

Paradigms for parasite conservation

Running Head: Parasite conservation

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Abstract

Parasitic species, which depend directly on host species for their survival, represent a major regulatory force in ecosystems and a significant component of Earth's biodiversity. Yet the negative impacts of parasites observed at the host level have motivated a conservation paradigm of eradication, moving us further from attainment of taxonomically unbiased conservation goals. Despite a growing body of literature highlighting the importance of parasite-inclusive conservation, most parasite species remain understudied, underfunded, and underappreciated. We argue the protection of parasitic biodiversity requires a paradigm shift in the perception and valuation of their role as consumer species, similar to that of apex predators in the mid-20th century. Beyond recognizing parasites as vital trophic regulators, existing tools available to conservation practitioners should explicitly account for the unique threats facing dependent species. We build on concepts from epidemiology and economics to introduce novel metrics of "margin of error" and "minimum investment" for parasite conservation. Once suitable parasites are identified, we describe methods for constructing population viability analyses for host-parasite assemblages. In the direst cases, ex situ breeding programs for parasites should be evaluated to maximize success without undermining host protection. Though parasitic species pose a considerable conservation challenge, adaptations to the conservation toolbox will help protect parasite biodiversity in the face of an uncertain environmental future.

Introduction

While conservation is founded on the preservation of biodiversity for the future, human health, as a rule, always takes precedence. Wildlife management divides biodiversity into threats and targets, and species that conflict with humans are labeled pests rather than priorities. However, the delayed realization that the pest eradication paradigm has unanticipated detrimental effects has forced practitioners to consider alternative approaches. Consequently, one of conservation's tasks is the identification of the prejudices of earlier paradigms, and the restoration of their casualties.

During the mid-19th century, for example, massive declines in herbivore populations on the American prairie forced carnivores to turn to livestock for sustenance, eliciting calls by ranchers and farmers for government-sponsored extermination (Bergstrom et al. 2013). At its peak, this management effort was responsible for the deaths of an estimated 21,000 wolves annually at the hands of government hunters (Mech & Boitani 2010). In 1963, under growing pressure from the environmental movement, an advisory group was tasked with reviewing the practices of the program. Upon their recommendations, and based on a growing body of literature on the negative impacts associated with predator removal (Hairston et al. 1960), eradication efforts were supplanted by a predator-inclusive paradigm that values the consumers' role in ecosystems.

Conservationists did not fully appreciate the ecological importance of apex carnivore species until after the decimation of many of these predator's populations on most continents (Berger & Wehausen 1991). Furthermore, a transformation in the public perception of predators occurred following the extirpation of many species of charismatic megafauna (Kellert et al. 1996; Messmer et al. 1999). These species are now often invoked in conservation efforts as keystone, umbrella, sentinel, flagship, and indicator species due to their ability to directly promote biodiversity in ecosystems through resource facilitation and

trophic stabilization (Sergio et al. 2008). Parasites may serve many similar functions, such as providing regular carrion for scavenger assemblages (DeVault et al. 2003) and structuring communities by indirectly affecting multiple trophic levels (Lafferty et al. 2008). A shift in the scientific and public perception of parasites is required as we recognize not only their intrinsic value, but also their role as trophic regulators. While parasitic species occur in almost every major animal clade, we present the case for rethinking the paradigms used for parasite conservation with a focus on invertebrate macroparasites, such as helminths and lice.

The advantage of apex predators over parasites in facilitating a paradigm shift is their charisma. Today, large carnivores attract huge amounts of funding and promote the idea of protecting large areas (Ray et al. 2013). Parasites, on the other hand, are not often praised for their aesthetic appeal outside the field of parasitology (Gómez & Nichols 2013; Lafferty 2014). The sperm whale roundworm, *Placentonema gigantissima*, for example, can grow up to nine meters in length, yet it is rarely considered alongside its cetacean hosts as one of the more interesting creatures in our oceans.

