

RESEARCH METHODS GUIDE

Leveraging Natural History Collections to Understand the Impacts of Global Change

Is the world wormier than it used to be? We'll never know without natural history collections

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Abstract

1. Many disease ecologists and conservation biologists believe that the world is wormier than it used to be—that is, that parasites are increasing in abundance through time. This argument is intuitively appealing. Ecologists typically see parasitic infections, through their association with disease, as a negative endpoint, and are accustomed to attributing negative outcomes to human interference in the environment, so it slots neatly into our worldview that habitat destruction, biodiversity loss and climate change should have the collateral consequence of causing outbreaks of parasites.
2. But surprisingly, the hypothesis that parasites are increasing in abundance through time remains entirely untested for the vast majority of wildlife parasite species. Historical data on parasites are nearly impossible to find, which leaves no baseline against which to compare contemporary parasite burdens. If we want to know whether the world is wormier than it used to be, there is only one major research avenue that will lead to an answer: parasitological examination of specimens preserved in natural history collections.
3. Recent advances demonstrate that, for many specimen types, it is possible to extract reliable data on parasite presence and abundance. There are millions of suitable specimens that exist in collections around the world. When paired with contemporaneous environmental data, these parasitological data could even point to potential drivers of change in parasite abundance, including climate, pollution or host density change.
4. We explain how to use preserved specimens to address pressing questions in parasite ecology, give a few key examples of how collections-based parasite ecology can resolve these questions, identify some pitfalls and workarounds, and suggest promising areas for research. Natural history specimens are 'parasite time capsules' that give ecologists the opportunity to test whether infectious disease is on the rise and to identify what forces might be driving these changes over time. This approach will facilitate major advances in a new sub-discipline: the historical ecology of parasitism.

KEYWORDS

disease, fluid-preserved specimen, museum, natural history collection, parasite, study skin, transmission

1 | INTRODUCTION

Disease ecologists have recently postulated that parasites may be on the rise (e.g. Harvell, 2019; Keesing & Ostfeld, 2021). This hypothesis is intuitively appealing; ecologists typically see parasitic infections as a negative endpoint and are accustomed to attributing negative outcomes to human interference in the environment, so it slots neatly into our worldview that habitat destruction, biodiversity loss and climate change should have the collateral consequence of causing outbreaks of parasites in established host–parasite relationships (distinguished from ‘emerging’ host–parasite pairs arising from spillover; see Keesing & Ostfeld, 2021). But theory suggests more complex effects of environmental change on parasite abundance, and empirical data to track parasite populations through time are entirely absent. Parasites are the ‘dark matter’ of ecosystems (Dobson et al., 2008); they are ubiquitous and abundant and they exert enormous influence on free-living species while remaining mostly unobserved. Knowing whether parasite abundance is increasing through time will allow us to anticipate and manage infectious disease threats; knowing whether parasite abundance is decreasing through time may allow us to intervene and rescue some of the ecological functions served by parasitic species, including host population regulation and facilitation of energy flow through food webs (Carlson, Hopkins, & Bell, 2020; Wood & Johnson, 2015). Here, we explore the potential utility of natural history collections for producing datasets that may allow us to test how the various forces that shape parasite populations interact to produce change in parasite abundance through time. We focus on average parasite abundance (after Bush et al., 1997), defined as the mean number of parasite individuals per

host. This metric encompasses both prevalence (the proportion of individuals infected) and intensity (the number of parasite individuals per infected host; Bush et al., 1997) and reflects the population status of parasites (Hechinger et al., 2008; Wood et al., 2013). New approaches that produce long time series of parasite abundance change will allow ecologists to test the appealing hypothesis that parasites are on the rise.

The abundance of parasites should be regulated by a combination of factors, including host density (e.g. Anderson & May, 1979; May & Anderson, 1979), host traits (e.g. immunity; Budischak et al., 2018; Cattadori et al., 2005) and survival of parasite transmission stages (e.g. McCallum et al., 2017; Pietrock & Marcogliese, 2003). But as global change impacts (i.e. pollution, habitat conversion, climate warming, invasive species) accumulate, these factors themselves will change in ways that may either increase or decrease parasite abundance (Figure 1). For example, pollutants can facilitate parasite transmission by eroding host immune defences that would otherwise allow the host to resist infection, while also retarding parasite transmission through direct toxicity to infectious life stages (Blanar et al., 2009; Lafferty, 1997; Vidal-Martínez et al., 2010). Reduction of host biodiversity can increase or decrease parasite transmission depending on the response of host abundance to community disassembly (Halliday et al., 2019; Mihaljevic et al., 2014; Rohr et al., 2019). Meanwhile, rising temperatures can affect parasite development directly or through intermediaries (e.g. host immunity or density), resulting in increases or decreases in parasite abundance (Claar & Wood, 2020; Lafferty & Holt, 2003; Morley & Lewis, 2014). Together, these studies provide valuable insight into the many ways in which various dimensions of global change could shape long-term

