

The path to host extinction can lead to loss of generalist parasites

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Summary

1. Host extinction can alter disease transmission dynamics, influence parasite extinction and ultimately change the nature of host–parasite systems. While theory predicts that single-host parasites are among the parasite species most susceptible to extinction following declines in their hosts, documented parasite extinctions are rare.

2. Using a comparative approach, we investigate how the richness of single-host and multi-host parasites is influenced by extinction risk among ungulate and carnivore hosts. Host–parasite associations for free-living carnivores (order Carnivora) and terrestrial ungulates (orders Perissodactyla + Cetartiodactyla minus cetaceans) were merged with host trait data and IUCN Red List status to explore the distribution of single-host and multi-host parasites among threatened and non-threatened hosts.

3. We find that threatened ungulates harbour a higher proportion of single-host parasites compared to non-threatened ungulates, which is explained by decreases in the richness of multi-host parasites. However, among carnivores threat status is not a significant predictor of the proportion of single-host parasites, or the richness of single-host or multi-host parasites.

4. The loss of multi-host parasites from threatened ungulates may be explained by decreased cross-species contact as hosts decline and habitats become fragmented. Among carnivores, threat status may not be important in predicting patterns of parasite specificity because host decline results in equal losses of both single-host parasites and multi-host parasites through reduction in average population density and frequency of cross-species contact.

5. Our results contrast with current models of parasite coextinction and highlight the need for updated theories that are applicable across host groups and account for both inter- and intraspecific contact.

Key-words: coextinction, conservation, host specificity, infectious disease, macroecology, pathogens

Introduction

Parasites are often viewed as negative aspects of ecosystems, as causes of disease and indicators of unhealthy environments. Infectious diseases of wildlife have been implicated in the declines of several free-living hosts (Smith, Acevedo-Whitehouse & Pedersen 2009; Heard *et al.* 2013) and as agents of many important diseases of humans and domesticated animals (Cleaveland, Lauren-

son & Taylor 2001). However, parasites are integral components of natural ecosystems with unique roles in food webs (Dunne *et al.* 2013), regulating community composition (Wood *et al.* 2007) and maintaining host genetic diversity (Altizer, Harvell & Friedle 2003). Furthermore, it has been speculated that loss of parasites may predispose hosts to infection by generalist parasites or emerging diseases (Dunn *et al.* 2009; Lloyd-Smith 2013) and thus have severe downstream effects. Recent efforts have therefore rallied for the inclusion of parasitic biodiversity in conservation efforts (Harris & Dunn 2010; Mihalca, Gherman & Cozma 2011; Moir *et al.* 2012; Gómez &

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Nichols 2013; Pérez, Sánchez & Palma 2013). Parasites are susceptible to many of the same threats affecting free-living species, but their added dependence on hosts suggests that parasites will be among the organisms most susceptible to extinction in the ongoing biodiversity crisis (Dunn *et al.* 2009; Colwell, Dunn & Harris 2012).

Parasite extinction risk depends on the number of hosts a parasite infects and the extinction rates of those hosts (Koh *et al.* 2004; Lafferty 2012). Recent models of parasite coextinction indicate that generalist parasites (those able to utilize multiple host species) are less susceptible to coextinction as they have alternative ways to complete their life cycles (Dunn *et al.* 2009; Lafferty 2012). However, local extirpations of infected host populations or preferred host species could result in parasite extinction well before the loss of all available host species as parasites are often unevenly distributed among host individuals, populations and species (Shaw & Dobson 1995; Poulin 2007; Moir *et al.* 2010; Välimäki *et al.* 2011). As the transmission of parasites depends in part upon sufficient contact among infected and susceptible hosts (McCallum, Barlow & Hone 2001), extinction processes may decrease the density or abundance of hosts below critical thresholds for parasites to transmit effectively (Deredec & Curchamp 2003; De Castro & Bolker 2005).