Parasitism, as a highly specialized life history, is a consistent part of natural ecosystems and has played a proportionate role in driving co-evolutionary radiation. Numerous examples illustrate the incredible diversity of form and function associated with a parasitic life history, including unique adaptations like behavior control, feminization and castration, and unparalleled complexity in life cycles (Poulin 2010). Despite their important role on organismal and evolutionary time scales, parasites are frequently equated with disease in current conservation applications, resulting in their eradication for the sake of host preservation. In the best cases, parasites are preserved to protect host immunity in reintroduced populations, as in the case of unique protozoans (identified as *Eimeria* sp.) in the black-footed ferret (*Mustela nigripes*) (Gompper & Williams 1998). However, in many cases, the extinction or extirpation of obligate parasites is merely a consequence, intended or

otherwise, of conserving megafauna hosts, as in the case of the louse *Colpocephalum californici* of the California condor (*Gymnogyps californianus*) (Koh et al. 2004) and the louse *Rallicola pilgrimi* of the little spotted kiwi (*Apteryx owenii*) (Rózsa & Vas 2015).

Although the benefits of parasites are an active topic of research, the negative impacts parasites can have, especially on humans, are conspicuous and well documented (Kuris 2012). Unfortunately, even when these costs and benefits of parasites can be measured, comparing them within the same value system is difficult, as it is impossible to determine the exchange rate between ecosystem health and human lives. Potential infection of livestock, fisheries, or humans by a pathogen may be enough to curtail parasite conservation efforts. For example, *Echinococcus granulosus*, a generalist tapeworm, has been found to be highly prevalent in canid species, but is frequently removed from wolves during translocation efforts (Lafferty 2014). The parasite has a more substantial effect on ungulates, manipulating their behavior and increasing their risk of predation by wolves. Thus, maintaining *E. granulosus* in the system may be beneficial for reintroduced wolves (Lafferty & Kuris 2014). The fact that humans and livestock can be accidental hosts of the tapeworm complicates matters, as introducing the parasite via wolves may have economic and human health ramifications (Corn & Nettles 2001). With wolf reintroduction already a contentious issue, conserving a zoonotic pathogen may undermine established conservation goals. Human economic concerns may also warrant parasite eradication, as in cases such as rinderpest, which threatened both wildlife and livestock (Mariner et al. 2012).

While exceptions for highly pathogenic or zoonotic parasites of hosts that are charismatic or the subject of high profile conservation efforts may be necessary, we encourage examination of the potential risk that losing parasite species may endanger hosts in the long run. By definition, parasites are exploitative, but recent research has highlighted the major role they play as catalysts in the evolution of host immunity, particularly through

interaction with the major histocompatibility complex (Kamath et al. 2014). In human populations, the “hygiene hypothesis” suggests that diminished pathogen/parasite exposure, often due to urbanization, has led to a steep increase in the frequency of allergies and autoimmune diseases such as Type 1 diabetes and multiple sclerosis (Yazdanbakhsh et al. 2002). Therapies for autoimmune diseases using helminths are currently being developed, such as using whipworm (*Trichuris suis*) to downregulate the patient’s immune response and achieve remission in Crohn’s disease (Summers et al. 2005). The immunoregulatory role of parasites is especially important in multi-species systems, where high parasite biodiversity is shown to have a dilution effect on chronic infections. Johnson et al. (2013) demonstrated that within-host parasite competition reduces rates of disease transmission in amphibian hosts, reducing limb deformations.

