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Parasites in a Changing World: Troublesome or in Trouble?

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Abstract

There are plenty of reasons to believe that parasite populations will respond to biodiversity loss, warming, pollution, and other forms of global change. But will global change enhance transmission, increasing the incidence of troublesome parasites that put people, livestock, and wildlife at risk? Or will parasite species decline in abundance—or even become extinct—suggesting trouble on the horizon for parasite biodiversity? Here, I explain why answers have thus far eluded us and suggest new lines of research that would advance the field. Data collected to date suggest that parasites can respond to global change with increases or decreases in abundance, depending on the driver and the parasite. The future will certainly bring outbreaks of some parasites, and these should be addressed to protect human and ecosystem health. But troublesome parasites should not consume all of our research effort, because this changing world contains many parasite species that are in trouble.

INTRODUCTION

For more than 20 years, ecologists have been asking whether parasitism is on the rise (1). As humans cause biodiversity loss, habitat destruction, warming, pollution, and invasion, do we thereby increase the likelihood of infection for ourselves, for our domestic animals, and for wildlife? It certainly seems like the answer is yes. After the COVID-19 (coronavirus disease 2019) pandemic and the many other outbreaks of infectious disease of the past decade (e.g., avian flu, swine flu, Middle East respiratory syndrome, Chikungunya, Zika, Lassa, Lyme, Hendra, Nipah), it should seem to anyone who is paying attention that problems caused by infectious disease are worse today than they have been in living memory. Consider Lyme disease. Between 1996 and 2022, the number of cases reported to the US Centers for Disease Control and Prevention increased from 16,455 to 62,551 (2). The actual number of contemporary cases might be even higher; an analysis of insurance claims suggests that there could be as many as 476,000 new cases per year in the United States alone (3). These data make it clear: Some parasites are undoubtedly on the rise. But is this the whole story? Do all parasites, or most, or the most pathogenic, benefit from global change?

I argue that the trajectory of parasitism does not point upward for all or even most parasites, and that we have been led astray, in part, by the composition of the existing literature. The literature is flawed in two ways. First, it contains information on a biased subset of parasite life: the handful of parasite species that are currently causing problems for people. And second, it contains information from a biased subset of time: the extremely recent past. In this review, I explain these biases, discuss what we learn about the trajectory of parasitism when we account for them, and propose some productive directions in which the field might proceed.

Here is how I believe the taxonomic bias may have arisen. Most ecologists want to make a difference in the world, to study something relevant and impactful; what better way to do this than to study a high-profile parasite that is considered an emerging threat to human health, livestock or agricultural productivity, or the conservation status of a valued wildlife species? In contrast, there are few professional incentives to study a parasite that is disappeared, disappearing, or holding steady. If ecologists prefer to study those parasites that are currently causing problems, they will disproportionately elect to study those parasites that are on the rise (**Figure 1*a***, *line i*), and as a result, the ecology literature will disproportionately represent those parasites. This creates a few problems. First, meta-analyses based on this literature (4, 5) will be biased toward parasites that are on the rise—a group that probably shares other traits in common, including the direction in which they respond to global change drivers. Second, without information on species that are not currently causing human or wildlife health problems, it is difficult to identify the traits that characterize a parasite likely to cause such problems. This is akin to performing an experiment without a control group—how will we anticipate and prepare for human and wildlife health emergencies without knowing which traits might predispose a parasite to an outbreak, and which traits might put the brakes on one? Third, without information on low-profile species that are not currently causing human or wildlife health problems (that is, the vast majority of parasite species), we understand how only a fraction of parasite biodiversity is changing as the world changes. It was once considered safe to ignore the hundreds of thousands of parasite species that have no impact on humans or their domestic animals, but that perspective is by this point quite outdated (6). It is increasingly recognized that parasites are ecologically important and that their loss might lead to the loss of important ecosystem services, including host population regulation, resource subsidies to consumers, competitive regulation of highly pathogenic parasites, and regulation of host immune responses (7). We need data sets that evaluate the trajectory of many parasite species simultaneously—ideally, a random cross-section of all the parasites in a given ecosystem.

I do not mean to suggest that a focus on flashy (i.e., dangerous, destructive, rapidly increasing) parasites is a shortcoming only in the research of others. This kind of bias has distorted

