The ghost of hosts past: impacts of host extinction on parasite specificity

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Abstract

A growing body of research is focused on the extinction of parasite species in response to host endangerment and declines. Beyond the loss of parasite species richness, host extinction can impact apparent parasite host specificity, as measured by host richness or the phylogenetic distances among hosts. Such impacts on the distribution of parasites across the host phylogeny can have knock-on effects that may reshape the adaptation of both hosts and parasites, ultimately shifting the evolutionary landscape underlying the potential for emergence and the evolution of virulence across hosts. Here we examine how the reshaping of host phylogenies through extinction may impact the host specificity of parasites, and offer examples from historical extinctions, present-day endangerment, and future projections of biodiversity loss. We suggest that an improved understanding of the impact of host extinction on contemporary host-parasite interactions may shed light on core aspects of disease ecology, including comparative studies of host specificity, virulence evolution in multi-host parasite systems, and future trajectories for host and parasite biodiversity.

Introduction

The Earth's biodiversity is in the midst of a crisis, with current rates of extinction that are conservatively 100 times faster than the normal background rate (Davis, Faurby, and Svenning 2018). Yet we are only beginning to understand the true scope of this crisis. Mammals are among the most well documented groups, and over a quarter of all mammal species are threatened with extinction (IUCN 2020). The loss of any one species will also impact affiliated species, including mutualists, commensals, and parasites, and when associations are obligate, we risk cascading extinctions. The intimate interactions between parasites and their hosts has led to the suggestion that parasites may comprise the majority of endangered species (Dunn et al. 2009), and increasing advocacy for the inclusion of parasites in global conservation planning (Carlson, Hopkins, et al. 2020). Yet even within mammals, one of the best-sampled host groups, it is unclear how many parasite species may be lost with future host extinctions (A. Dobson et al. 2008; Carlson, Dallas, et al. 2020), what effect losses of hosts and their parasites will have on the ecological structure of communities, or how patterns that we observe in contemporary communities may be related to losses of hosts and parasites in the recent past.

Parasites play critical roles in ecological communities through impacts on host populations and structuring food webs (Hudson and Greenman 1998; Dunne et al. 2013). However, in comparison with their hosts, parasite extinctions are notoriously difficult to observe (Galetti et al. 2018), though some can be inferred through analysis of ancient samples (Taglioretti, Fugassa, and Sardella 2015; Lafferty and Hopkins 2018). Beyond direct observation, the coextinction of parasites along with loss of their hosts (Stork and Lyal 1993) have been studied via comparative analyses of threatened and non-threatened hosts (Altizer, Nunn, and Lindenfors 2007; Farrell et al. 2015), and simulations that identify likely coextinctions resulting from future host extinctions (Koh et al. 2004; Dunn et al. 2009; Strona, Galli, and Fattorini 2013; Harris and Dunn 2013; Dallas and Cornelius 2015). Both of these approaches commonly assume a complete extinction of parasites when, and only when, all of their documented hosts have gone extinct (Colwell, Dunn, and Harris 2012). However, multi-host parasites may require multiple hosts to maintain a net reproductive rate greater than one, suggesting that the extinction of even a single host may imperil a parasite (Holt et al. 2003; Dobson 2004; Fenton et al. 2015). Moreover, the extinction of some of their hosts also impacts the ecology and evolution of multi-host parasites through altering the adaptive landscape across available hosts (Williams 2012). Host extinction therefore not only has the potential to result in parasite extinction, but may alter host specificity, and shift the evolutionary landscapes shaping future parasite evolution. Predicting the impacts of host extinctions on host specificity becomes especially muddied when we expand our notion of host specificity beyond the number of host species infected.

Host specificity is a fundamental property of parasites, and can be quantified by the richness, evenness, or the ecological or evolutionary diversity of host species that a parasite infects (Poulin, Krasnov, and Mouillot 2011). Parasite species can display various degrees of specificity, from infecting a single host species (i.e., a specialist parasite) to infecting multiple host species (i.e., a generalist parasite). Among generalist parasites the degree of specificity can also vary dramatically. Using phylogenetic distances among hosts to measure specificity, a parasite infecting the same number of hosts may infect only closely related hosts or infect hosts from across multiple, distantly related clades (Poulin, Krasnov, and Mouillot 2011; Park et al. 2018). The degree of host specificity is a product of historical associations of parasites with their hosts, including processes of co-speciation and parasites shifting to infect novel hosts (Page 1993; Cooper et al. 2012). Identifying the set of host species that a parasite could infect given suitable opportunity (i.e., the potential host range of a parasite) allows us to infer ancestral host-parasite associations (Martínez-Aquino 2016), and make crucial predictions of the potential for emergence in novel hosts (Woolhouse and Gowtage-Sequeria 2005; Elmasri et al. 2020) and likely impacts following cross-species transmission (Brierley, Pedersen, and Woolhouse 2019; Farrell and Davies 2019; Guth et al. 2019).

Predictions of unobserved host-parasite associations are often based on an assumption that present day associations accurately reflect potential host ranges (Becker et al. 2020; Elmasri et al. 2020; Wardeh, Sharkey, and Baylis 2020). However, host range is a dynamic property of parasites that evolves through cospeciation, host shifts, and the gains and losses of hosts over varying timescales (de Vienne et al. 2013; Wells and Clark 2019; Doña et al. 2019; Braga et al. 2020; 2021). Changes in parasite host specificity as a result of host-switching and shifting geographic ranges have attracted considerable attention by researchers (Charleston and Robertson 2002; Hoberg and Brooks 2008; Johnson, Weckstein, Meyer, et al. 2011; Doña et al. 2018; Engelstädter and Fortuna 2019; Schatz and Park 2021), whereas extinction history has tended to be overlooked. Similar to the impact of host-switches, if recent historical host extinctions have reshaped contemporary host-parasite associations, we may be misled as to the intrinsic specificity of parasites. For example, the extinction of an evolutionarily distinct host may shift our perception of a parasite from being a phylogenetic generalist to a phylogenetic specialist. We use the term apparent specificity to reflect host specificity inferred from current documented host-parasite associations. Identifying the ways in which host specificity may have been influenced by past host extinction is important for quantifying risks of parasites establishing on novel hosts, and predicting how selection on multi-host parasites may shift in response to future host extinctions.