Although theory suggests that coextinction of hosts and parasites is a common phenomenon, empirical support is scarce and only a few instances of coextinction have been documented (Dunn *et al.* 2009; Moir *et al.* 2010). An analysis of parasite richness among wild primates revealed that threatened host species were associated with fewer parasite species compared to non-threatened hosts (Altizer, Nunn & Lindenfors 2007). This result supports coextinction theory; however, the proportion of specialist parasites was not significantly different, suggesting that host declines lead to the loss of both specialist and generalist parasites. A similar result was found among acacias and the phytophagous insects that feed on them (Powell 2011). A recent study of fish parasites found that specialist parasites tend to use hosts with low vulnerability to extinction (Strona, Galli & Fattorini 2013), which may be additional support for the loss of specialist parasites from threatened hosts. Conversely, a study of viral richness in bats found the opposite trend with threatened bat species harbouring increased richness of viruses (Turmelle & Olival 2009). These conflicting results highlight the need for an improved understanding of coextinction and host–pathogen dynamics in declining host populations.

Here, we contrast patterns of single-host vs. multi-host parasites among threatened and non-threatened wild ungulates and carnivores. Although host range can be considered as a continuous variable, multi-host parasites may also infect hosts with different risks of extinction, which makes it difficult to predict coextinction risk based solely on the number of hosts per parasite. However, single-host parasites must go extinct before or immediately upon the loss of their sole host. We use phylogenetic comparative

methods to evaluate whether single-host parasites are less common among threatened hosts compared to non-threatened hosts, as we expect host species with small or declining populations to be less likely to support viable populations of single-host parasites. We focus on wild ungulates and carnivores because of the availability of data and their shared evolutionary histories with domesticated mammals.

Materials and methods

PARASITE RECORDS

Records of parasitic organisms reported from free-living carnivores and terrestrial ungulates (Perissodactyla + Cetartiodactyla minus cetaceans) were obtained from the Global Mammal Parasite Database (Nunn & Altizer 2005) and Huang *et al.* (2015) which include papers published up to 2010; accessed 15 October 2013. This data base documents host–parasite associations and encompasses both micro- and macro-parasites including viruses, bacteria, protozoa, fungi, helminths and arthropods. We restricted reports to wild populations of hosts sampled within their native ranges. Host Latin binomials were standardized Wilson & Reeder (2005). Parasites reported to genus level or higher were excluded from the analyses. Only reports with prevalence greater than zero were included. Parasites were classified as single-host if associated with only one host species in the data set and multi-host if associated with more than one host species.

HOST TRAITS

To quantify host extinction risk, we employed the categorical threat status reported by the 2014 IUCN Red List of Threatened Species (International Union for the Conservation of Nature (IUCN) 2014). We converted IUCN status to a binary variable with species listed as Least Concern (LC) or Near Threatened (NT) considered ‘Non-Threatened’, and species listed as Vulnerable (VU), Endangered (EN) or Critically Endangered (CR) considered ‘Threatened’. Hosts with the status of Data Deficient (DD), Extinct in the Wild (EW) or Extinct (EX) were excluded from our analysis. To limit temporal mismatches in the reporting of parasites and changes in IUCN status, two species reported to have genuine changes in status between the 2010 and 2014 editions of the IUCN Red List were assigned their 2010 status. The IUCN also provides information on species population trends, which was converted into a binary variable with species listed as either decreasing or not decreasing (i.e. increasing or stable) to capture decreases in host abundances where rate of decline may be below thresholds necessary to be considered threatened (Mace *et al.* 2008).

To control for additional host traits that have been shown to correlate with both extinction risk and parasite richness in mammals (Nunn *et al.* 2003; Ezenwa *et al.* 2006; Lindenfors *et al.* 2007; Cardillo *et al.* 2008), we included data on average adult female body mass (g), geographic range area (km²) and average population density (number of individuals km⁻²) per host species from the PanTHERIA data base of mammalian life-history traits (Jones *et al.* 2009). Additional population density estimates for ten species in the order Carnivora were obtained from grey literature.