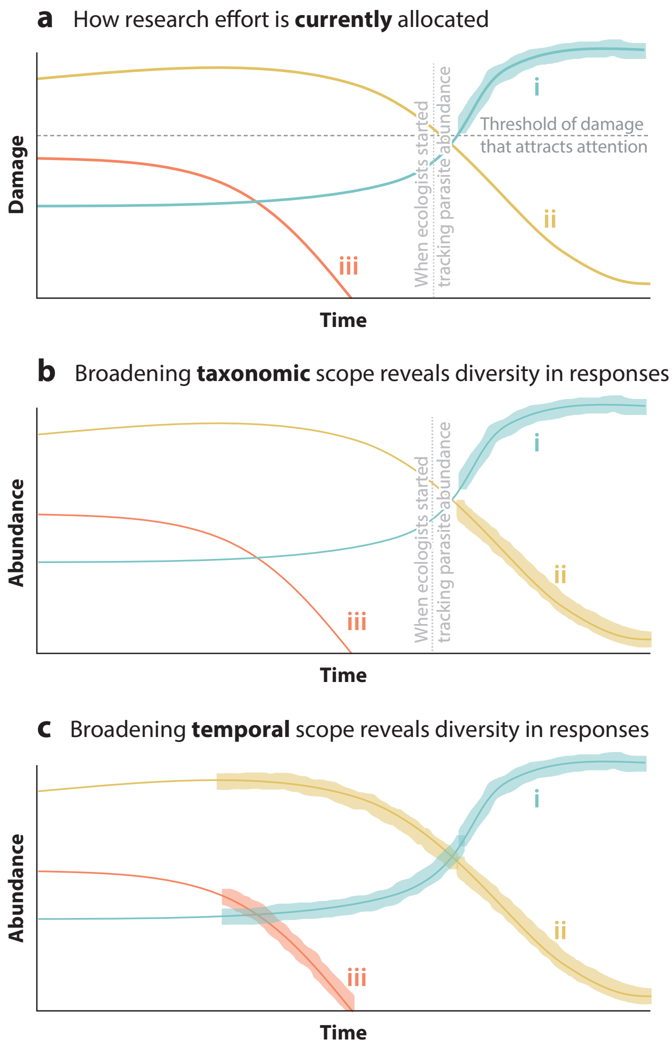

Figure 1

(*a*) Ecologists generally collect data on parasites that are dangerous for human, domestic animal, or wildlife health. These parasites attract the attention of scientists (*shaded* band) when the amount of damage done to human or animal health passes some threshold (*line i*). The problem with this approach is that only those parasites that increase in abundance cause sufficient damage to attract research attention. Parasites that are declining in abundance (*line ii*) or that are extinct (*line iii*) go unstudied. Even parasites that were formerly abundant (*line ii*) may not be tracked, because useful data on parasite burdens are rarely available from before the development of modern ecological sampling methods (∼1960s). (*b*) By removing the requirement that parasites must cause some unusual damage to attract research attention and thereby broadening the taxonomic scope of parasites studied, we may discover a diversity of responses to global change among parasites. (*c*) By removing our reliance on old data sets to reconstruct past parasite abundance, we can access information that predates modern ecological interest in parasites. This will enable us to access information on parasites that were never quantified at past time points, including those that are currently extinct or very rare (*line iii*). Such long-term data sets can be reconstructed by performing sampling in natural history collections or using molecular methods.

conclusions from my own papers. In my earliest sortie into the field of historical ecology, I came across an old data set that had been moldering in the basement of the Washington Department of Fish and Wildlife (WDFW) headquarters. The data set pertained to a series of research cruises conducted in 1949 and 1952, which assessed the prevalence of a large and easily visible nematode parasite (then called *Philometra americana*; the current nomenclature is *Clavinema mariae*) among English sole (*Parophrys vetulus*) in Puget Sound, Washington, USA. The parasite is not dangerous for people, but it looks extremely unappetizing, so it was causing many filets to be condemned and costing fishermen a lot of money. I had been looking for old data sets documenting the abundance of any parasite in any host in any aquatic ecosystem and had—until the WDFW data set—come up empty-handed, so I was excited to find out just how things had changed since these mid-century cruises. My team was able to replicate the old sampling methods and describe how the prevalence of the parasite had changed over the 68 years between 1949 and 2017. We found an eightfold increase in the abundance of the worm over this period (8). Judging from this single paper, one might suspect that parasites are on the rise in Puget Sound; after all, it was our only peek into how the burden of parasitism had changed in the region, and the increase observed in *C. mariae* was substantial. But a few years later, my group conducted a much larger study that put the findings from this single parasite species into context (9). When we performed parasitological dissections of Puget Sound fish specimens originally collected between 1880 and 2019 and held in natural history collections, we included English sole among the 8 fish species sampled. We sampled all the metazoan parasites of 699 individual fishes across these 8 species. Again, we found that *C. mariae* increased in abundance over time, but we also found that its trajectory was quite unusual among the parasite species detected; most of the parasites, including several others from the same host species (10), declined over time. Of the 88 total parasite species we detected, *C. mariae* was 1 of 10 that increased over time; another 32 declined, and the overall trend across parasite species was toward decline (9).

I do not think it is an accident that a historical data set happened to exist for one of the few parasite species in the region that was increasing in abundance, and for no other parasite species. The WDFW commissioned a cruise to investigate *C. mariae* in the late 1940s precisely because it was causing problems for fishermen (**Figure 1*a***, *line i*). Parasites that are declining (**Figure 1*a***, *lines ii*,*iii*) do not cause problems for fishermen. Therefore, we should assume that, wherever we are relying on data that pass through a filter of human interests, we are not getting an unbiased picture of how parasite communities are changing. Human interests can perform this filtering in various ways. They influence the availability of historical data, as in the case I describe here, but they also decide what gets studied and permanently documented in the literature, introducing the same bias into meta-analyses of that literature. It is good that we are targeting our science to address societal concerns about human, livestock, and wildlife disease issues. But what facts are we missing about nature when we allow ourselves to extrapolate from the flashy parasites to the rest of parasite life (**Figure 1**)?

The second reason we have the mistaken impression that parasites are on the rise is temporal bias: Vanishingly few long-term data sets document these changes. In lieu of studies comparing past and present burdens of parasites, parasite ecologists (including myself) have relied largely on space-for-time substitutions, in which a contemporary study is conducted in paired areas. Those areas spared from human impacts are employed to stand in for a past, presumably more pristine ecosystem, and those exposed to those impacts show us how things look today. Space-for-time substitutions are very helpful for dissecting the influence of particular drivers on ecosystem change, isolating, for example, the influences of fishing (11), deforestation (12–14), and human population density (15) on parasite burdens. But long-term ecosystem change is always caused by multiple drivers. For an example, allow me to critique one of my own research projects, which