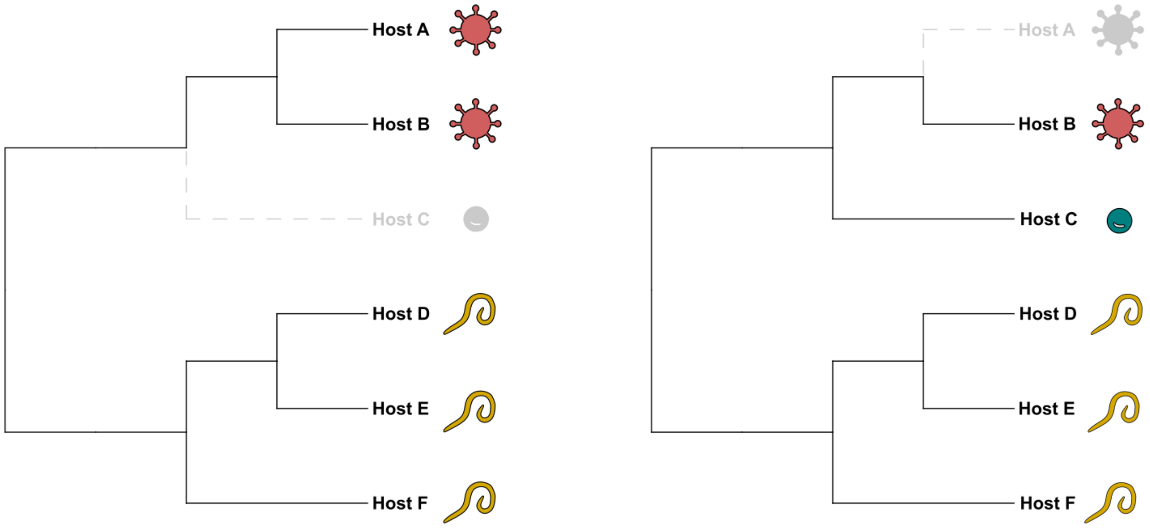
Here we examine how host extinction may shape patterns and perceptions of parasite host specificity and alter emergent patterns of parasite diversity and distribution at broader scales. We first summarize theoretical predictions on the consequences of host extinction, then showcase examples of these through the lenses of both historical mammal extinctions and projected future extinctions based on contemporary threat status. Although these patterns are complex, we highlight how host extinction can lead to both increases and decreases in apparent parasite host specificity, demonstrate how host specificity may be impacted by non-random host extinction, and consider implications for projecting how host specificity might respond to future host extinctions. Finally, we discuss the impacts of host extinction on parasite ecology and evolution, with a focus on altering costs of generalism versus specialism, parasite fitness, transmission potential, and virulence evolution. While current coextinction theory largely addresses parasite extinction resulting from host extinction, we suggest that expanding this framework to include contemporary measures of host specificity, and theory underlying co-adaptation and virulence evolution in multi-host systems will be crucial to understanding how biodiversity loss impacts infectious diseases more broadly.

Proximate impacts of host extinction on parasite host specificity

The concept of parasite coextinction was first formulated as the extinction of a host-specific parasite with the loss of its sole host (Windsor 1990; Stork and Lyal 1993) (Fig. 1A). While assumed to be quite common, coextinction events are rarely documented (Rózsa and Vas 2015). A classic example of coextinction is the loss of the host-specific California condor louse (*Colpocephalum californici*) which went extinct after California condors (*Gymnogyps californianus*) became extinct in the wild and surviving individuals were deloused during a captive breeding and reintroduction program (Dunn 2009). Beyond coextinction, host extinction may result in a formerly multi-host parasite being constrained to infect a single host species (Fig. 1B). This was the case for two species of passenger pigeon louse (*Columbicola extinctus* and *Campanulotes defectus*) that parasitized both the passenger pigeon (*Ectopistes migratorius*) and another closely related species (Price, Clayton, and Adams 2000; Dunn et al. 2009). Ironically, this was initially presented as a classic example of parasite coextinction as these two parasite species had only been described on the passenger pigeon and were presumed extinct with the pigeon (Stork and Lyal 1993), and only later were they found alive and parasitizing another host species. In hindsight, if the full host ranges had been known, these parasites would have been considered to be multi-host parasites, and now constrained to single-host specialists after the extinction of the passenger pigeon. For parasites that infect more than two hosts, host extinction in the absence of host jumps will always reduce host richness, thus increasing perceived taxonomic specialisation. However, the loss of a host species may increase or decrease the average phylogenetic distances among extant hosts (Figs. 1C & 1D), shifting our perception of the phylogenetic host breadth of the parasite. The directionality of the shift in phylogenetic host breadth is highly context dependent, which we explore further below.

A) *Loss of single host parasite*

B) *Generalist becomes specialist*



C) *Decreased phylogenetic distance among hosts*

D) *Increased phylogenetic distance among hosts*

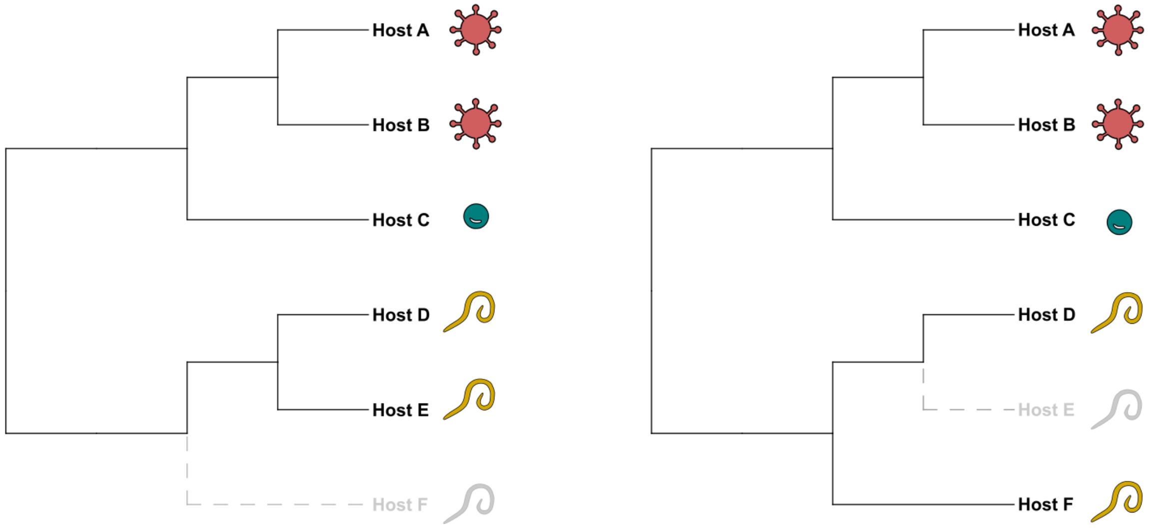


Fig. 1 Examples of how host extinction can impact parasite specificity. Each coloured shape represents a hypothetical parasite species, with their positions reflecting interactions with hosts alongside the host phylogeny. Each extinction scenario involves the loss of one host species (depicted by grey dashed lines). Depending on the original set of host-parasite interactions, the extinction of a host species may result in the loss of a single-host parasite, an example of coextinction (A), the reclassification of a former generalist to a single-host parasite (B), or more subtle changes in which the average phylogenetic distances among hosts may decrease (C) or increase (D) among the remaining hosts.

Ghosts of hosts past

Building a greater understanding of coextinction and our perceptions of contemporary patterns of the host specificity of parasites may be achieved through studies of historical host extinctions. Looking to the past, we may be able to find support for parasite extinctions following known host extinctions, and identify cases in which historical extinctions likely influenced contemporary host specificity. As host species are pruned from the tree of life, those that survive can become increasingly isolated in the phylogeny, especially if they are nested within clades where extinction has been rampant (Pavoine et al. 2019). The apparent phylogenetic specificity of the parasites found on them will therefore also change over time.