At the ecosystem scale, parasites play the role of “ecological puppeteers,” effecting major changes under the guise of their host species, making their value significant but difficult to measure (Lefevre et al. 2009). By some metrics, parasites represent the dominant force shaping ecosystems. For example, parasites constitute a large portion of biomass in most systems and can be responsible for up to 78% of trophic interactions in some food webs (Lafferty et al. 2006). By mediating interactions between free-living species through apparent competition (Hatcher et al. 2012), they may be as important in their regulatory effects as wolves, cougars, or any other apex carnivore. Moreover, behavior-altering parasites may increase the flow of energy throughout trophic levels where such transfer might not otherwise exist (Kuris et al. 2008). For example, camel crickets and grasshoppers infected with nematomorph parasites (*Gordionus* spp.) are 20 times more likely to jump into a stream, where their biomass constitutes up to 60% of the energy intake of endangered fish populations (Sato et al. 2011). Often, the parasite species that have the greatest ecosystem impacts tend to be small and virulent rather than intrinsically impressive, like the sperm

whale roundworm mentioned earlier. Thus, competing prioritization schemes based on intrinsic versus functional value are likely to emphasize a different subset of parasites from any given ecosystem.

As studies demonstrating the vital role parasites play in ecosystem health and functionality emerge, we encourage the development of conservation tools that enable practitioners to become more discerning when prioritizing and executing parasite conservation efforts. A shift in mindset is just the first step in preserving these vital elements in many ecosystems; successful parasite conservation requires adapting and expanding the tools available to conservation practitioners. Incorporating parasites into the conservation agenda represents the next step in the iterative process through which conservation has expanded from resource management to the protection of previously maligned and misunderstood consumer species like large carnivores.

The Conservation Toolbox

The majority of the methods used in conservation biology were developed without explicitly considering the many dependent species that constitute vital elements of any ecosystem. We propose a series of shifts in the way we apply several of our most established tools for conservation, in order to incorporate parasite species that have been previously overlooked. Most fundamental to this is the identification of the subjects requiring protection. As discussed by Costello et al. (2013), naming species is required for the development of conservation plans, but the rate at which species are described may be overtaken by extinction rates in the direst cases. Consequently, concurrent to naming and cataloging parasite biodiversity, conservation practitioners are faced with the challenge of rapidly identifying which species are at the greatest extinction risk.

Parasites face the unique conservation challenge of dependence on a sustainable antagonistic interaction. However, in unstable cases where there is an immediate tradeoff between host population health and parasite persistence, eradication of the parasite is often suggested in the hope of preserving the host, despite the cost to ecosystem function and diversity (Fig. 1) (Stringer & Linklater 2014). In these cases, parasite eradication may even be vital to hosts' survival: for instance, Zhang et al. (2008) report that the host-specific intestinal nematode, *Baylisascaris schroederi*, was the greatest threat to giant pandas, accounting for 50% of reported mortality during their study. In cases like this, parasite conservation will inevitably upset the public, posing serious ethical challenges.

Recommendations made using the newly adapted conservation toolbox should abide by the precautionary principle, particularly concerning issues of human health. Incomplete knowledge of parasite life histories and complex multi-species interactions create the potential for unanticipated consequences, and we warn that conservation of even the most endangered and intrinsically valuable parasite should be reconsidered if the parasite potentially threatens human health. For example, despite the diversity and unique biological attributes of haemosporidian blood parasites, the conservation of malaria given its global mortality rate is obviously unjustifiable from a human health perspective. Despite these risks, we must not dismiss all zoonotic diseases as lost causes. Rather, we can reduce the odds of mismanagement and the potential for emergence of novel pathogens by including epidemiologists and public health specialists in risk analysis and conservation planning. This way, ecologically important parasites like *Echinococcus granulosus* can be protected, maximizing the services they provide to natural ecosystems while minimizing risk to humans. Once the risks have been adequately considered, parasites can be effectively incorporated into the mainstream conservation agenda through their inclusion in economic valuation,

population viability analysis, ex situ conservation efforts, and open-source data management databases.