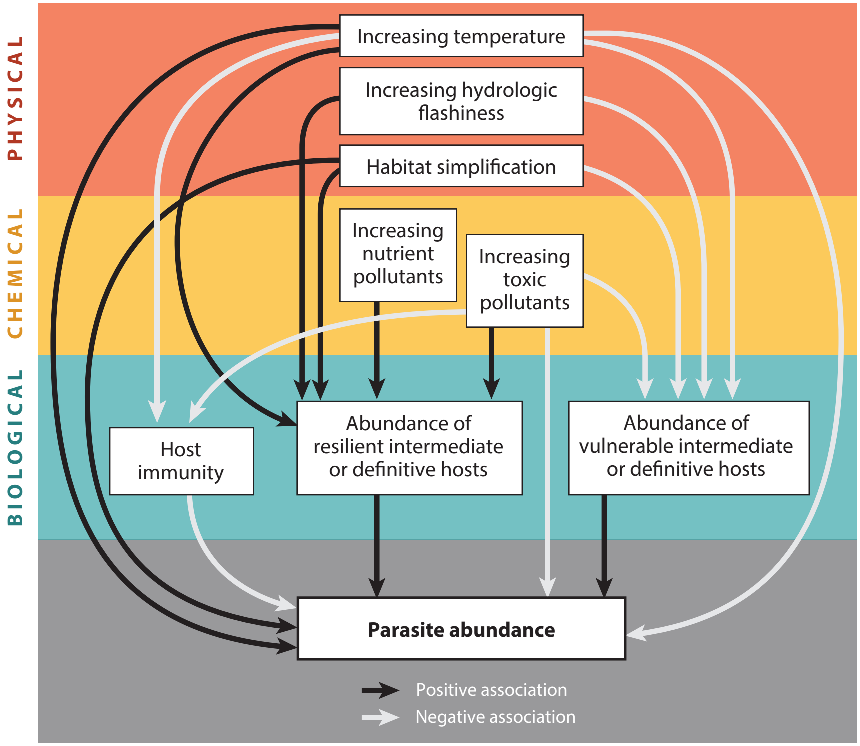

Figure 2

What is the net effect of global change on parasite abundance? This path diagram illustrates some of the mechanisms by which physical, chemical, and biological changes may produce change in parasite abundance (in this case, in freshwater ecosystems). For each path (i.e., arrow), color indicates whether the relationship between two variables is positive (*black*) or negative (*grey*). To assess the overall net effect of one variable on another, signs along each compound path (i.e., all paths between two endpoints) are multiplied. Space-for-time substitutions can isolate individual pathways and quantify the strength of links between variables. But the net, or overall, effect of global change on parasite burden is difficult to quantify without long-term data to reveal parasite population responses to many stressors acting simultaneously. Reproduced with permission from Reference 20; copyright 2023 Wiley.

investigates how fishing pressure influences parasite burden using entire fished and unfished islands as replicates (16). Although this is a helpful way to study how fishing and its knock-on effects (e.g., changes in fish community composition) might impact parasite burden, the unfished islands do not resemble pristine ecosystems of the past in other dimensions, including climate, ocean pH, concentrations of toxic chemicals, productivity, island size (due to sea level rise), frequency of intense storms, and many other factors that may influence parasite burden. Empirical, field-based studies on how parasites respond to human impacts are almost entirely these kinds of space-for-time substitutions. Given that these studies isolate only one driver at a time, is it any wonder that we are still in the dark about how parasite populations have changed over time? What is the net effect of the many stressors operating on parasites simultaneously (**Figure 2**)? Parasites might be resilient to one stressor, but they are like any other group of species: Add stressors, and there will tend to be more losers and fewer winners. Only measurements of actual change in parasite abundance through time can encompass all of the many stressors that accompany global change, and only with these data will we appreciate the full extent of parasite biodiversity decline.

In addition, we cannot measure in a contemporary space-for-time substitution a parasite species that is extinct. Any undocumented parasite extinctions, of which there might be many (17–19), can be detected only with long-term data (**Figure 1*c***, *line iii*).

To truly understand how parasites are changing as the world changes, we need to address two priorities: We must measure the net impact of ecosystem change on a parasite population across time (i.e., look at actual change rather than isolating individual drivers in space-for-time substitutions), and we need to measure that trajectory for multiple parasite populations (i.e., not just the highest-profile parasites). There is only one problem: We still lack long-term data, even for the highest of high-profile parasite species. We cannot return to the past to goad parasitologists of the nineteenth and twentieth centuries to collect data on a broad cross-section of parasite biodiversity. Is there any way to resurrect these data today, or is the opportunity to know parasite burdens of the past lost forever?

The historical ecology of parasitism is a young subfield, but it has already made some fundamental discoveries about parasites of the past and established some promising pathways for resurrecting more information. The discipline focuses on changes in parasite burden over the past few hundred years, distinguishing it from archaeoparasitology (hundreds to thousands of years) and paleoparasitology (thousands to millions of years) (20). The primary innovations have come from the use of natural history collections and from genomic tools. Here, I review the state of the science: what we know about how parasite burdens of wildlife have changed over the past 200 years, and where we need to go next. These studies allow us to understand whether, in a changing world, parasites are going to be troublesome, in trouble, or both.

TROUBLESOME OR IN TROUBLE? WHAT WE LEARN WHEN WE. . .

. . .Broaden the Taxonomic Scope of Parasite Species Assessed

For studies evaluating parasite responses to global change, the more complete and unbiased the sample of parasite species, the more representative the results will be of what we should expect, parasitologically speaking, in a changing world. What would we learn if we did not select focal parasites but instead tracked multiple parasite species simultaneously?

There is one corner of the literature where it has always been common to conduct studies across a taxonomically diverse group of parasites: Papers investigating the impacts of pollution on parasitism have diffused their focus across a broad cross-section of the parasite tree of life. This literature shows that parasites vary widely in their responses to pollutants, with responses determined by the interaction of parasite identity and pollutant type (21, 22). For example, acanthocephalan parasites tend to respond positively to pulp mill effluents but negatively to pesticides (23, 24). Trematode parasites respond negatively to many pollution pressures, including crude oil, acid rain, thermal effluent, pulp mill effluent, polychlorinated biphenyls, pesticides, and heavy metals (23). Meanwhile, the protozoal parasites tend to do well in polluted environments, responding positively to crude oil, thermal effluent, and pulp mill effluent (24). Where many parasite taxa seem to reach agreement is in their response to nutrients; parasite populations tend to respond positively to nutrient enrichment (23–25), at least until that enrichment tips over into extreme eutrophication and parasites can no longer persist in host-depleted, hypoxic environments (26). Some sources suggest that parasites with complex life cycles (i.e., parasites that are transmitted from one host species to another host species in an obligately required sequence) may be more responsive to nutrient enrichment than are directly transmitted parasites [i.e., parasites that can be transmitted between conspecific hosts (27)], possibly because nutrients favor low-trophic-level intermediate hosts that are needed for the transmission of complex life cycle parasites. The literature on parasites and pollution is clear: Responses vary depending on parasite taxonomic identity and pollution type. No one parasite taxon is representative of the responses to pollution of all (or even most) parasite taxa, and many parasite taxa are probably on the decline as pollution pressure mounts.

Parasites are often considered only as threats to the conservation of their hosts (28). In some cases individual parasite species have risen precipitously in abundance and, in the process, caused spectacular declines in their hosts (29–33). But broadening our view to a more biodiverse slice of parasite life shows that, on average, the fate of a parasite tends to track the fate of its host, such that hosts in decline have parasites that are also in decline. In a meta-analysis, Altizer and colleagues (34; see also 35) discovered that species richness of parasites, including viruses, protozoa, and worms, was lower in threatened than in nonthreatened primate species, suggesting that, as hosts dwindle in geographic range and population density, their parasites decline—irrespective of parasite taxonomic identity. In another meta-analysis of parasites infecting animal, plant, and fungal hosts, Kamiya et al. (36) showed that host density is strongly positively correlated with parasite presence across both metazoan and nonmetazoan parasites. In a study of 1,273 mammal species, Nikc et al. (37) found that viral diversity decreased as the host species' threat level increased, suggesting that viral extinctions may have occurred in the past as threatened species diminished in density. Of course, host bottlenecks can hand some rapidly evolving parasites a temporary selective advantage, as a high diversity of immune genes is part of what allows hosts to keep up with parasites in the coevolutionary arms race between host and parasite (38). But in a world where biodiversity is in decline (39), there is good reason to believe that the parasite species of declining hosts are also themselves in decline.