One approach to quantify how host extinction drives the phylogenetic distances among species is through the measure of evolutionary distinctiveness (ED) (Redding and Mooers 2006). This measure, widely used in conservation prioritization (Redding and Mooers 2006; Isaac et al. 2007; Redding, DeWolf, and Mooers 2010; Pearse et al. 2015; Perrault, Farrell, and Davies 2017) divides the total branch lengths of a phylogenetic tree among the tips. Each species is apportioned an amount of phylogenetic diversity, typically measured in millions of years of evolution, based on the sum of the branch lengths from the tip to the root of the tree, discounted by the number of shared descendents subtending from each branch. In this way, species that branched off deeper in the tree and have few or no extant relatives are considered to have high ED, whereas species in a young clade that recently underwent rapid speciation without much extinction would have low ED.

Evolutionary distinctiveness has been shown to be negatively related to parasite species richness per host (Huang et al. 2015; Park et al. 2018), indicating that hosts more isolated in the mammal phylogeny have fewer parasites. This may result from different (and non mutually exclusive) processes. Phylogenetic distance among hosts is negatively related to the propensity for parasite sharing (Davies and Pedersen 2008; Huang et al. 2014; Braga, Razzolini, and Boeger 2015), such that hosts isolated in the phylogeny may be less likely to be infected by multi-host parasites. One mechanism for this is the tendency for high ED hosts to have unique physiologies or life histories which may make them less likely to gain parasite species via host switching events (Antonovics et al. 2013). A less considered explanation is that more evolutionarily distinct hosts may have lost parasites because of the extinction of closely related species which acted as maintenance hosts. Following from the idea that single-host parasites will be lost with the extinction of their sole hosts, clades that have undergone large numbers of species extinctions are likely to have seen the coextinction of multi-host but clade-specific parasites. Thus, surviving hosts have both fewer close relatives (high ED) and fewer clade specific parasites which would otherwise be maintained in more species-rich clades via frequent cross-species transmission.

While increasing evolutionary distinctiveness may result in a reduction in parasite species richness per host, the remaining parasites may become apparent phylogenetic specialists or generalists depending on the initial host-parasite interactions before extinction (Fig. 1). For example, loss of a host’s close relatives might leave parasites stranded on these newly isolated hosts, if they are unable to evolve to infect additional host species (see Johnson, Weckstein, Bush, et al. 2011). In this case, host extinction may result in an increase of single-host parasites on distinct hosts (Fig. 1B) or they may appear to have lowered phylogenetic host specificity if parasite populations still persist on more distantly related hosts (Fig. 1D). Alternatively, if evolutionarily distinct hosts are more likely to be threatened with extinction (Cadotte and Davies 2010), these hosts today may have already undergone severe population declines in the recent past, and thus host fewer specialist or generalist parasites, depending on host and parasite life histories (Altizer, Nunn, and Lindenfors 2007; Farrell et al. 2015).

To explore empirical examples in which host extinction may have impacted contemporary patterns of host specificity, we pair a global database of contemporary mammal host-parasite interactions (Farrell et al. 2020, based on data amalgamated from Gibson, Bray, and Harris 2005; Wardeh et al. 2015; Olival et al. 2017; Stephens et al. 2017) with data on mammal host extinctions (Faurby and Svenning 2016) and the Phylogenetic Atlas of Mammal Macroecology (PHYLACINE) (Faurby et al. 2018). PHYLACINE includes harmonized data on mammal traits, geographic distributions, and phylogenetic relationships for all mammals since the last interglacial period (~130,000 years ago until present), including extinct species. We use these data to identify illustrative examples, and demonstrate concepts that may be expanded upon to investigate the impact of host extinction on parasite specificity. With these data we can calculate the evolutionary distinctiveness of species before and after extinction, taking their difference as a measure of gains in ED and their increasing phylogenetic isolation. Over this time period there are 352 documented mammal extinctions, which resulted in ED shifts for 551 extant mammals (Fig. 2). The majority of these ED gains are less than 1 million years (Fig. 2), but some species have seen large gains in ED on the order of tens of millions of years of added distinctiveness (Table 1). As these hosts have lost close relatives, we suggest that the impacts of historical host extinction on parasite host specificity may be gleaned from investigating the ecology and evolution of parasites surviving on them. In the next section we use a case study of an elephant tapeworm to demonstrate how this approach may generate new hypotheses of how host extinction may impact host specificity through altering parasite distributions, and ultimately shift selection pressures on surviving parasites.

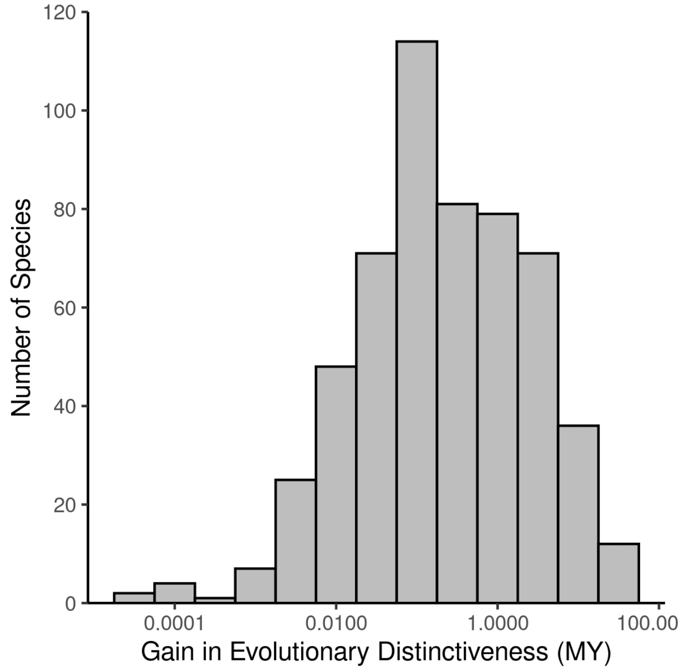


Fig. 2 Distribution of gains in evolutionary distinctiveness (ED) for extant mammal species resulting from mammal extinctions over the past 130,000 years. Gains in ED were calculated using the “equal-splits” approach (Redding 2002, Redding and Mooers 2006) and by subtracting contemporary ED measures per species from ED calculated including extinct taxa. Data from the PHYLACINE dataset (Faurby et al. 2018) and Faurby and Svenning (2016).