Including Parasites in Economic Valuation

Parasitic species occupy a unique space in the public's perception of "nature." Their negative impacts on human health and economics are particularly salient (Gómez & Nichols 2013), while their diversity and functional role in ecosystems remain unrecognized by most. Some proponents of economic valuation metrics argue that they inherently account for the value of the ecological relationships underlying a threatened or endangered species (White et al. 1997), but it seems unlikely that parasites' ecological role will be thoughtfully considered in any method of appraisal. At the scale of a single interaction, it is difficult to untangle the positive effects a parasite might have from the costs they incur to ecosystem services provided by the host. Measuring the impacts that parasites have on their hosts and trophic webs will likely require manipulative experiments, which may be an infeasible step in conservation planning for already endangered species. Within the time frame dictated by co-extinction rates, it is unlikely that many parasites will be sufficiently studied; if we hope to utilize the existing economic valuation framework to revise policy in the short term, we may need to turn to proxy methods such as metrics of connectedness in networks (Mougi & Kondoh 2012) to evaluate their functional roles and assign monetary values.

Previous efforts at disease and parasite eradication offer an idea of the economic cost of the potential alternative to conservation. Complete eradication has proved difficult and costly in the past, with smallpox and rinderpest being the only examples of successful campaigns thus far (Barrett 2004; Mariner et al. 2012). For example, approximately \$350 million have been spent on the effort to eradicate Guinea worm disease (*Dracunculus medinensis*), a macroparasite that infected nearly 3.5 million people each year when the effort

first began (Callahan et al. 2013). In cases in which human health is not directly impacted, maintaining parasite population levels, rather than advocating for increase as we would for most other threatened species, may represent the most cost-effective and acceptable strategy. Evidence from successful maintenance of parasites during captive breeding programs suggests that the costs may actually be negligible for some species (Izdebska 2006).

Thus, we propose shifting efforts away from costly broad-scale eradication efforts, and advocate for a framework that values hosts and parasites as species assemblages and measures their total net economic significance. With imperfect knowledge of host-parasite interactions, it may be impossible to accurately value the independent and interacting effects that each has on the other's ecosystem services. Consequently, we propose the treatment of host-parasite interactions (HPIs) as a unit of conservation, maximizing important criteria like host immunity and intrinsic value while carefully monitoring any added risk stemming from the interaction. We predict that in cases where coevolution and equilibrium population dynamics are important factors, preserving HPIs will be synonymous with effective host conservation.

Including Parasites in Population Viability Analysis

Population viability analysis (PVA) is a mainstay of conservation biology and has been applied to assess a wide range of taxa (Boyce 1992). In its simplest form, this approach takes population survey data and projects the probability that a population will persist over a given time frame based on variation in the population's growth rate, a starting population size, and some threshold at which extinction is assumed to occur (Dennis et al. 1991). The extinction risk of a population of interest can then be estimated by simulating multiple populations and assessing the number that go extinct over the time frame of interest (typically 100 years).

Currently, the majority of parasite involvement in PVA focuses on the effect of parasite extirpation on host persistence odds (Gerber et al. 2005). A simple starting goal for expansion of the concept would be developing tools to adjust the extinction threshold of the host PVA to reflect the minimum population size that an associated parasite species requires to persist. However, applying PVA methods to host or parasite populations alone is insufficient for a framework that considers hosts and parasites as assemblages. Rather than a modified host PVA, we argue that a more dynamic joint approach better accounts for the natural oscillations that characterize antagonistic species interactions. In the simplest case, where a specialist parasite exploits a single host, epidemiological tools like the host density threshold and the intrinsic rate of increase can be used to find the sustainable limits of host-parasite equilibrium (Fig. 2). When faced with the divergent choice between eradication and mutual preservation, we argue that the ideal joint PVA has the capacity to measure both the additional investment required to maintain parasites and the assumed liability for disease-driven host extinction, informing conservation efforts.