Whereas the literature on pollution and endangered hosts has sampled across a broad swath of parasite diversity, resulting in a broad understanding of parasite responses, other literatures have focused narrowly on a small subset of parasite life, often species with zoonotic potential, experimental tractability, or both. Much ink has been spilled on the biodiversity–disease relationship, which describes how biodiversity loss influences parasite transmission. This literature focuses disproportionately on Lyme disease (*Borrelia burgdorferi*), which is an enormous public health problem in the northeastern and midwestern United States (3) but represents only one of countless parasite species that occur in those regions. I will not relitigate old arguments about whether Lyme disease risk in fact increases or decreases with biodiversity loss (40–43). But I will wonder: What would we find out about the biodiversity–disease relationship if we explored it beyond a handful of high-profile, experimentally tractable parasites? Below, I provide a few examples of what we could learn from such an effort.

One of my own past studies was devised specifically to assess how biodiversity might influence zoonotic disease burdens across an agnostic sample of human-infecting parasite species (44). We chose the 24 parasites the World Health Organization considered to be the most burdensome. We then explored how the global burden of each parasite had changed between 1990 and 2010 using data from the Global Burden of Disease database and tested whether those changes were correlated with changes in country-level economics, urbanization, population density, temperature, precipitation, forestation, or biodiversity. Increasing biodiversity increased the burden of one group of parasites (the foodborne trematodes) and decreased another (filarial nematodes causing lymphatic filariasis) but had no effect on any of the remaining 22 parasites. Surprisingly, forestation had a net positive effect across parasite taxa, suggesting that a prime mechanism for terrestrial biodiversity conservation—protecting forests—could actually work against public health goals. This study also suggested that forest loss might cause declines in the abundance of many parasites—even for parasites of a host species (humans) that remains extremely abundant as forest habitat is lost. I am by no means bemoaning any such decline of human-infecting parasites; in my book, these parasite species deserve annihilation. But I am pointing out that, when we explore responses to global change across a large swath of parasite biodiversity, we can sometimes find surprising amounts of vulnerability to global change among parasites, even for those parasites that infect a very high-density host (people).

Another informative example comes from the Kenya Long-term Exclosure Experiment (KLEE), a manipulative experiment in which large animals have been excluded from 1-ha plots at Mpala Research Center in Kenya. Because biodiversity loss tends to eliminate large-bodied animals first (45), this design is used to experimentally investigate the ecological impacts of biodiversity loss. Young and colleagues have tracked the effects of the KLEE manipulation on rodent-borne pathogens. They found that the exclusion of large animals increases the abundance of rodents by reducing the competition for food resources that rodents experience, which increases the per-unit-area abundance (but not necessarily the per-capita abundance) of many rodent-borne parasites, including *Bartonella* (46); *Borrelia*, *Theileria*, and *Hepatozoon* (47); *Coxiella burnetii* and *Rickettsia* spp. (48); and three nematode parasites found in rodent intestinal tracts, *Neoheligmonella* sp., *Trichuris* sp., and *Syphacia muris* (49). What I have always wondered is, what if we tracked parasites other than those that infect rodents? If there were a way to assess the total parasite community inside and outside the KLEE exclosures (for example, using environmental DNA screening of fecal, insect, or soil samples), what differences would be detected? Within exclosures, there would probably be fewer complex life cycle parasites that require large-bodied hosts at some stage in their life cycles—for example, the protozoan *Toxoplasma gondii*, which uses rodents as intermediate hosts but requires a cat definitive host; the cestode *Echinococcus* spp., which can use rodents as intermediate hosts but require a canid definitive host; the cestode *Stilesia hepatica*, which uses oribatid mites as intermediate hosts but requires a ruminant definitive host; or the trematodes *Fasciola gigantica* and *Gastrodiscus* spp., which use snails as intermediate hosts but require ruminant and equid definitive hosts, respectively. In the exclosures, I would also expect to see zero of the directly transmitted parasite species that are host-specific to large-bodied hosts, for example, nematodes in the genera *Oesophagostomum* or *Borrostomum*. I understand why the focus to date has been on rodents: They carry many parasites that are a danger to people, and they are easy to sample inside and outside of exclosures. But what we have missed in focusing only on rodent parasites is a full picture of how biodiversity loss impacts the entire parasite community. Some of the parasites that I predict might not be found in the KLEE exclosures have zoonotic potential, so using the KLEE experiment to draw the conclusion that large wildlife elimination generally exacerbates human disease transmission is, I think, premature—precisely because of the narrow taxonomic focus on rodent-borne parasites.

Sometimes, broadening the taxonomic scope beyond a focal parasite reveals that the focal parasite's responses are largely representative. Johnson's work on amphibian parasite communities in ponds of California's East Bay region has explored the links between host biodiversity and parasite transmission, providing insight into how global biodiversity change might change the trajectory of parasite populations. With a combination of field sampling, laboratory experimentation, and mesocosms, Johnson's group has demonstrated convincingly that ponds containing more amphibian species tend to have lower burdens of the trematode parasite *Ribeiroia ondatrae*, which can cause limb malformations in the amphibian host. This effect appears to occur through transmission interference (whereby the addition of noncompetent host species allows trematode larvae to be wasted and thereby diverted away from competent host species) and susceptible host regulation [whereby the addition of noncompetent hosts caps the abundance of competent hosts (50–53)]. Later work, which expanded the scope of studies beyond *R. ondatrae*, indicated that the same negative biodiversity–disease results were obtained for some of the other trematode parasites that inhabit the same amphibian hosts in the same ecosystem, including *Alaria*, *Cephalogonimus*, and *Echinostoma* (54, 55). In this system, the multiple parasite players appear to diverge not in their responses to the diversity of their snail or amphibian hosts but in their response to the diversity of birds. In a manipulative experiment in which bird visitation was either doubled by the addition of perching and roosting habitat or left unchanged, even *R. ondatrae* did not display the expected negative biodiversity–disease relationship (56). Both *Cephalogonimus* and *Ribeiroia* responded positively to bird augmentation; *Clinostomum*, *Echinostoma*, *Haematoloechus*, and the protozoan *Opalina* responded negatively; and *Alaria* and the protozoan *Nyctotherus* were equally abundant between bird-augmentation and control treatments. Broadening the view beyond *R. ondatrae* and into the diversity of other food web players offers a more complex picture of how changes in biodiversity affect parasite populations.

