



Succinctus

Estimates of coextinction risk: how anuran parasites respond to the extinction of their hosts



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ABSTRACT

Amphibians are known as the most threatened vertebrate group. One of the outcomes of a species' extinction is the coextinction of its dependents. Here, we estimate the extinction risk of helminth parasites of South America anurans. Parasite coextinction probabilities were modeled, assuming parasite specificity and host vulnerability to extinction as determinants. Parasite species associated with few hosts were the most prone to extinction, and extinction risk varied amongst helminth species of different taxonomic groups and life cycle complexity. Considering host vulnerability in the model decreased the extinction probability of most parasite species. However, parasite specificity and host vulnerability combined to increase the extinction probabilities of 44% of the helminth species reported in a single anuran species.

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Biodiversity is declining at alarming rates, similar to those of historical mass extinctions (Stork, 2010). Rapid changes in atmospheric conditions, habitat fragmentation, pollution, invasive species and pathogens, individually and collectively, represent a greater threat to existence than most living species have previously experienced (Barnosky et al., 2011). Amphibians are much affected by the current biodiversity crisis, with well-documented recent extinctions in response to such stressors (Pounds et al., 2006). At least 32% of existing amphibians are at threat from extinction (Stuart et al., 2004) and numerous populations are facing major population declines, morphological deformities and severe pathogen infections (Daszak et al., 2003).

One of the outcomes of a species' extinction is the coextinction of its dependants, which is one of the most common, but least understood, routes to biodiversity loss (Brook et al., 2008; Dunn et al., 2009). When one thinks about extinction, parasite species are generally seen as one of the threats that free-living organisms have to face in a changing world. However, parasite species may be

more prone to, and affected by, extinction than free-living organisms (Moir et al., 2011). Parasite extinction may first seem beneficial to hosts, especially those endangered, but some long-term consequences might be severely disadvantageous, such as a loss of genetic diversity of their hosts or increased abundance of other pathogenic parasites (Altizer et al., 2003; Dobson et al., 2008). For instance, Altizer et al. (2003) showed that exposure to parasites maintains host allelic diversity and sexual recombination, which is related to resistance and immune defence against pathogens in a wide range of host species. Parasite diversity is also linked to ecosystem health, as parasite species richness affects the robustness, stability and persistence of food webs (Dunne et al., 2013; McQuaid and Britton, 2014).

Coextinctions are often difficult to document and models estimating coextinction rates may therefore be useful in predicting and preventing future biodiversity loss (Colwell et al., 2012). These estimates are influenced by host and parasite traits and by the interactions between them. The degree of host specificity is a key factor in determining coextinction risk, since parasites with restricted host relationships are more likely to become extinct with their hosts (Dobson et al., 2008; Lafferty, 2012). Parasite extinction likelihood may also vary with their host's vulnerability to extinction (Lafferty, 2012). Hence, assuming that extinctions are not

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random in nature, and that hosts vary in their likelihood of becoming extinct, provides a more realistic scenario of how parasite biodiversity will respond to host extinctions (Moir et al., 2010). Here, we use data on the helminth parasites of South American anurans to explore the relationships between parasite specificity and host vulnerability in determining parasite coextinction rates.

We compiled reports of helminth parasites of amphibians from South America from a recently published list (Campião et al., 2014). This list reports 298 helminth taxa in 186 amphibian species. We conducted the analysis with amphibians of the order Anura only, and excluded all reports in which the host or parasite were not identified to species. It was assumed that a parasite species would persist if at least one of its host species persists. Assuming that host extinction events are statistically independent (Sodhi et al., 2008), this means that the probability Q_i that parasite species i persists can be expressed as

$$Q_i = 1 - \prod_{j \in H_i} (1 - q_j),$$

where q_j is the probability that host species j is extant and the product runs over the set H_i of all hosts of parasite species i . We modeled host extinction as a Markov process with rate r_j , i.e. we assumed that the probability that the species becomes extinct in the time interval $(t, t + dt)$, provided it is extant at time t , is $r_j dt$. This means that the probability that host species j is extant after time t satisfies $\frac{dq_j}{dt} = -r_j q_j$, and by solving this we find that the probability $q_j(t)$ is given by $e^{-r_j t}$. By assuming particular relationships between the host extinction rate r_j and host traits, we were able to study how parasite extinction probabilities varied under different scenarios for host extinction.