STATISTICAL ANALYSES

Generalized Estimating Equations (GEEs) (Paradis & Claude 2002) were used to explore relationships between host traits and univariate responses of (i) proportion single-host parasites, (ii) richness of single-host parasites and (iii) richness of multi-host parasites. GEEs offer a flexible and unified method allowing the specification of non-normal error structures for binomial and count data as well as correcting for phylogenetic non-independence. All analysis was conducted in R v.3.1.0 (R Core Team 2014).

To control for uneven sampling of parasites among hosts, we included as a covariate the number of citations per host (Altizer, Nunn & Lindenfors 2007) as reported in the ISI Web of Knowledge using the Latin binomial of each species in either the title or topic fields. Citation counts as well as estimates of body mass, geographic range and population density were log-transformed prior to analyses.

As ungulates and carnivores differ significantly with respect to their life histories, ecology and predictors of extinction risk, we conducted models separately for each group, though the number of hosts per parasite was taken from the merged host–parasite lists of both groups. Before model fitting, we checked the predictors for collinearity by estimating the variance inflation factors (VIFs). In all cases, VIFs were less than three, indicating no significant effect of collinearity (Belsley, Kuh & Welsch 1980).

Full models including all predictor variables were first fit with the `geeglm` function in the package `geepack` (Højsgaard, Halekoh & Yan 2006). For proportion of single-host parasites, we used counts of single-host and multi-host parasites as the response and specified a binomial error structure with a logit link function. To determine whether or not changes in the proportion of single-host parasites were being driven by changes in the richness of single-host or multi-host parasites, we fit separate models with richness of single-host and multi-host parasites, respectively, as response variables assuming a Poisson error structure.

For each of the full models (6 in total), we estimated Pagel's lambda as a measure of phylogenetic signal in the residuals using the `fitContinuous` function in the package `Geiger` (Harmon *et al.* 2008) and most current inclusive estimates of phylogeny. We used a species-level mammal super tree for ungulates (Fritz, Bininda-Emonds & Purvis 2009) and a more recent species-level tree for the order Carnivora (Nyakatura & Bininda-Emonds 2012). To correct for phylogenetic non-independence in model residuals due to shared evolutionary histories among hosts, the respective trees were transformed using the estimated lambda value from model residuals (Revell 2010) with the function `transform.phylo` in the package `Geiger` (Harmon *et al.* 2008). We then refit the models using the `compar.gee` function in the package `ape` (Paradis, Claude & Strimmer 2004) specifying the phylogenetic covariance structure from the transformed phylogeny.

SENSITIVITY ANALYSES

As a full suite of predictors was not available for every host species, sample sizes were maximized by removing predictors with $P > 0.1$ and the above procedure correcting for phylogenetic non-independence in the residuals repeated. The reduced models often allowed for increased sample sizes and thus comparison across a larger number of host species. Threat status and citation count were forced into all models. We additionally

fit bivariate models which included only threat status and citation count as predictors to explore the effect of threat status in the absence of ecological covariates. To determine whether patterns differed by parasite type, parasites were categorized as either micro-parasites (bacteria, viruses, fungi, protozoa) or macro-parasites (helminths, arthropods), and models re-run separately for each parasite type. This distinction represents a functional difference whereby micro-parasites tend to have shorter life cycles and directly reproduce in their definitive hosts (Anderson & May 1991), which may cause the two groups to respond differently to host extinction.

Results

A total of 13 724 reports of host–parasite associations were used, representing 4098 unique confirmed host–parasite associations among 235 hosts and 1384 parasites. This resulted in 729 single-host and 656 multi-host parasites. A total of 95 ungulate and 140 carnivore host species were included, of which complete covariate data were available for 68 and 64, respectively (see Appendix S1 in Supporting information for the data frame used in these analyses). In both groups, mean multi-host parasite richness per host appears lower among threatened hosts when examining data uncorrected for sampling effort or ecological covariates (Fig. 1).