Parasite responses to climate change appear to be diverse (5, 57–61), although this was recognized only recently, displacing earlier predictions that parasite burdens would generally increase with warming temperatures (62). The aforementioned global analysis of directly measured burdens of the 24 most burdensome human diseases found that some parasites responded positively to warming, whereas others responded negatively (44). In a global meta-analysis of the impact of temperature on prevalence of wildlife parasites, Cohen et al. (5) found that responses of parasites to warming depended upon both the parasite's identity and the region (i.e., tropical versus temperate zone). For example, helminths increased in response to increasing temperature across both tropical and temperate regions, whereas fungal parasites increased with increasing temperatures in temperate regions but precipitously declined with increasing temperatures in tropical regions—a finding consistent with deep-time studies of fungal abundance and global temperature (63). It is easy to pick and choose individual species that respond positively to climate change; these portentous results get a lot of attention, and the message dovetails with the environmentalist sensibilities of most ecologists. But when a broader range of parasite taxa are considered, we see that climate change is likely to bring both more and less infection to human and wildlife hosts, depending on the parasite you choose to study.

In conclusion, those literatures that encompass a greater scope of parasite biodiversity appear to find both greater diversity in parasite responses to global change and a greater proportion of parasites responding negatively to global change drivers. This work is increasingly clarifying that, although some parasites will absolutely cause trouble for human lives and livelihoods as the world changes, many others might quietly disappear.

. . .Measure Actual Change in Parasite Burden Through Time

Studies designed as space-for-time substitutions can isolate individual drivers of change in parasite burden, but they are no substitute for measuring actual change over time—change that might be caused by many drivers simultaneously (**Figure 2**). If we really want to know whether the world is wormier than it used to be, then we need some information on how things used to be. Studies of long-term change in parasite burden are rare, but there are a few examples—and each has provided surprising insights into how global change reshapes parasite communities.

The largest long-term data set of wildlife parasite abundance ever assembled revealed a steep decline in parasite burdens through time (9). As mentioned above, my team performed parasitological dissections of Puget Sound fish specimens originally collected between 1880 and 2019 and held in natural history collections, sampling all the metazoan parasites of 699 individual fish across 8 fish species. Our analysis of the resulting data yielded a surprising result: Parasite burden declined between 1880 and 2019, particularly among those parasites with complex life cycles involving three or more obligately required host species. The declines were closely correlated with sea surface temperatures, suggesting that climate change might interrupt parasite life cycles, particularly for those parasites with many potential points of failure in the life cycle (64). Imagine if we had instead tried to answer the same question with a study that used data only from contemporary ecosystems.

Because parasite life cycles play out over such broad spans of space and time and involve taxonomically diverse (and sometimes large-bodied) hosts, there are few opportunities to design a manipulation or even a space-for-time substitution that can encompass sufficient space and time to realistically simulate impacts of the driver of interest on parasites. Imagine, for example, a field experiment that tested the same effect as the one demonstrated by Wood et al. (9). It would have needed to experimentally warm up a stretch of Puget Sound big enough to encompass one turn of a tapeworm life cycle, which could involve planktonic copepods, pelagic schooling fish, large groundfishes, and sharks—that is, extremely vagile animals. And it would have needed to do it for a few years. Even if the funding existed to support such a logistically complicated experiment, the authorities that govern scientific use of natural resources would probably not permit it. A space-for-time substitution would have required that we find regions of Puget Sound warming at different rates; then we would need to track the trajectories of parasite burden across those regions by collecting fish and performing parasitological dissections on them. To detect an effect in such a study, we probably would need to collect data for at least a decade, probably much more—a timeline made nearly impossible if it depended on any currently available funding schemes, which generally demand much quicker return on investment. Not only are these alternative options logistically impossible, they also provide much less bang per buck. By generating a 140-year data set, we also gave ourselves the option to be agnostic as to the driver of change. We did not have to design the study around one specific hypothesized driver (e.g., climate) but instead were able to screen for the effects of multiple drivers simultaneously (**Figure 2**). We were able to ask how things have changed, and why. It is a powerful question, and one that can be answered only with long-term data.

Parasitological dissection of museum specimens is not the only way to build long-term data sets of parasite abundance. This has also been done successfully through then-and-now comparisons (65), in which studies conducted at a past time point are repeated using the same methods in contemporary ecosystems, and through meta-analysis (66, 67). In one then-and-now comparison, Keas & Blankespoor (68) replicated a study originally conducted in 1936 in Douglas Lake, Northern Michigan. The richness of trematode species infecting a common snail (*Stagnicola emarginata*) had been halved (from 16 to 8 species) and overall trematode prevalence reduced from 61% to 13% over the half-century that elapsed between "then" and "now," an effect that they attributed to increasing development around the lake. In a meta-analysis, Egizi & Maestas (69) compiled literature reports of grouse ticks (*Haemaphysalis chordeilis*) from across the United States and Canada, finding that positive reports have declined and negative reports have increased since 1965, an effect the authors attribute to declines in the tick's preferred game bird hosts caused by the loss of North America's grassland habitats. One of the most important functions these long-term data sets serve is their utility for counteracting the "shifting baselines" phenomenon (70). The term is normally used to describe the ratchet effect by which humans use their own personal experiences as a yardstick to measure ecosystem integrity, and thereby fail to appreciate the distance between the ecosystems of their childhood and the "pristine" state of that ecosystem (71, 72). Here I use it to refer to the ratchet effect by which parasitologists use their own personal experiences as a yardstick to measure what is normal in parasite populations, and therefore fail to appreciate how much change in parasite populations preceded their entry into the profession. There is only one way to help us all shift our baselines back to where they belong: data from before we were born (or trained).