The dynamics of generalist parasites within ecosystems are far more difficult to model. In such cases, the odds of parasite persistence are distributed across a set of variably suitable hosts, necessitating a parasite PVA that integrates multiple simultaneous joint PVAs. Conversely, parasites with multi-stage life cycles or free-living stages can face compounding and distributed risk across each sequential host, requiring an approach that accounts for contact and transmission dynamics between levels (Rudolf & Lafferty 2011). A solid foundation in system dynamics allows for incorporation of additional corrections; for example, assessing the tradeoffs between parasite costs and benefits both at an individual scale (bolstering host immunity; Johnson et al. 2013) and at a population scale (in regulation of species interactions).

Typically, parasites lack long-term population data, which poses a challenge for fitting dynamical models that accurately measure or estimate demographic and epidemiological parameters. Unlike the approach taken in the US Endangered Species Act of setting a critical population size and adhering to that threshold (Rohlf 1991), parasites will likely require an ongoing periodic reassessment of what constitutes stable populations (and acceptable risk to humans) given current environmental conditions and host densities. However, as the challenge of reintroducing gray wolves into Yellowstone National Park illustrates, it is likely more feasible to expend resources to prevent an unpopular species from disappearing in the first place than to try to return it after its disappearance.

Including Parasites in Ex Situ Conservation:

In cases where the conservation status of a host becomes dire enough that the survival of a species is contingent on its removal from the wild and management in captivity (ex situ conservation), parasites are often eradicated to reduce risks to captive populations (Stringer & Linklater 2014). This systematic eradication has been responsible for the regional extirpation and extinction of parasites (Jørgensen 2014), which in some cases leads hosts to be more susceptible upon reintroduction. For example, when gray wolves were reintroduced to Yellowstone, the removal of parasitic mites increased the susceptibility of wolves to viral pathogens (Almberg et al. 2012). However, in addition to maintaining parasites that are beneficial to their host species, conservation efforts must treat endangered parasites of endangered hosts as worthwhile targets in their own right, supplanting the paradigm that parasite eradication is synonymous with disease control in threatened hosts. Fortunately, the costs of parasite eradications are well enough studied that current conservation best practices are perhaps more advanced in ex situ protocols than other parasite conservation tools. For example, the IUCN Guidelines for Reintroductions and Other Conservation Translocations

even advocate for re-introducing parasites along with translocated hosts after a period of absence (Jørgensen 2014).

Despite these guidelines, most interest thus far has been on utilizing parasite conservation as a tool for host preservation, and implementation strategies for critically endangered hosts are not formalized. Jørgensen (2014) highlights the potential for conflicts that arise when conserving several parasite species within a single host species, drawing on the case study of the host-specific louse, *Felicola isidoroï*, of the critically endangered Iberian lynx (*Lynx pardinus*). While captive breeding represents the best chance for *F. isidoroï* to be saved, a plethora of disease-carrying generalist ectoparasites make delousing a requisite part of the lynx's conservation plan. Pérez et al. (2013) suggest extreme measures: to work around delousing, they recommend transferring *F. isidoroï* by hand from wild lynx into captive breeding stock. As this example highlights, developing conservation plans that benefit both hosts and parasites of conservation interest requires attention to the broader ecological context.

Maintaining complex HPIs with proper environmental conditions for parasite transmission will likely be economically and spatially restrictive when hosts are being bred in captivity. In situations where parasites cannot be feasibly maintained in captive host populations or established in phylogenetically-related alternative hosts in the wild, options for truly ex situ conservation should be explored (Fig. 3) (Silverman et al. 2001). These may come in the form of Ark projects (Soulé et al. 1986), in which the parasite is removed entirely from its host and supported using artificial methods. The goal of any such effort should be reintroduction into natural host populations upon their recovery, as maintaining parasites as “museum species” (i.e. those that only remain in zoos or laboratories) will be costly and only serve research purposes. However, due to our incomplete knowledge about the roles of

specific parasites in their natural systems, ex situ conservation measures should be taken at every opportunity to maintain any parasite that cannot justifiably be conserved on its host.