Species	Common name	ED extant	ED pre-extinction	ED gain
Elephas maximus	Asian elephant	47.69	10.00	37.69
Solenodon cubanus	Cuban solenodon / almiqui	66.45	32.60	33.85
Dugong dugon	Dugong	60.50	30.86	29.64
Loxodonta africana	African bush elephant	47.69	19.86	27.83
Macrotis lagotis	Greater bilby	45.85	19.73	26.12
Tachyglossus aculeatus	Short-beaked echidna	74.61	49.04	25.57
Hippopotamus amphibius	Common hippopotamus	33.28	9.14	24.14
Zaglossus bruijnii	Western long-beaked echidna	39.05	16.62	22.43
Tapirus indicus	Malayan tapir	40.52	20.37	20.15
Choloepus didactylus	Linnaeus's two-toed sloth	25.59	7.31	18.27

Table 1 Extant mammal species with the largest gains in evolutionary distinctiveness (ED) over the past 130,000 years (see Fig. 1 for the full distribution).

Geographic discontinuity and the mystery of the elephant tapeworm

The species with the largest increase in ED is the Asian elephant (*Elephas maximus*), the only extant member of its genus. The Asian elephant is more closely related to extinct mammoths than African elephants (*Loxodonta africana*) (Palkopoulou et al. 2018), another species with large ED gains over the past 130,000 years (Table 1). Currently listed by the IUCN as Endangered and with a declining population trend (Choudhury et al. 2008), Asian elephants are known to host at least 36 parasite species, 22 of which are only documented with this host species (Farrell et al. 2020). Among these parasites is the elephant tapeworm (*Anoplocephala manubriata*). Both Asian and African elephants are host to the eponymous cestode (McAloon 2004; Perera et al. 2017), even though these host species live on different continents, with no part of their geographic ranges overlapping. This raises a number of questions as to the ecology and evolutionary history of *A. manubriata*, and how disconnected species across the globe are infected by the same parasite. Although the taxonomy and biology of this parasite are rarely studied, the elephant tapeworm has been shown to use Oribatid mites as obligate intermediate hosts (McAloon 2004), and phylogenetic analysis of tapeworms taken from Asian elephants were placed as sister taxa to *Anoplocephala sp.* infecting Equids (Perera et al. 2017).

One possible explanation for the unusual distribution of *A. manubriata* might be circumglobal transmission. Some intermediate hosts of elephant tapeworms have distributions that span continents (McAloon 2004). As Oribatid mites commonly occur in soil communities, their general mechanisms of dispersal are relatively unknown, but some species have the ability to survive long-distance wind dispersal (Lehmitz et al. 2011) and are speculated to undergo trans-oceanic dispersal via seabirds or ocean currents (Starý and Block 1998). Although tapeworm populations in Asian and African elephants may be connected through rare cross-continental dispersal events, an alternative (and non-mutually exclusive) explanation is that the host range of the elephant tapeworm we see today is a relic of historical host extinctions.

Over the past 50,000 years we have seen the extinction of a suite of megafauna (Barnosky 2008), including elephantids that roamed throughout Eurasia (Fig. 3) (Palkopoulou et al. 2018; Faurby et al. 2018), which may have acted as alternative hosts and bridged the now disconnected ranges of African and Asian elephants (Palkopoulou et al. 2018). Would these lost elephantids also have been host to the elephant tapeworm? If so, the elephant tapeworm may be an example of a parasite which has seen a reduction in host richness, but an increase in the mean evolutionary distance among its hosts (Fig. 1D). If true, elephantid extinctions may have changed the host landscape such that the elephant tapeworm is now isolated on two distinct and disjunct host populations. Unfortunately, precise data on historical ranges of hosts is unavailable beyond hindcasted distributional models encompassing large amounts of uncertainty, even for species with prolific fossil records (Lorenzen et al. 2011). In the case of the elephant tapeworm, the current distributions of elephant species do not overlap, and would not be connected if extinct elephantids roamed the world today (see Fig. 3). However, examining the hindcasted distribution of the woolly mammoth (Mammuthus primigenius) (see Nogués-Bravo et al. 2008), this species (and potentially the historical distribution of other extinct elephantids) is likely to have bridged the distributions of the African and Asian elephants.

A more prosaic explanation is that the elephant tapeworm story is simply a case of mistaken identity; that elephant tapeworms in Asian and African elephants are morphologically similar, yet genetically distinct species. Expanding the study by Perera et al. (2017) to explicitly include tapeworms from African elephants would perhaps resolve this. Currently, poor parasite taxonomy challenges our ability to reconstruct historical and contemporary patterns of parasite sharing, with viruses being particularly problematic as they were historically defined by the host in which they were isolated (Fauquet 2008). As the availability of parasite phylogenies become increasingly available (see Pfenning-Butterworth et al., this issue), we will be able to identify cases in which parasite evolution is driven by host extinction.

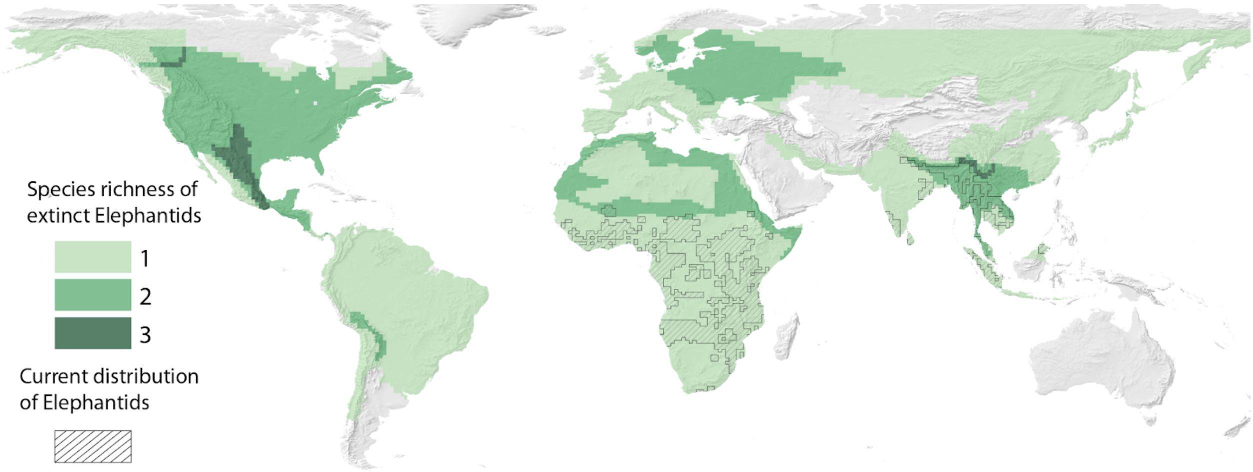


Fig. 3 Distributions of species richness of extinct species from the Elephantidae family (green shades) and of current species of elephants (black stripes). The distribution of Asian elephants and Afican elephants would not be bridged by extinct elephantids in today's climate. Extinct species include: *Cuvieronius hyodon, Elephas antiquus, Elephas cypriotes, Elephas iolensis, Elephas maximus, Elephas mnaidriensis, Elephas namadicus, Elephas naumanii, Elephas tiliensis, Loxodonta africana, Mammut americanum, Mammuthus columbi, Mammuthus exilis, Mammuthus primigenius, Notiomastodon platensis, Stegodon florensis, Stegodon orientalis, Stegodon trigonocephalus.* Data are from Phylacine 1.2 (Faurby et al. 2018). Distributions for species are based on models of where these species would live presently and without anthropogenic pressures, indicating that species richness of extinct elephants indicates where those species would live today, not where they were historically distributed.