Longer time series provide even better historical context, encompassing more human-driven ecosystem change and facilitating estimation of parasite population sizes in the absence of human impacts. Unfortunately, longer time series are vanishingly rare. One major exception is this: Gastropod shells sometimes encode reliable indicators of infection, and because they persist in fossil and archaeological deposits, they can be used to track temporal change—at least for the small subset of parasite species that leave these traces. For example, distinctive pits in the shells of the economically important Adriatic bivalve *Chamelea gallina* reliably indicate the presence of trematode infections. The abundance of pits on *C. gallina* shells has declined over the past 2,000 years, such that today's most-infected sites are less than half as infected as those from 543 BCE (73). The authors of this study interpret the decline as a response to the urbanization of the Adriatic, reflecting pollution pressure that began in Roman times and ramped up with the Industrial Revolution. Similarly, Olympia oyster (*Ostrea lurida*) shells from the US Pacific Northwest retain traces of burrows and blisters caused by shell-boring spionid polychaetes. Until recently, many suspected that shell-boring polychaetes were invasive species brought to the region through the receipt by Pacific oyster farms of oysters from other infested regions (e.g., the US east coast, Hawaii, Japan). But analysis of fossil, archaeological, and modern Olympia oyster shells reveals that these contemporary aquaculture pests are not new to the region. According to the fossil evidence, they have been present for at least 80,000 years (J. Martinelli, A. Bonifate, L. Simonitis, I. Holland Lulewicz, et al., manuscript in review). Time series that reach deep into the past can therefore answer questions that shorter time series cannot, especially in regions where human impacts are long-standing (i.e., where time series need to encompass the deep past to reveal prehuman ecosystem states) or where the provenance of a parasite species is in question.

Long-term data are particularly useful for parsing the drivers of parasite burdens. For example, low-latitude regions are hot, poor, and biodiverse, and the people who live there have high burdens of zoonotic parasites, on average. Are the high parasite burdens observed near the equator due to temperature, because parasites develop faster at high than at low temperatures? Are they due to the high biodiversity of nonhuman animals, which provide a source and a reservoir of parasite propagules? Perhaps it has something to do with poverty, which deprives people of access to clean water, sanitation, and medical care, and which increases malnutrition, reducing resistance to infection? With static data, there are few options for parsing among these potential drivers because they are hopelessly collinear with one another. However, long-term temporal data can allow some of this collinearity to be loosened, because having multiple time points allows each spatial location to serve as its own control, reducing collinearity that arises due to space. For example, two countries might have similar levels of biodiversity due to their close proximity, but their temporal trajectories of biodiversity change will depend on environmental laws and regulations, which might diverge. With temporal data, a researcher can ask not "Are hosts in a high-biodiversity location more burdened by parasites than hosts in a low-biodiversity location?" but "As biodiversity declines through time, how does parasite burden change?" By looking at change over time, the researcher can perform as many natural experiments as there are spatial locations, and observe the outcome of each, and their analysis can summarize over all of those independent experiments to reveal general patterns across spatial locations. This was the rationale behind the analysis of the 24 most burdensome human diseases that I reference above, which looked at change over time between 1990 and 2010 (44). In that study, we conducted both a purely spatial analysis and a temporal analysis; the temporal analysis gave us different answers than we would have obtained had we not been able to achieve any time depth in our data set. Specifically, the temporal analysis pointed to increasing urbanization and wealth as key drivers of declining parasite burdens.

Long-term data sets can even reveal parasite extinctions—events that would never be detected without data from the time period in which the parasite was still extant (**Figure 1*c***, *line iii*). For example, ancient DNA resurrected from prehistoric human coprolites and corpses reveals microbial species that have never been detected in humans living today (74–76). These extinct bacterial species are a mixture of parasites, commensals, and mutualists that probably were driven to extinction by improvements in sanitation or the advent of antibiotics (77). A menagerie of extinct nematodes, trematodes, and protozoa were detected in coprolites produced by New Zealand moas between the years 678 and 1440 AD (78)—before all seven moa species went extinct in the 1400s (79). Given the obligate dependence of many parasites on their hosts and the fact that many hosts have already become extinct, there really should be more documented parasite extinctions than there are; this shortfall of documented parasite extinctions has been called the "paradox of missing coextinctions" (17, 18). We will never know whether it arises because parasite extinctions are difficult to document or because they truly are rare, unless we develop more long-term data sets.

Detecting metazoan parasites in preserved specimens is generally straightforward, requiring only a microscope and morphological species diagnosis. Developing long-term data sets can be more difficult for viral, bacterial, fungal, and protozoal parasites, which can only in rare instances be identified using visual diagnosis alone. But although it is difficult to resurrect intact DNA sequences from old, chemically preserved, and degraded specimens, it is not impossible. Molecular techniques are now sufficiently advanced that parasite DNA has been resurrected from coprolites deposited in the late Pleistocene (80) and from formalin-fixed specimens that used to be considered unusable for DNA analysis (81). Protozoal parasites like malaria can be detected in mosquito specimens held in entomological collections (82), the Lyme disease bacterium has been detected in mouse skins from the late 1800s (83), and the 1918 flu virus variant that killed 50 million people was resurrected from contemporaneously collected bird skins (84). Not only can parasite DNA be sequenced from old specimens with increasing ease and decreasing cost, we can also now make inferences about the effective population size of a parasite at past time points using only sequences contained in modern populations. For example, the sequences of modern *B. burgdorferi* (85–87), Powassan virus (88), and the ticks that vector both parasites (89) indicate past population bottlenecks coincident with the height of agriculture in the northeastern United States. Significant challenges remain for reconstructing trajectories of change through time for viral, bacterial, fungal, and protozoal parasites (81, 90, 91), but molecular and computational advances are making such projects both cheaper and easier.

Long-term data sets show parasite populations in their historical context, allowing us to ask whether what we see today is normal. They can help us narrow in on the causes of parasite population change and reveal parasite extinctions. And they are possible to build for metazoan parasites as well as protozoa, fungi, bacteria, and viruses. The picture painted by the few long-term data sets that exist is not one of surging parasite populations. We do indeed see parasites that are on the rise, but also those that are on the decline, extinct, or waxing and waning over the decades in response to various drivers. The next trick will be to identify the parasite traits, drivers, and environmental conditions that predict a positive versus negative outcome for a given parasite population.

HOW TO ADDRESS OUTSTANDING QUESTIONS

Recent advances clearly demonstrate the complexity of parasite responses to global change. But it is not enough for us to throw up our hands and say, "It's complicated!" The next step for this field is to make sense of this complexity, to move toward an ability to predict, for a given parasite and a given environmental driver, what the outcome is likely to be (see the sidebar titled Outstanding Questions). To move toward this end goal, we need to proceed along three fronts.

