed and (c) TES removed.

patterns of diversity for affiliated parasite assemblages. Nor have many studies considered the implications of changing patterns in biological diversity for human health (although see [30]). Here, we show that even in the simplest possible case, the simulated extinction of carnivore hosts can alter the composition, relative proportion and spatial patterns of zoonotic parasites. While it is unrealistic to imagine that large numbers of carnivore species will go extinct in North America in the near future, local extinctions of carnivores are common and our results suggest these local extinctions

affect not just the ecological roles of carnivores as predators, but also their ecological roles as (alternate) hosts.

When hosts went extinct, the extinctions of parasites were not random with respect to the type of parasite or whether a parasite was zoonotic. In some groups, for instance nematodes, zoonotic parasites were more likely than non-zoonotic parasites to go extinct (figure 1b), which might actually be beneficial to humans. Conversely, in other groups, zoonotic parasites are likely to be proportionally more common as more carnivores become extinct, whether locally or globally.

Zoonotic viruses, in particular, tend to be generalist, and so are robust to individual host extinctions. They persist even when host extinctions are common. This is potentially troublesome because many emerging diseases in humans and wildlife are zoonotic viruses [28,31,32].

We also found that the extinction or extirpation of carnivores has the potential to alter geographical patterns of zoonotic exposure (figure 4). Put another way, the geography of risk to humans from zoonotic disease will change as a function of changes in carnivore host populations, like those that happen owing to local extinctions, reintroductions or even changes in response to climate change. The precise spatial patterns of zoonotic parasites and exposure to humans that resulted from continent-wide extinctions depended greatly on which hosts were lost. The effects on zoonotic species richness overall from the extinction of carnivore hosts of conservation concern, such as the red wolf or Canada lynx, were minimal because rare hosts tended to have few unique zoonotic parasites. But the 'hotspots' of risk for humans were geographically reduced. By contrast, losing widespread hosts such as the red fox or American mink reduces the number of zoonotic parasites and alters the geographical distribution of zoonotic-rich areas. Some parasites predicted to go extinct will persist in other non-carnivore hosts, whereas other parasite species that require a mammalian carnivore to complete their life cycle (for example the nematode *Echinococcus granulosus*) would be completely extinguished from wild animal populations within the geographical boundaries of our study.

In our models, we assumed that as carnivores went extinct, their associated specialist parasites would succumb to the same fate as their hosts. Surprisingly, given the number of documented or predicted animal and plant extinctions, few empirical examples of parasite coextinctions have been recorded [4,25]. One reason for the rarity of observed coextinction events may be that rare hosts tend to have relatively fewer specialist parasites [22,33]. Even if hosts with specialist parasites go extinct, it is not necessarily a foregone conclusion that their parasites will also go extinct. Alternatively, when host populations dwindle, parasites may switch to more abundant hosts even if the abundant hosts are less preferred, as has been argued to have been the case with the transition of bedbugs from bats to humans [34]. In the modern context, abundant alternative hosts onto which parasites might switch are most likely to be our domesticated species or humans. It is possible that many of the non-zoonotic species in our database might, when faced with a rare host, switch to humans. Events in which parasites have 'jumped' onto humans from rarer original hosts include HIV-1, SARS, Ebola and Hendra virus [13,15,26,28]. Clearly, not all rare parasites are equally likely to switch to humans and evaluating life-history attributes can help elucidate

likely scenarios based on transmission mode, evolutionary capacity and geographical proximity [29,35]. With geography, it is useful to consider not just the locations of zoonotic hotspots or rare zoonotic species, but also how those regions overlap with human populations. The distributions of carnivores overlap some of the most densely populated regions. Such overlap raises concern about just how often zoonotic parasites switch to alternative hosts when their normal primary host's populations decline.

Although the association between host and zoonotic parasite species richness is clear, whether parasite-rich areas equate to greater risk to human health remains unanswered. At least at fine spatial scales and for some vector-borne diseases, biodiversity can buffer or 'dilute' the impacts of zoonotic diseases for humans [36–39]. A regional study in Africa also showed a negative relationship between wildlife species richness and bovine tuberculosis [40]. If the dilution hypothesis was to apply at the spatial scale and the parasite assemblage included in our study, it would suggest that host extinctions would increase the risk to humans from those zoonotic parasites that persist because the hosts that went extinct no longer dilute the impacts of such parasites. However, in some cases, species composition rather than species richness *per se* determines the effects of biodiversity on disease [41]. Our results, in part, corroborate this statement in as much as removing widespread hosts versus TES hosts had differential effects on zoonotic species richness and distribution. In addition, at a large scale, parasite prevalence and diversity appear to be positively rather than negatively correlated [42]. Likewise, we might expect geographical variation in the prevalence of certain zoonotic parasites to be associated with overall zoonotic species richness in North America. Regardless of whether dilution or amplification occurs, what remains conspicuous in our results is that hosts vary in their contribution to human health risks. Anticipating changes in host composition in future environments may help inform both parasite conservation and disease mitigation efforts.

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