In statistical tests, threatened ungulates harbour a significantly higher proportion of single-host parasites compared to non-threatened ungulates [Fig. 2a, Appendix S2 (Table 1) in Supporting information]. This result is supported by the finding that threatened ungulates harbour a significantly lower richness of multi-host parasites compared to non-threatened ungulates (Fig. 2c), whereas single-host parasite richness was not significantly associated with threat status (Fig. 2b). Multi-host parasite richness was significantly negatively associated with threat status and a decreasing population trend, and significantly positively associated with range area, body mass and

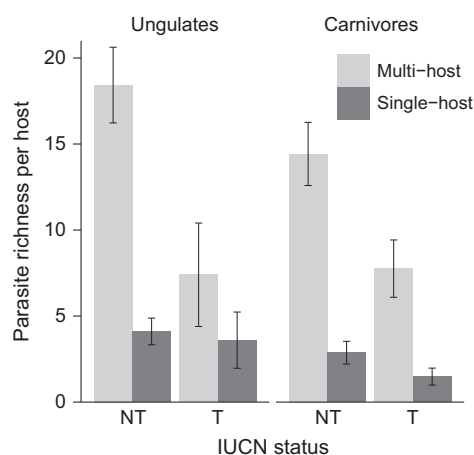


Fig. 1. Average parasite richness per host for multi-host and single-host parasites, sorted by host group and threat status (NT = Non-threatened; T = threatened), see “Materials and methods” for details. Error bars represent standard errors.