More Time Series Across More Parasite Species

There are some tantalizing long-term time series of parasite abundance change, data sets that clearly show us that surprises are in store when we quantify parasite populations of the past (9). But in reality, these time series pertain to at best a few hundred parasite species, when hundreds of thousands exist on Earth (92). To draw robust inferences about which parasites are likely to increase and which are likely to decline in response to global change, we need better sampling across parasite taxonomic groups.

OUTSTANDING QUESTIONS

- What factors predispose parasites to positive/negative temporal trajectories?
  - Parasite traits (19, 64)
    - **Life cycle complexity:** Are complex life cycle parasites likely to decline in response to global change, due to the many potential points of failure in their life cycles?
    - **Host specificity**: Are host specialist parasites likely to decline in response to global change, due to their obligate dependence on only one or a few hosts? Are generalists likely to increase, due to their comparative flexibility to track the abundance of hosts that are increasing?
    - **Taxonomy**: Are metazoan parasites likely to decline in response to global change, due to their long generation times and slow rates of evolution? Are viruses and bacteria, with their shorter generation times and higher mutation rates, better poised to capitalize on global change impacts?
  - Host traits
    - **Threat status**: Are parasites of threatened or endangered hosts likely to decline in response to global change, or will immunocompetence declines in endangered populations benefit their parasites?
    - **Body size:** Are parasites of large-bodied hosts likely to decline because large-bodied hosts themselves are likely to decline (45)?
  - Global change drivers (96)
    - **Land use change**: Will parasites respond to habitat fragmentation with increases in abundance (e.g., due to the concentration of hosts in declining habitat areas) or decreases (e.g., due to reductions in host density)? Will habitat edges be parasite rich or parasite poor? Will the conversion of land from natural ecosystems (e.g., forests, grasslands) to human-dominated ecosystems (e.g., agricultural fields) increase parasite burdens or decrease them?
    - **Overexploitation**: Will the reduction in host density caused by overexploitation cause a concomitant reduction in parasites of the exploited hosts? Will compensatory release of other hosts lead to increases in the abundance of parasites of those other host species? Given this churn of hosts, what is the net effect of overexploitation on the parasites in an exploited ecosystem?
    - **Climate change**: Will climate change shift parasite ranges poleward? Will it favor some parasite species and drive others outside of their thermal tolerance limits?
    - **Invasive species**: Does the replacement of parasite-rich native host species with parasite-poor invasive species (which bring with them only a fraction of their native parasites due to founder effects) result in lower overall parasite abundance in invaded compared to noninvaded ecosystems? Is this effect offset by the introduction of non-native parasite species?
    - **Pollution**: We already know that the responses of parasites to pollutants depend on the parasite taxon and the pollutant type. But parasites in nature are exposed to more than one pollutant at once. What is the net effect, in nature, of this slurry of pollutants on parasite abundance?
- There are some clear historical inflection points for free-living biodiversity; for example, severe depletion of many marine species began after European colonization in North America and Australia (97). Have there also been major historical inflection points for parasite biodiversity change? What historical developments have had the greatest impact on parasite abundance?

(*Continued*)

(*Continued*)

- Many time series of parasite burden point to parasite decline, something that has long been predicted (64, 98) but has amassed serious evidence only recently. Are parasites, as some have argued (9, 99–101), the most endangered group of species on Earth?
- Can parasite communities be restored? Will parasite restoration be a natural consequence of ecosystem restoration, or do special measures need to be taken to encourage the process of parasite population reestablishment?

Extend Time Series Deeper into the Past

Time series clearly give us a lot of useful information about parasite change. The deeper into the past those time series can stretch, the more historical environmental change they encompass, and the closer we can get to quantifying the parasite communities of a "pristine" ecosystem. I put pristine in quotation marks because I realize that there is no one ideal ecosystem state; that ecosystems have been shaped by humans since our species evolved; and that separating our impact on ecosystems fails to recognize that we, as a species, are a part of the ecosystems we inhabit. The further we get into the past, the more ecosystem states we encompass, including those that predate European and US colonialism, the Industrial Revolution, and World Wars I and II—historical developments that left deep marks on ecosystems. We can never point to one "pristine" ecosystem, but the further back a time series stretches, the more highly resolved the picture that emerges of what ecosystems might have looked like before these exceptionally destructive historical developments occurred.

Develop Time Series that Can Experimentally Address Specific Global Change Drivers

Historical environmental data can sometimes be used to find correlations between parasite abundance and past ecosystem changes (9). But appropriate historical environmental data will not be available in every ecosystem, and even where they are available, causation cannot be inferred using only these observational data.

However, time series can be developed that allow improved experimental control and therefore improved ability to infer causation. This can be done by identifying regions that naturally differ in their exposure to a global change driver of interest (e.g., climate warming, urbanization, pollution) and quantifying the trajectory of parasite populations in the impacted and control region, before and after the driver occurred. I call these retrospective control–impact studies (i.e., before–after–control–impact or BACI studies in which time is continuous rather than discrete). For example, my group is currently following up on the finding that climate drives declines in complex life cycle parasites (9) by developing a time series of parasite burden for fishes collected in rapidly and slowly warming regions of the Gulf of Alaska (93) from the 1920s to the present day. If climate is in fact a cause of long-term decline among complex life cycle parasites, then complex life cycle parasites should have steeper declines in the rapidly warming regions than in the slowly warming regions. This is still a correlational study, and causation still cannot be inferred with full confidence, but with a retrospective control–impact study we can have slightly more confidence in the causal role of the predictor variable than we might in a simple correlation (9).