Non-random extinction and the reshaping of host and parasite assemblages

Extinction is a non-random process, with some clades and some areas more extinction prone than others (Purvis, Agapow, et al. 2000; Cardillo et al. 2006; Fritz and Purvis 2010; Ana D. Davidson et al. 2017). Since the Cenozoic, mammals have faced extinction as a result of anthropogenic pressures, and climatic and environmental change (Nogués-Bravo et al. 2008; Lorenzen et al. 2011). These impacts have affected large-sized species more intensely (Cardillo et al. 2005) and their intensity is non-randomly distributed across space (Morales-Castilla et al. 2012). Today larger-bodied host species and host species with narrow geographic ranges or climatic niche tolerances suffer from disproportionately greater extinction risk (Purvis, Gittleman, et al. 2000; Cardillo et al. 2008; A. D. Davidson et al. 2009; Olden, Hogan, and Zanden 2007; Böhm et al. 2016; Collins et al. 2018). Because the attributes that predispose some species to higher risk of extinction than other species are typically conserved on the evolutionary tree of hosts, the process of extinction can result in large loss of phylogenetic diversity (Heard and Mooers 2000; Davis, Faurby, and Svenning 2018) and reshape the phylogenetic tree structure of survivors (Davies and Yessoufou 2013). These same host traits also co-vary with parasite richness across host species (Kamiya et al. 2014), for example, primates and carnivores with larger body sizes and larger geographic ranges also tend to host more parasite species (Nunn et al. 2003; Lindenfors et al. 2007). Thus, the process of extinction may jointly reshape extant host phylogenetic structure and within-host parasite diversity, both mediated through host species traits. However, the direction of trait effects can be complicated: although both large geographic extent and larger body size are associated with higher parasite diversity, hosts with large ranges have reduced extinction risk, whereas hosts with large body size have higher extinction risk.

While host trait predictors of parasite richness have been explored for different parasite taxa (Kamiya et al. 2014; Morand 2015), less work has explored how host traits contribute to variation in the richness of specialist vs generalist parasites. Observations that the relationship between host extinction risk and the ratio of specialist to generalist parasites differs (Farrell et al. 2015) suggest that drivers of parasite loss may differ between these classes of parasite, and thus we might also predict drivers of parasite richness would differ similarly. Testing this prediction requires that we have a robust metric of parasite specificity that is insensitive to recent host extinctions. Exploring how contemporary parasite specificity varies with host traits can provide a potential signal of the effect of non-random host extinction. However, it may simply be infeasible to separate the effects of host traits on determining parasite encounter and transmission from the longer-term evolutionary consequences of extinction-driven specialization.

Theory may be of some assistance in separating these effects, clarifying implicit assumptions, and guiding future predictions. For example, simple mathematical models suggest that large-bodied hosts are more likely to be infected by generalist parasites than small-bodied hosts. This is based on an assumption that large-bodied hosts are a better resource for parasites, thus making the cost of generalism (poorer adaptation to any individual host) easier to pay (Walker et al. 2017). This would suggest that biased extinctions of large-bodied hosts may more likely result in increases in apparent specificity, rather than in coextinction. However, this model also identifies cases where that pattern could reverse, and large-bodied hosts would be more likely to be infected by specialist parasites. Empirically, there is evidence for large-bodied hosts being more heavily infected by generalist parasites in some systems (Walker et al. 2017), and more heavily infected by specialist parasites in other systems (Sasal et al. 1999; Desdevises, Morand, and Legendre 2002; Krasnov et al. 2006).

Ghosts of future extinctions

Considering that the loss of even a single host may impact the apparent host specificity of parasites in multiple ways (Fig. 1), it is difficult to outline clear predictions for formal comparative analyses investigating the impact of extinction on present day host specificity. The shift in the phylogenetic signature of a parasite across the host phylogeny will depend on which host species is lost from the phylogeny, and different parasites will be impacted differently with the loss of the same host species, depending on their initial phylogenetic host range. However, we may study the impacts of extinction on host specificity through the lens of the current biodiversity crisis. Parallel to earlier studies examining the potential for parasites to go extinct with the loss of their hosts (Koh et al. 2004; Dunn 2005; 2009), we may similarly erode existing host-parasite networks and examine resulting impacts on host specificity, however these approaches tend to ignore the potential for parasite host-switches. To demonstrate, we can examine future impacts of biodiversity loss on the host specificity of mammal parasites by removing sets of hosts based on their IUCN status, with all critically endangered hosts removed first, followed by those in categories with decreasing risk of extinction (Fig. 4A). Exploring the mean pairwise phylogenetic distance among hosts (MPD) as a metric of host specificity, we see that the majority of parasites experience little change with future host extinctions, but there are a few with large changes in MPD. As additional hosts with lower risk of extinction are lost, more extreme reductions in MPD are seen, while other parasites will see increases in MPD.

In the previous example, all hosts are removed simultaneously, based on their risk of extinction, but in reality host extinctions will have an ordering, which will result in different trajectories for changes in phylogenetic host specificity as hosts are lost. Figure 4B illustrates the variable trajectories that shifts in MPD can take as the hosts for a single parasite go extinct. Each line represents a single randomized order of host extinction, indicating that the order of host extinction may result in increases or decreases in apparent specificity. While this is a simple example to illustrate this phenomenon, future studies may examine these patterns in increasingly realistic contexts of non-random and projected host extinctions, or consider simulated extinctions in the context of a host community network and incorporating additional interactions among hosts.