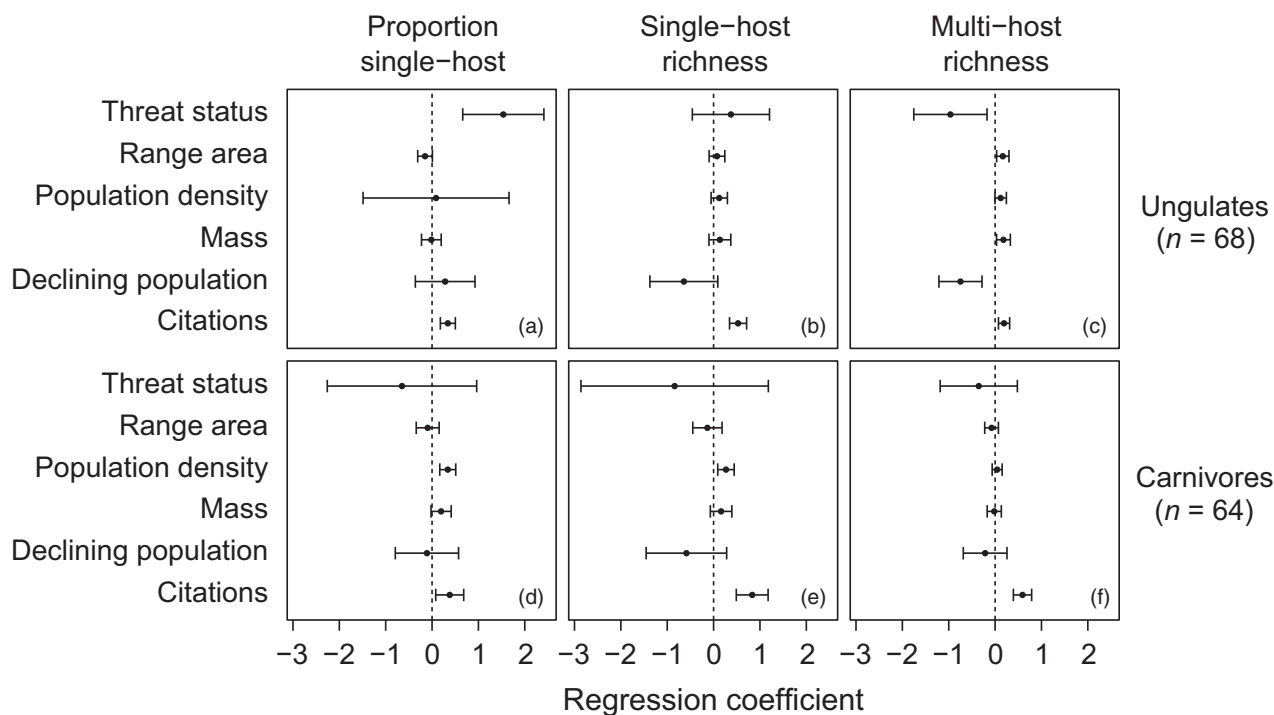


Fig. 2. Estimated regression coefficients from Generalized Estimating Equations for ungulate (a–c) and carnivore (d–f) hosts. Columns represent response variables. Error bars represent 95% confidence intervals.

citation count (Fig. 2c). The significance and direction of predictors did not vary between full [$n = 68$; Fig. 2, Appendix S2 (Table 1) in Supporting information] and reduced models [$n = 68$ –93; Appendix S2 (Tables 2 and 3) in Supporting information], except for threat status in the bivariate model of multi-host parasite richness, which became marginally non-significant ($P = 0.073$). In contrast, single-host parasite richness did not correlate significantly with any of our ecological predictors. The significance and direction of predictors did not vary between full models when classifying parasites as either micro- or macro-parasites [Appendix S2 (Table 4), in Supporting information].

Among carnivores, we found no significant effect of host threat status on the proportion of single-host parasites, the richness of single-host or the richness of multi-host parasites [Fig. 2d–f, Appendix S2 (Tables 2 and 3) in Supporting information]. However, both the proportion of single-host parasites and richness of single-host parasites were positively associated with population density (Fig. 2d,e). The richness of multi-host parasites was not significantly predicted by any of our ecological variables (Fig. 2f). As for ungulates, the significance and direction of predictors did not vary between full [$n = 64$; Appendix S2 (Table 1) in Supporting information] and reduced models [$n = 64$ –140, Appendix S2 (Tables 2 and 3) in Supporting information]. While the significance and direction of predictors was similar for models predicting the proportion of single-host parasites and the proportion of single-host macro-parasites, the proportion of single-host micro-parasites among carnivores was not significantly

predicted by any of our ecological predictors [Appendix S2 (Table 4) in Supporting information].

Discussion

We found host extinction risk to be a significant predictor of the proportion of single-host parasites among ungulates, but not carnivores (Fig. 2). Although current theory predicts that threatened hosts should have decreased proportions of single-host parasites (Dunn *et al.* 2009; Lafferty 2012), we found no trend within carnivores and the opposite trend within ungulates. For ungulates, we suggest this result can be explained by the disproportionate loss of multi-host over single-host parasites. For carnivore hosts, threat status was not a significant predictor of the proportion of single-host parasites or the richness of either single-host or multi-host parasites. Our results suggest a need for improved theory on the process of coextinction and highlight the necessity of challenging models with empirical data.

Recent models of coextinction operate under the assumption that parasites will be lost from a system when all of their potential hosts go extinct (Colwell, Dunn & Harris 2012). However, these models focus only on the outcome after complete host extinction, whereas a species will frequently experience significant contractions in abundance and range size well before it finally becomes extinct. Here, we used IUCN Red List status and data on host population trend to document this path towards extinction. Our study provides added evidence that models of parasite coextinction with host decline may differ from models based solely on host extinction.

Why does threat status result in a disproportionate loss of multi-host parasites in ungulates but not carnivores? It is possible that this contrast reflects differences in the major threatening processes or life-history traits between the two groups. If ungulates and carnivores are listed under different Red List criteria, this might explain differences in loss of parasites with extinction risk. Indeed, a greater proportion of threatened ungulates included in this study are listed because of an observed reduction in population size (Criterion A1, A2, or A4): 14 out of 20 ungulates opposed to 13 out of 29 carnivores. While this difference is not statistically significant (Pearson's $\chi^2 = 2.10$, $P = 0.147$), it may indicate that threatened ungulates have more often experienced significant reductions in abundance and geographic range.