The anuran geographic range was adopted as a measure of host vulnerability and this was modeled as $r_j = c/\log(A_j)$, where A_j is the geographic range of species j and c is a constant. This means that the chance of that species becoming extinct increases as geographic range declines and $q_j(t)$ is now given by $e^{-\frac{ct}{\log(A_j)}}$. Several other factors might be important in determining amphibians' vulnerability to extinction. Here, we focused on geographic range because it is positively correlated to species' niche breadth and abundance (Slatyer et al., 2013), being the most important driver of amphibian extinction risk (Sodhi et al., 2008; Cooper et al., 2011; Whitton et al., 2012; Ficetola et al., 2015), and is known for all host species in the dataset. Geographic range data were compiled from International Union for Conservation of Nature (IUCN, <http://www.iucnredlist.org/technical-documents/spatial-data>) records. We do not have any specific information on the time scale for host extinction, so we are unable to estimate the constant c that determines the extinction rates. Rather than choosing explicit but arbitrary values for c and t , and determining the probability of parasites becoming extinct after this time, we instead assumed that a particular fraction of the hosts had become extinct. As described above, the probability that host j is extant at time t is $q_j(t)$, so the mean number of extant host species after time t is

$$S(t) = \sum_j q_j(t) = \sum_j e^{-\frac{ct}{\log(A_j)}}$$

where the sum runs over all host species. Both $q_j(t)$ and $S(t)$ depend only on the product ct , so a non-linear equation solver can be used to numerically find the value of ct corresponding to a particular value of $S(t)$, and hence determine the parasite's extinction probabilities at the point when a particular number of host extinctions have taken place.

We used Mann–Whitney U tests to compare extinction rates between different parasite specificity groups (generalists and specialists). We also tested whether a parasites species had

particularly high or low extinction probabilities, given its number of hosts. To do this, bootstrap distributions of the extinction probabilities were generated by randomly resampling, with replacement, the geographic ranges A_j (and, hence, extinction rates r_j) of the host species. This allows testing of the null hypothesis that there is no association between host vulnerability and particular parasite species or groups. To assess the effect of host vulnerability on the extinction probabilities of the parasite species, the observed estimates were tested to confirm whether those had a significant tendency to be greater or smaller than the medians of the bootstrap confidence intervals (CIs), using a chi-square test. Differences amongst parasite taxonomic groups (Acanthocephala, Cestoda, Monogenea, Nematoda, Trematoda) were tested with a Fisher's exact test.

A re-sampling (permutation) process was used to compare the extinction probabilities amongst helminth taxonomic groups, and between species with direct and indirect life cycles. This was tested with a re-sampling ANOVA, where we considered different percentages of host species becoming extinct, and a nested relationship between helminth life cycle and taxonomic group. We did 1000 re-samplings, with replacement. Since information on the life cycle of anuran parasites is scarce, the literature was searched for each family and it was assumed that all helminths of a given family would have the same type of life cycle, i.e. direct or indirect. This analysis was conducted with 181 helminth species, because some species in the dataset are inquenda or insertae sedis and were removed.

The data set comprised 157 anurans and 194 helminth species. The number of hosts to which a parasite is associated (parasite specificity from here on) was on average 3.7 (SD = 6.68); 52% of the helminth species were associated with a single host species. Monogenea were the most specialised parasites, while Nematoda were the most generalist (Table 1). Parasite species associated with few hosts had higher extinction probabilities (Fig. 1). The vulnerability of hosts associated with specialist (one host) parasites did not differ from other hosts ($U = 2670$, $P = 0.5638$). Notwithstanding, 75% of the extinction probabilities generated by the null model were higher than expected if the actual geographic range of each host species was considered ($\chi^2 = 45.55$, degrees of freedom (df) = 1, $P < 0.001$). This indicates that most helminths depend on hosts with a higher than average vulnerability to extinction. However, 44% of the specialist parasites had significantly greater extinction probabilities ($\chi^2 = 6.01$, df = 2, $P = 0.049$), with Monogenea being the parasite group most negatively affected by their hosts' vulnerability (i.e. extinction probability was increased; Fisher's Exact Test for Count Data $P = 0.02$).

Forty-six percent of the helminth species reported have a direct life cycle. Hence, extinction probabilities varied amongst helminth species of different taxonomic groups and life cycle complexity (Fig. 2) with a significant interaction between these factors (Table 2). Therefore, the extinction probabilities tended to be

Table 1

Number of hosts reported in helminth species of different taxonomic groups of parasites from South American anurans.

Reported hosts	Number of helminth species in each taxonomic group				
	A	C	M	N	T
1	2	6	10	58	35
2	0	1	1	14	12
>2	3	1	0	33	18
Total	5	8	11	105	65
Mean of reported hosts (\pm S.D.)	3.4 \pm 2.6	2.1 \pm 2.61	1.1 \pm 0.28	3.9 \pm 7.53	2.2 \pm 2.1

A, Acanthocephala; C, Cestoda; M, Monogenea; N, Nematoda; T, Trematoda.

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