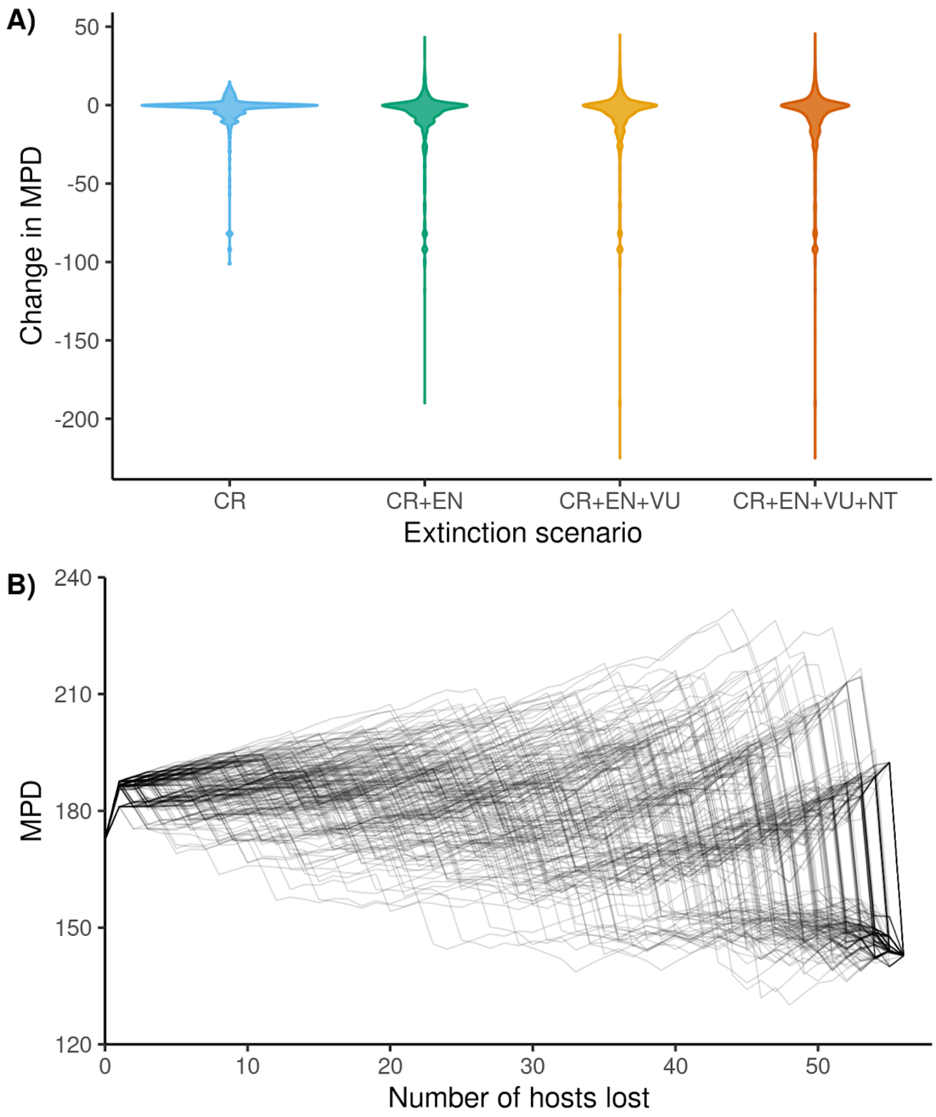


Fig. 4. A) Changes in host specificity measured as the mean pairwise phylogenetic distance among hosts (MPD) as hosts are removed according to their IUCN status (CR = Critically Endangered, EN = Endangered, VU = Vulnerable, NT = Near Threatened). Extinction scenarios from left to right remove additional mammal hosts according to their current status. To improve visibility, changes in MPD of zero are removed before plotting. These represent parasites with MPD unchanged by future extinction events. Domesticated species and data deficient (DD) species are not assessed by the IUCN and were assigned a status of Least Concern (LC), thus retaining them in each extinction scenario. The host phylogeny and IUCN statuses are taken from PHYLACINE and paired with the host-parasite association data in Farrell et al. (2020). B) Changes in host specificity of *Trypanosoma cruzi* measured as the mean pairwise phylogenetic distance among hosts (MPD) as hosts are increasingly lost via extinction. Each line represents a single simulation with a different randomized order of extinction for documented hosts, excluding humans and domesticated species. We use *T. cruzi* to illustrate this because it infects a large number and phylogenetic diversity of host species. 200 simulations are depicted.

To further explore projected changes in host specificity for particular parasites, we examine differences in MPD as a measure of host specificity among extant hosts and after projected host extinction (Fig. 5A). Assuming a simulated extinction event leaving only hosts assessed as Least Concern (LC) or Data Deficient (DD) by the IUCN, we see that the majority of parasites fall on the 1:1 line, indicating that future extinctions will not have a consistent directional impact on phylogenetic host specificity. Nonetheless, phylogenetic specificity will change for a large number of parasites. Among those parasites impacted, some generalists will be reduced to single-host parasites (those with MPD of zero after host extinction), some will become "apparent specialists" (reduction in MPD), and others will become "apparent generalists" (gains in MPD). Examples of increasing apparent specialism and generalism can be seen with extinctions among the hosts of the nematode *Ophidascaris robertsi* and the trematode *Neodiplostomum intermedium* (Fig. 5B). Both parasites infect Australian mammals including marsupials and native placental rats. However, future host extinctions are likely to trim away internal branches among hosts of *Ophidascaris robertsi* leading to increased phylogenetic distances, while all of the marsupial hosts of *N. intermedium* will be lost and lead to greatly increased phylogenetic specificity. Although the number of projected host extinctions is high, the ecology of *O. robertsi* may be relatively unimpacted as extinctions do not prune large swathes of the host tree, multiple sister taxa are projected to survive, and mammals are only intermediate hosts for this parasite which uses pythons as a definitive host (Gonzalez-Astudillo et al. 2019). However, as *N. intermedium* uses mammals as definitive hosts, the large phylogenetic distances between Australian eutherian rats and marsupial hosts could mean that the projected extinction of the *Dasyurus* hosts will dramatically shift the selective landscape of the parasite.

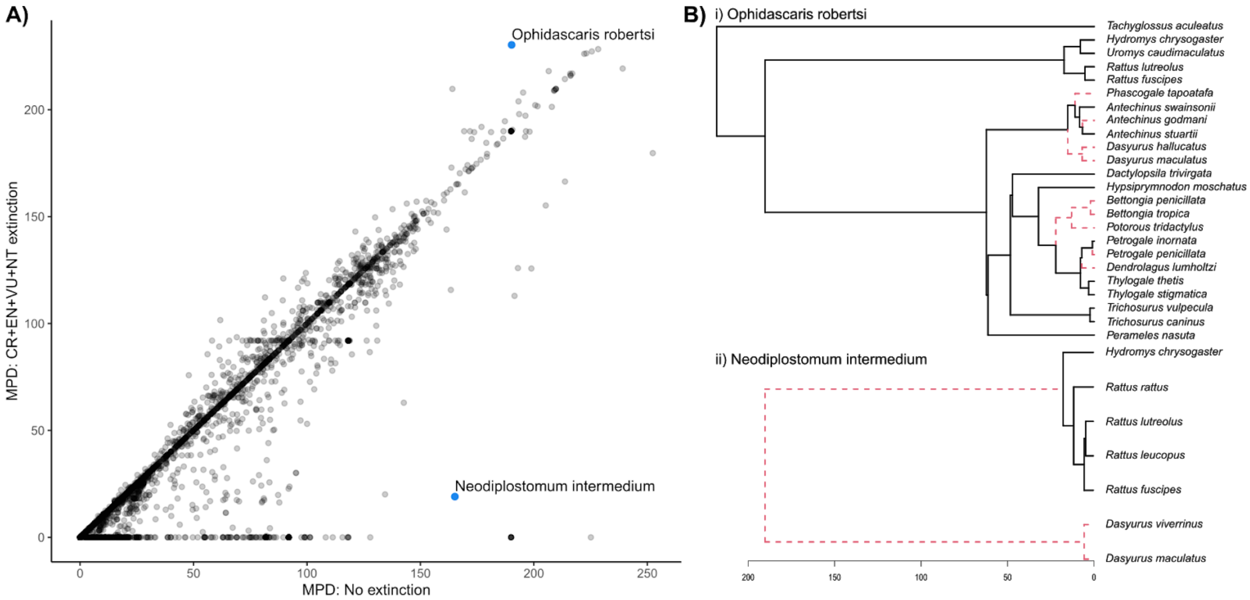


Fig. 5 A) Host specificity of parasites, measured as the mean pairwise phylogenetic distance (MPD) among contemporary hosts (x-axis), and assuming the extinction of all mammals except those categorized as Least Concern (LC) or data deficient (DD) by the IUCN (y-axis). B) Examples of future host extinctions on the phylogenetic relationships among hosts for i)