Even in situations where ex situ conservation is successful, issues may arise surrounding reintroduction, namely potentially divergent evolutionary trajectories between host and parasite and risk of invasion. Parasites evolve in conjunction with the internal environments of their hosts (Koskella & Lively 2007). Hosts that have been living without a specific parasite could be colonized with other parasites that may outcompete the original organism upon reintroduction (Fenton & Perkins 2010). Furthermore, hosts separated from their native parasite assemblage may then be especially susceptible to virulent infections by the reintroduced parasite (Aiello et al. 2014). Most megafauna conservation efforts that involve relocation of animals include deworming and vaccination of hosts (Cunningham 1996). We should instead establish protocols for maintaining both the internal and external environments of conserved megafauna species. These efforts should include consistent testing of introduced and potential native hosts to determine if parasites are experiencing immunological release into new, naïve hosts (Cunningham 1996).

Including Parasites in Open-source Data Management Systems

In developing a plan for parasite preservation, the allocation of limited conservation funds requires a triage system that includes hosts' environmental sensitivity. Yet, complex, multi-host life cycles obscure the correlation in vulnerability between parasites and any given host. As the case of the Iberian lynx highlights, considering single host-parasite pairs is often insufficient to devise accurate conservation plans, and association data is required to inform conservation work. At a broader scale, understanding the risk parasites face from threats like climate change or habitat loss requires information regarding distributions, prevalence, and host specificity that has never been compiled in one definitive source. At the time of

publication, long-term parasite ecology datasets are limited, and integration across platforms is virtually nonexistent. Major data sources like the Global Biodiversity Informatics Facility (www.gbif.org) and the Encyclopedia of Life (www.eol.org) decouple parasites from their hosts, and though parasite diversity databases exist, they tend to be specific to particular groups of hosts, especially at the class or order level (e.g. the Global Mammal Parasite Database [Nunn & Altizer 2005], FishPEST [Strona & Lafferty 2012], or the Global Cestode Database [Caira et al. 2012]). Some of the best databases are also worryingly out of date with respect to the rate of species description, such as the Host-Parasite Database curated by the British Natural History Museum, last updated in 2003 (Gibson et al. 2005).

Taxonomic data on host affiliations and phylogenetic relationships can help fill in some of these gaps in parasite biology (Dunn et al. 2009; Rózsa & Vas 2015). In cases where systematic data are inaccurate or poorly integrated, vulnerability assessments are correspondingly questionable. For instance, the louse *Columbicola extinctus* was believed to be endemic to the passenger pigeon *Ectopistes migratorius* and to have gone extinct (Stork & Lyal 1993), but genetic data later revealed *C. extinctus* is extant on the band-tailed pigeon *Columba fasciata* (Clayton & Price 1999). To solve some of these problems, online data repositories containing information on taxonomy should be integrated with host and parasite phylogenies.

Making existing spatial data more freely available to researchers in conjunction with existing open source databases and museum collections will also accelerate progress and reduce costs in time, money, and computing power. In particular, distributional data is still needed for the identification of biodiversity hotspots based on high levels of parasite richness and/or endemism (Myers et al. 2000). Existing efforts to catalogue host-parasite records in a spatially-explicit manner are ongoing and incomplete. Moving forward, this process may

benefit from collaboration with medical researchers, coopting infrastructure for monitoring important infectious diseases (e.g. the Gideon database; Smith et al. 2007).