Host geographic range is a key predictor of parasite species richness (Kamiya *et al.* 2014). Broad ranging species are also more likely to overlap with other host species, increasing opportunities for infection with multi-host parasites (Gregory 1990). Overlap in host geographic range is a significant predictor of parasite community similarity in carnivores (Huang *et al.* 2014) and primates (Davies & Pedersen 2008), and similarly among sympatric African bovids, habitat overlap is positively correlated with increased prevalence of multi-host gastrointestinal parasites (Ezenwa 2003). Geographic range is often used as a proxy for the amount of interspecific contacts experienced by a given host, while population density is used to represent the amount of intraspecific contact. However, as extinction processes can reduce both species' abundances and range (Price & Gittleman 2007; Hayward 2009), it is not immediately obvious how population density will respond, especially when host individuals are unevenly distributed throughout a species' range.

Among ungulates, group living is common and is hypothesized to provide benefits via reduction in predation pressure (Averbeck *et al.* 2012). In some cases, human hunting and habitat degradation have even resulted in increased group sizes, which is hypothesized to allow greater vigilance and predator avoidance (Averbeck *et al.* 2012). It is possible, therefore, that extinction drivers might decrease total abundance of species by reducing the total number of groups, while maintaining the number of individuals per group. If this is the case, the number of intraspecific contacts among individuals may stay relatively constant as species decline. We suggest that the path to extinction in ungulates may follow this trajectory. In threatened ungulate species, local densities may remain high due to pressure to maintain minimum group sizes and thus allow intraspecific contact rates sufficient to support single-host parasites, while reduction in total range size will result in a loss of multi-host parasites.

In contrast with ungulates, only 10–15% of carnivores are known to live in social groups (Gittleman 1989). The natural rarity of carnivores may lead to species being placed on the IUCN Red List solely because of living at critically small population sizes. Additionally, species

which have undergone a historical decline but currently have range and population sizes above critical thresholds will not be considered threatened (Mace *et al.* 2008), which may be the case for many large carnivores (Ripple *et al.* 2014). Consequently, threat status in carnivores may not be a reliable proxy of recent population decline. It is understandable then that direct measures of population density are a better predictor of parasite assemblages in carnivore hosts, with those species living at higher densities able to support a higher proportion and richness of single-host parasites.

While these explanations fit the known ecologies of these two host groups, comparative analyses are inherently susceptible to issues of data quality. It is possible that insufficient sample size or mismatched data may lead us to miss important patterns, but it is unclear how these issues would bias our results so as to cause the observed differences between carnivores and ungulates. We have shown that the response of parasite assemblages to host decline depends upon the interaction between intrinsic attributes of hosts and extrinsic drivers of extinction. As changes in both geographic range and population density during host decline impact parasite transmission, gathering additional baseline data on host population densities is therefore essential for predicting coextinction events.

Considering the important roles parasites play in ecosystems and the burdens they cause for wildlife, domesticated animals and humans, it is vital that we better understand how anthropogenic changes to natural ecosystems alter host–parasite dynamics. The loss of multi-host parasites may have detrimental outcomes to ecosystems, including facilitating disease emergence (Johnson 2013). Determining how anthropogenic and biological factors interact to alter host–parasite systems can aid in the prediction of disease emergence through future host shifts, or increased prevalence of endemic diseases, an important consideration for the proactive surveillance of emerging pathogens (Farrell, Berrang-Ford & Davies 2013). Generating a broader understanding of host–parasite coextinction dynamics will be critical for prioritizing surveillance efforts in the face of shifting species ranges and expansion of human land use practices. Anthropogenic activities not only directly contribute to species loss, but have the potential to bring previously isolated host populations into contact and create novel opportunities for cross-species transmission and exacerbation of existing threats. Our results indicate that there is an urgent need to develop new theories of parasite transmission and loss in declining hosts, but more critically this theory needs to be tested against empirical data which we currently lack.

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Data accessibility

Data available in Appendix S1, Supporting information.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Dataframe used in the analyses (.csv).

Appendix S2. Model results in Tables S1–S4.