Ophidascaris robertsi (i), and ii) *Neodiplostomum intermedium*. Extinct lineages are denoted by red dashed lines, and represent the loss of species assigned IUCN categories other than Least Concern (host phylogeny and IUCN statuses are taken from PHYLACINE and paired with the host-parasite association data in Farrell et al. (2020). Scale bar represents millions of years.

Impacts of host extinction on parasite ecology & evolution

Host extinction and the coextinction of dependent parasites will impact the structure and function of ecosystems (Dunn et al. 2009; Lafferty 2012; Dallas and Cornelius 2015), and may shift the distributions of zoonotic diseases (Harris and Dunn 2013). In addition to complete host loss, there can be large impacts due to changes in host populations as they decline to extinction. These include reductions in host and parasite abundance, leading to reduced population densities or range sizes. At the extreme, for parasites that are “obligate” multi-host parasites (where “obligate” refers to a situation where the net reproductive rate of the parasite on any individual host is less than one, so that parasite maintenance requires multiple hosts; Fenton et al. 2015), host population declines may lead to parasite extinction well before any host actually goes extinct. We are already seeing evidence of such changes in many host populations (IUCN 2020; UNEP 2019; WWF 2020), and these host declines have been marked by the loss of parasites in threatened species (Altizer, Nunn, and Lindenfors 2007, Herrera et al., this issue) and changes in the proportion of generalist versus specialist parasites in some host groups (Farrell et al. 2015). In the latter case, these changes likely result from shifting intra- and interspecific contact rates among hosts, which may have proximate impacts such as shifting parasite distributions, population sizes, and relative rates of host exposure. While it is clear that host extinction will influence parasite abundance, whether extinction increases or decreases transmission will depend on specifics of the system and how it impacts the relative abundance of competent hosts. In instances where parasites lose hosts that support onward transmission, we may see reduced transmission potential, whereas the extinction of off-target or dead-end hosts may allow for the maintenance of robust parasite populations within more competent reservoir hosts. Further, parasite life histories, such as transmission mode, may evolve in tandem with shifting host specificity (Antonovics et al. 2017), and are likely to mediate this effect. For many parasites, transmission is only weakly or not impacted by reductions in host density, and in extreme cases, such as vector-borne or strongly frequency-dependent transmission, reduced host density can improve transmission (Bjørnstad, Finkenstädt, and Grenfell 2002; Hopkins et al. 2020).

Transmission Frequency

Whether host extinction increases or decreases parasite transmission will impact changes on evolutionary timescales (Day et al. 2020) and may impose new selection pressures on parasite evolution (Smith et al. 2012). For example, host extinction may limit gene flow among previously connected parasite populations, promoting specialization of parasites on their newly isolated hosts. For many infectious organisms, and especially those with short generation times such as viruses and bacteria, this isolation could lead to allopatric speciation, a process that would be reflected in congruent tree shapes in co-phylogenetic analyses (Clayton et al. 2003, Pfenning-Butterworth et al. this issue). This process of host extinction leading to parasite specialization and speciation may be quite common, but the lack of robust parasite fossil records and data on historical hosts make this difficult to identify. Future co-phylogenetic methods may benefit by modelling the impacts of host extinctions, as reconstructions may be differentially impacted by the loss of closely versus distantly related host-species (Santichaivekin et al. 2020). For relatively long-lived parasites, such as cestodes, including the elephant tapeworm discussed above, we may be able to identify examples where parasites are in the process of speciation. The longevity of adult tapeworms in their definitive hosts is quite variable, surviving from weeks to multiple decades up to the lifespan of the host (Sandground 1936). The long generation times of some tapeworms might not allow sufficient time for divergence following historical extinctions and subsequent geographic isolation of their host species. This may be the case for the elephant tapeworm, but further research on maximum longevity, population genetics, and phylogenetic analyses of both the Asian and African populations would be needed.

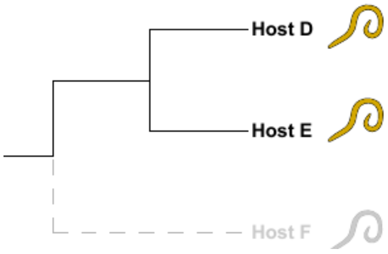
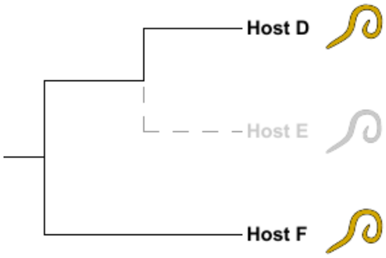
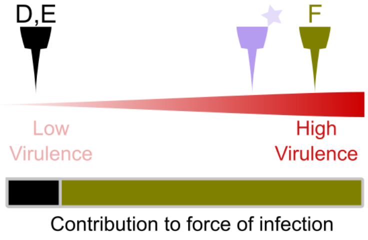
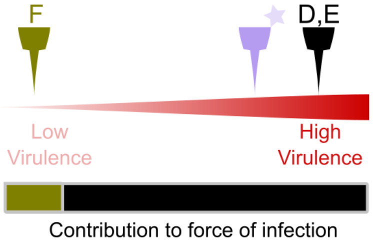
Costs of Generalism

As host extinction drives increasing phylogenetic isolation of host species, this is likely to alter the costs of generalism, potentially promoting further parasite specialisation and speciation, and also shift the optima for virulence and transmission across extant hosts (Antonovics et al. 2013; Leggett et al. 2013; Farrell and Davies 2019). Multi-host parasites are often assumed to experience a cost of generalism, the increased transmission opportunities associated with additional host species trading off against fitness benefits gained by specializing on any particular host species (Woolhouse 2001; Parrish et al. 2008; Antonovics et al. 2013; Leggett et al. 2013). Costs of generalism can take two forms; one is a more global cost in which having multiple hosts reduces the potential for co-evolution with any one host, meaning generalists may not be as well adapted to their hosts, on average, when compared to specialist parasites. The other form that a cost of generalism may take is greater variation in fitness across hosts, with parasite adaptation to novel hosts resulting in reduced fitness in original hosts (Ebert 1998), with the magnitude of this trade-off increasing with phylogenetic distance between hosts (Antonovics et al. 2013). Due to either or both of these costs, generalist parasites are therefore likely to have lower fitness in any given host than is possible in a single-host relationship, which is offset by the demographic advantage of an expanded reservoir of available hosts (Gandon 2004). In this context, the influence of host extinction on parasite mean fitness will depend precisely on which hosts are lost, the evolutionary distances between extant hosts, and the types of costs of generalism that were being paid (e.g., if they were reasonably well adapted to any host in the system).