Galvanizing Support for Parasite Conservation

The vital first step in effectively incorporating parasites into existing conservation schemes is a shift in the minds of practitioners around the world. The success of parasite conservation programs, however, will be contingent upon extensive public outreach. We hope calling attention to parasite diversity will catalyze a shift much like the transformation of public perception of top carnivores. Just as wolves or big cats captivate the minds of school children, so too can the fungus that turn ants into “zombies” (*Ophiocordyceps camponoti-balzani*) or the isopod that eats and replaces the tongue of a fish (*Cymothoa exigua*). Though museums and zoos represent the primary means by which the public is exposed to global biodiversity, parasite collections are seldom displayed or receive little attention, reducing awareness and utility of these resources to non-parasitologists. The variety of parasite life styles represents an unparalleled evolutionary opportunism and creativity that constitutes a critical and unsung component of the diversity of life (though recent media coverage has stimulated discussions on this subject; Jones 2015). At the present time, the conservation agenda expressed by academia and NGOs overlooks this realm of biodiversity, making advocacy for parasite biodiversity intractable. Biodiversity is no longer a concept endemic to academic discussions, but has become almost synonymous with the idea of nature itself and should be broadened to include parasites. Engaging the public on the importance of parasites and expanding the conservation toolbox will bolster efforts to combat the greatest threats to biodiversity.

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Figure Captions

Figure 1. Four conceivable outcomes for parasite conservation, taken from four case studies (clockwise from upper left): the co-threatened *Gyrostigma rhinocerontis* (Oestridae: Diptera) bot-fly parasite introduced to new areas in conjunction with reintroduction efforts for the critically endangered black rhinoceros (*Diceros bicornis*) (Stringer & Linklater 2014); the louse *Columbicola extinctus* rediscovered on the band-tailed pigeon (*Columba fasciata*) subsequent to the extinction of the passenger pigeon (*Ectopistes migratorius*) (Clayton & Price 1999); the extinct pair *Rallicola extinctus* and its host the huia (*Heteralocha acutirostris*) (Pizzi 2009); and the extinct louse *Colpocephalum californici* of the currently critically endangered California condor (*Gymnogyps californianus*) (Koh et al. 2004).





	Host conserved	Host extinct
Parasite conserved	 <p>Ideal circumstances: both are saved Charismatic megafauna with vital highly-specific parasites</p>	 <p>Reintroduction into alternative hosts OR Rediscovery after host extinction</p>
Parasite extinct	 <p>Current conservation paradigm Parasite a human health risk or otherwise unsuitable candidate</p>	 <p>Current paradigm when host conservation proves unsuccessful</p>

Figure 2. Presenting host-parasite cycles in phase space highlights some of the more immediate challenges to joint population viability analysis. The standard model for host-

parasite dynamics includes an equilibrium population size H^* for hosts and P^* for parasites (cf. Anderson & May 1978). Population viability analysis typically includes some number N_C that is the critical population size or pseudo-extinction threshold, below which populations cannot be recovered (P_C, H_C). It is also especially useful to define the host density threshold (H_{DT}), representing the minimum host population size necessary to sustain $P > P_C$. We similarly define the concept of maximum sustainable parasite population (P_{MAX}), above which the rate of parasite increase becomes unsustainably high and shifts hosts (and parasites) towards extinction. Using these, we define two primary metrics for successful cost-benefit analysis. First, the *Minimum Investment* for parasite conservation is the number of extra hosts necessary to maintain viable parasite transmission ($H_{DT} - H_C$). Second, the epidemiological *Margin of Error* is the degree of flexibility between parasite populations maintained at equilibrium and host endangerment ($P_{MAX} - P^*$). This *Margin of Error* can be treated as a measure of joint conservation risk proportional to the degree of demographic stochasticity in a host-parasite system. In cases where *Minimum Investment* is low and *Margin of Error* is high, parasite conservation may require little to no additional effort at all relative to existing host conservation efforts.