Rivers lend themselves to retrospective control–impact studies. Riverine fishes are well represented in natural history collections, providing ample specimens that can be mined for parasitological data (providing continuous data across a broad temporal scope), and with their directional flow, rivers can serve as their own controls, as long as specimens have been collected both above- and below-stream of the impact under investigation (control/impact). My lab is currently exploring the response of parasite populations to industrial pollution by performing parasitological dissections of fishes collected from 1963 to 2005, above and below a pulp mill on the Pearl River in Louisiana (**Figure 3*a*,*b***). We are also exploring the response of parasite populations to urbanization by

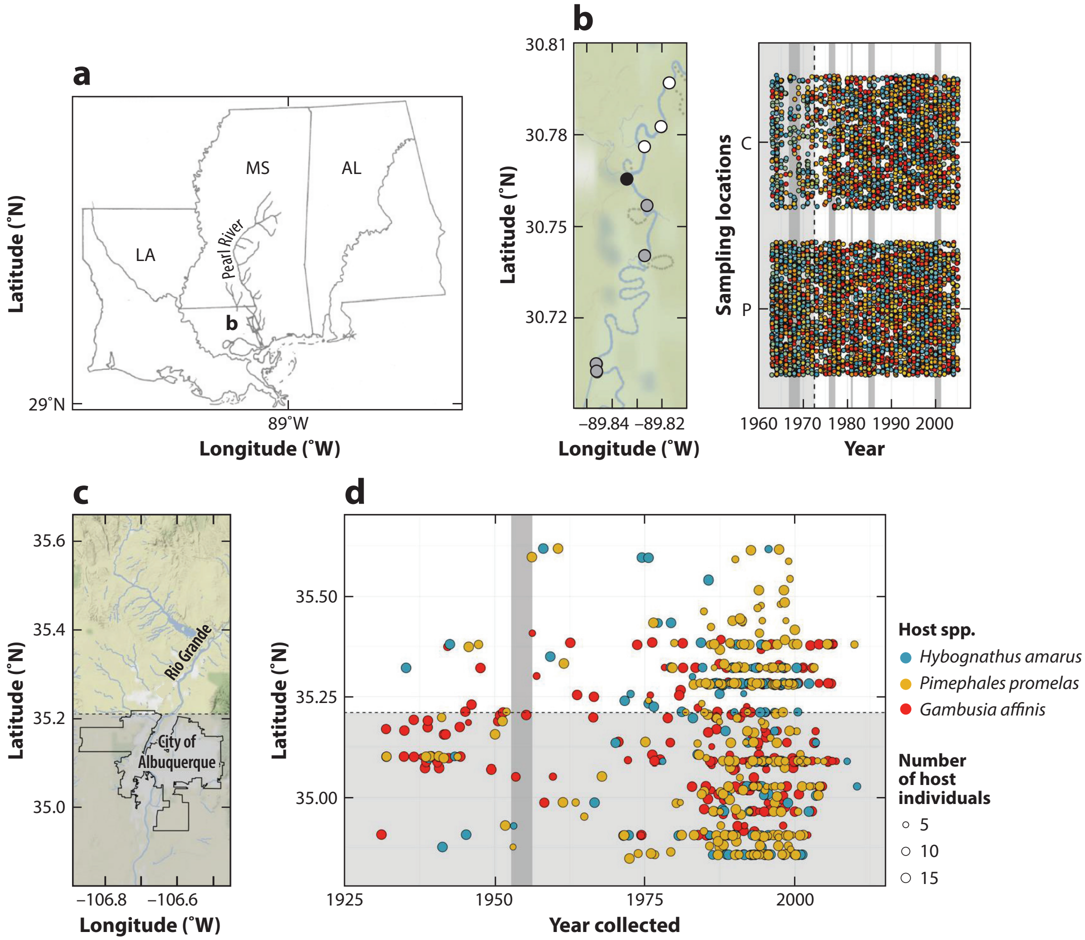

Figure 3

Study design for two retrospective control–impact studies that allow researchers to isolate the impact of a particular global change driver on parasite burden, separating its influence from background change. (*a*) Study area for retrospective control–impact study of pulp mill effluent impacts on parasite burden of fishes in the Pearl River, Louisiana, and (*b*) sampling locations (white markers = control, grey markers = polluted) and pulp mill (*black marker*) with plots of specimen availability. For plots, each point is a lot (i.e., a jar of fish) held in the Tulane University Biodiversity Research Institute Ichthyology Collection, and each color is a different fish host species (of 10 species to be targeted). The dashed line indicates implementation of the CWA in 1973, the light grey shading indicates the period before CWA implementation, and the dark grey vertical bars indicate droughts. (*c*) Study area for retrospective control–impact study of urbanization impacts on parasite burden of fishes in the Rio Grande, New Mexico. The map indicates two regions: control, north of the dashed line, upstream of the North Diversion Channel (i.e., the Albuquerque outfall that contributes the greatest discharge by volume to the Rio Grande), and urbanized, south of the dashed line, below North Diversion Channel. (*d*) Fish specimens available for dissection at the University of New Mexico Museum of Southwestern Biology from control and urbanized regions. Each point is a lot (i.e., a jar of fish) held at the Museum, with size proportional to the number of individual fish in the lot. X and Y positions are jittered to allow visualization of overlapping points. The dark grey vertical bar indicates the 1953–1956 drought. Abbreviations: C, control sites; CWA, Clean Water Act; P, polluted sites.

performing parasitological dissections of fishes collected from 1931 to 2010 above and below the City of Albuquerque's main diversion channel into the Rio Grande in New Mexico (**Figure 3*c*,*d***). These retrospective control–impact studies will allow our team to isolate "background" parasite population change (i.e., what happens upstream of the impact) from change occurring as the result of the targeted driver (i.e., what happens downstream of the impact). The result will be the world's first glimpse into how pollution and urbanization have reshaped parasite assemblages through time, in concert with the many global change drivers simultaneously acting on these systems.

This experimental design is easily replicated. All an interested ecologist would need to do is identify a source of historical parasite data (94) and figure out how to obtain those data from sites that experienced a global change impact of interest and matched control sites that did not experience that impact (or experienced it to a lesser degree). Natural history collections make this easy, because specimens are abundant (20, 95), but the approach could be taken anywhere a source of historical parasite data is identified.

CONCLUSION

Are parasites in a changing world likely to be troublesome, or in trouble? The answer: yes. Both things are happening. Both things need to be addressed.

Many parasites are on the rise, and some of those parasites are dangerous for the health of humans, domestic animals, and endangered wildlife. We absolutely must address the threat that these parasites pose.

However, our extreme focus on this small subset of parasite life has blinded us to something important. There is a lot more variability in parasite temporal trajectories than we expected a decade ago. Among the few long-term, multispecies data sets that now exist, there are a substantial proportion of parasite species in decline. It is too soon to say with high confidence, but the early indications point to major declines in parasite biodiversity. Given that parasites constitute half of all animal species, that could mean that, by the numbers, parasite biodiversity loss is Earth's most critical biodiversity crisis. A key challenge for the coming years will be to amass data fast enough to understand and respond to this potential conservation crisis—a crisis that has gone almost entirely unrecognized. Until now.

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