Virulence

Parasite fitness relies on successful transmission, which requires the exploitation of host resources and ultimately results in damage to hosts, termed ‘virulence’. For many parasites, greater host exploitation facilitates increased transmission, but if viruence is too high, then transmission may be reduced due to shorter infection duration (Anderson and May 1982; Frank 1996). For multi-host parasites, there may be a unique optimal virulence that maximizes transmission on each individual host (Gandon, 2004). If parasites are constrained to a single level of virulence (i.e., they cannot plastically adjust their strategy to the current host), then parasites will evolve an intermediate virulence, influenced by the relative contribution of each host species to the total force of infection, that maximizes fitness across their host species, but achieves optimal virulence in none (Williams 2012). By changing the epidemiological contribution of each species, host extinction is likely to shift the selective landscape for parasites, leading to changes in virulence as parasites adapt to track the optimal virulence of the surviving hosts.

Depending on the relative contributions of different host species to transmission, as well as the optimal virulence within each, the extinction of a particular species may lead to the evolution of increased or decreased virulence on remaining hosts. In Table 2 we explore possible evolutionary outcomes of host extinction assuming three host species, the potential for onward transmission in each host, and a single optimal virulence expressed in each host species that maximizes total transmission. Few empirical studies have examined how phylogenetic distance among hosts is linked to parasite virulence, but studies of zoonoses and multi-host domesticated animal parasites found that increased evolutionary distance among hosts is associated with greater potential for virulence, but at the cost of reduced transmission (Farrell and Davies 2019; Guth et al. 2019). Predicting the evolution of virulence in multi-host systems is a complex challenge, but as biodiversity loss dramatically restructures host-parasite associations and humans become increasingly isolated in the tree of life, understanding how parasite virulence may evolve in response to host extinction is increasingly important.

Virulence scenario (pre-extinction)	**Extinction scenario**	
 The red bar indicates the degree of virulence ▼ indicates optimal virulence for host species F ▼ indicates optimal virulence for host species D & E ▼ indicates the parasite's evolved optimal virulence across all hosts, prior to extinction  The relative sizes of black and green bars indicates the relative contribution of each host clade to the force of infection	 Decreased phylogenetic distance among hosts after extinction of host F	 Increased phylogenetic distance among hosts after extinction of host E
	Virulence is far from optimal on the remaining hosts. Parasite may go extinct if virulence cannot be downregulated to optimal for hosts D + E.	The evolutionary impact of losing a host that contributed relatively little to the force of infection may be minimal. However, the relative weighting of species F may be expected to increase, which would generate selection for increased virulence.
	The evolutionary impact of losing a host that contributed relatively little to the force of infection may be minimal. However, the constraints that circulation in species F imposed on the evolution of virulence have been removed, so we may predict an increase in virulence.	The evolutionary impact of losing species E will depend on the relative contributions of D and E to the force of infection. If only their combined influence outweighed the contribution of F, then we would expect selection for decreased virulence.

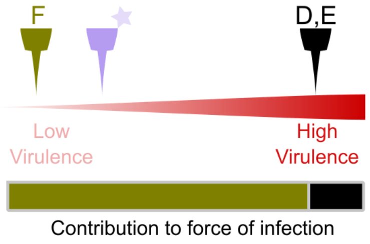
	Virulence is far from optimal on the remaining hosts. Parasite may go extinct if virulence cannot be upregulated to optimal for hosts D + E.	The evolutionary impact of losing species E will depend on the relative contributions of D and E to the force of infection. If only their combined influence outweighed the contribution of F, then we would expect selection for decreased virulence.

Table 2. Examples of how parasite virulence might evolve in response to host extinction. The first column indicates the initial state of each system prior to extinction, including the optimal virulence for each host clade if this was the sole host, and the evolved optimal virulence expressed across all hosts. In these examples optimal virulence is skewed towards the single-species optimum for the host clade that contributes the most to force of infection. The second and third columns outline the shifts in the system resulting from two extinction scenarios in which the phylogenetic distances among hosts is either decreased or increased. With the extinction of a given host, in general we would expect virulence to evolve towards the optimal virulence for the remaining species, though this is dependent on the initial state of the system. This framework closely follows the theory in Williams (2012).

Conclusion

The current biodiversity crisis is reshaping the tree of life, shifting realised parasite host specificities and the adaptive landscapes of contemporary parasites. Here we demonstrate that the impacts of host extinction on phylogenetic measures of host specificity are context-specific, with host extinction potentially leading to both increases and decreases in generalism of parasites. We suggest that these changes in specificity are likely to have complex impacts on parasite evolution, including further evolution of specialist or generalist strategies, and the shifts in parasite virulence. We show that past extinctions may have reshaped host-parasite associations, and thus care should be taken when drawing inference from present-day patterns of host specificity. In the case of more recent host extinctions, parasites today may appear more or less specialized, masking an intrinsic ability to infect novel host species, and altering our perceptions of their potential host ranges.

Just as past extinctions have shaped present day host-parasite interactions, ongoing biodiversity loss will continue to shape disease dynamics into the future. Beyond extinction, climate change induced range shifts may promote host-parasite sharing and novel interactions never seen before in evolutionary history (Morales-Castilla et al., this issue). Infectious diseases act as synergistic drivers of host extinction, with impacts due to infectious diseases increasing as populations decline to extinction (Heard et al. 2013). Host extinction is likely to decrease global parasite richness through coextinction of specialist parasites (Dunn et al. 2009), but generalist parasites are most often associated with host declines (Pedersen et al. 2007). The relative loss of specialist parasites may remove protective effects of co-adapted parasites and expose hosts to more virulent parasites through the reduction of immune cross-protection and opening of new niches for generalist parasites (Lloyd-Smith 2013). When shifting to novel hosts, parasites may display increased virulence due to a lack of co-evolutionary history between host and parasite (Woolhouse et al. 2005), and host extinctions may also select for increased parasite virulence in some systems, exacerbating disease-mediated host declines. While current theory is well developed for single-host single-parasite systems, expanding on theories of host specificity, co-adaptation, and virulence evolution in multi-host systems is crucial for better understanding how biodiversity loss impacts infectious diseases, and mitigating disease impacts as we navigate the current biodiversity crisis. We note that many of the concepts discussed here for host-parasite systems may also be applied to symbionts in general, offering new avenues for future research into the cascading impacts of host extinction.

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Data Accessibility

Data and R scripts to reproduce the figures are available at https://github.com/DiseaseMacroecology/ghost-host and 10.6084/m9.figshare.14573787

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