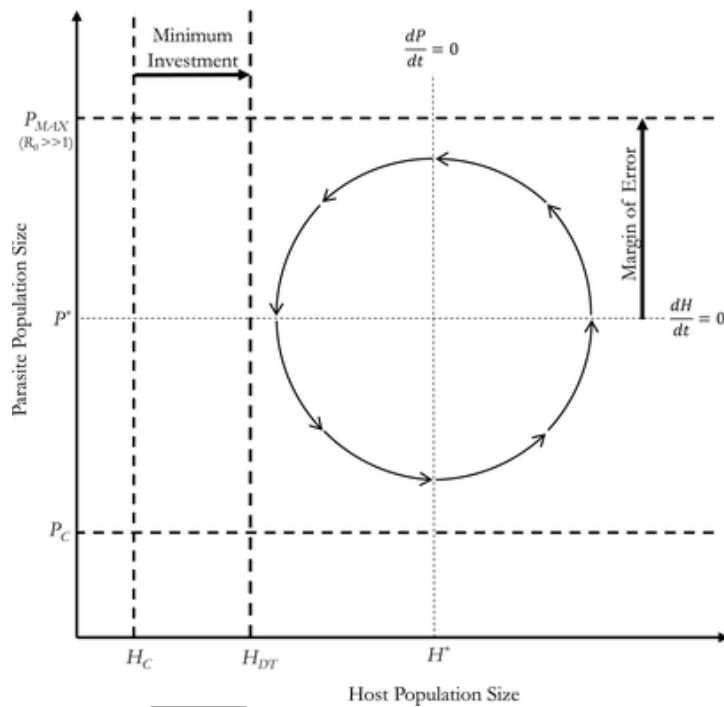
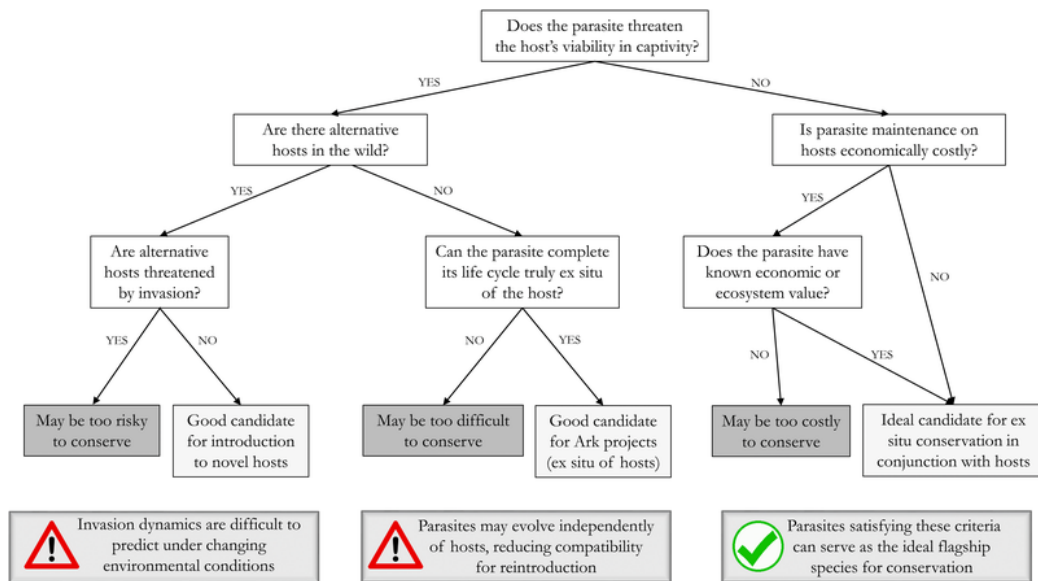


Figure 3. Ex situ conservation of parasites is one of the most risky elements of parasite conservation. We advocate for a cautious approach that limits potential risks to hosts while maximizing the return on conservation investments using a decision-making process as exemplified here. For parasites that complement their hosts' conservation goals, it may be easiest to simply maintain them together in captive breeding programs. However, in cases with higher risk or more obvious conflicts of interests, preserving parasites ex situ from their hosts may be the best option. While the authors are not aware of any large-scale projects of this sort, it is easy to conceive of a collection of in vitro adults (e.g. for readily cultured cestodes) or earlier developmental stages (e.g. eggs or protozoan cysts) similar to large seed bank projects. For the most limited groups, introduction into novel hosts may be necessary, though this may represent the riskiest strategy available for ex situ conservation of parasites.



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