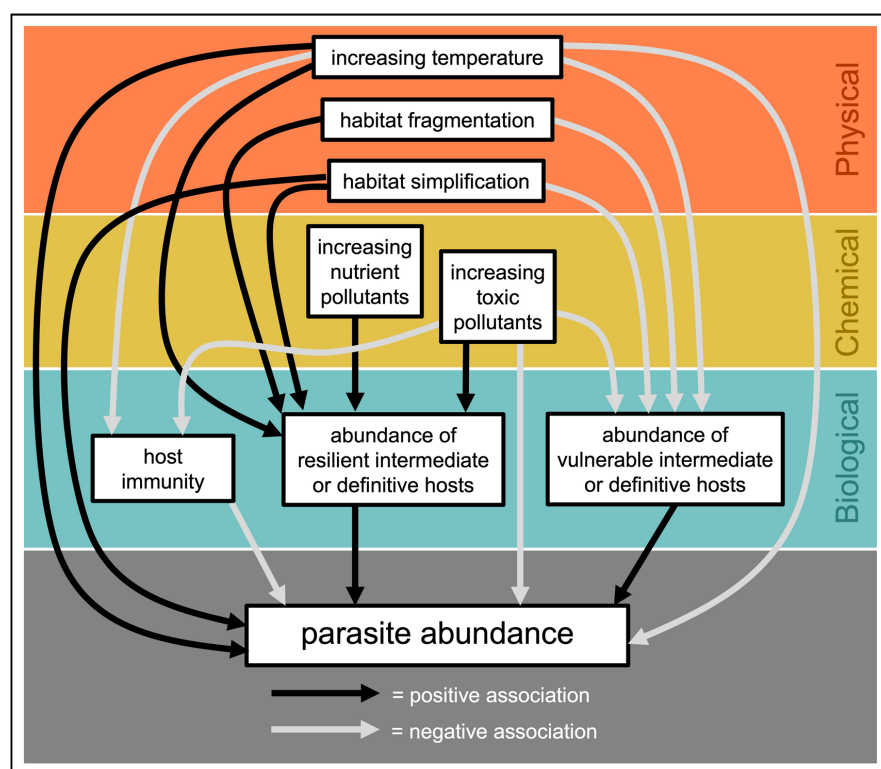


FIGURE 1 What is the net effect of global change on parasite abundance? This path diagram illustrates some of the mechanisms by which physical, chemical and biological changes to ecosystems may produce change in parasite abundance. For each path (i.e. arrow), colour indicates whether the relationship 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. Some biological mechanisms (e.g. invasive species) will directly affect the abundance of intermediate or definitive hosts; they may have negative (e.g. invasive outcompetes competent intermediate host and thereby reduces its abundance) or positive (e.g. invasive serves as a competent intermediate host) effects on parasite abundance.

trajectories of parasite abundance. But in real ecosystems, these facets of global change manifest simultaneously; although there is increasing recognition of the potential for interactions among stressors (Crain et al., 2008; Dieleman et al., 2012; Jackson et al., 2016; Orr et al., 2020), parasite ecologists have not yet seized the opportunity to understand which of these mechanisms are most important in shaping trajectories of parasite population change in nature.

To date, studies of global change impacts on parasitism have focused on exploring individual mechanisms in isolation and summing their effects to predict the net effect on temporal trajectories of parasite abundance (Cable et al., 2017; Didham et al., 2007), which may underestimate the impact of global change (Orr et al., 2021). This choice has been made for practical reasons: until now, there have been almost no opportunities to measure how wildlife parasite populations are actually changing on multi-decadal time scales (Harmon et al., 2019). In fact, one of us (CLW) has been searching for a decade for datasets that quantitatively (i.e. with sufficient host and infection parameters) document the abundance of aquatic parasites at any historical time point in any ecosystem and for any host species and any parasite species. She has found only two suitable datasets: one from 1949 to 1951 (Howard et al., 2019) and another from 1969 to 1970 (Quinn et al., 2021). Among papers on parasites in fishes, the average length of a study described by the authors as 'long term' is 12.4 years (Fiorenza, Leslie, & Torchin, 2020). If we are to test the hypothesis that the world is getting wormier, we need a new way to quantify the historical abundance of parasites—a data source that gives us a much deeper temporal and broader taxonomic scope.

Thanks to the foresight of past generations of scientists and naturalists, today there exists an affordable, broadly accessible, low-tech solution for generating highly resolved, long-term data on the abundance of parasites: parasitological examination of specimens preserved in natural history collections (DiEuliis et al., 2016; Fiorenza, Leslie, & Torchin, 2020; Harmon et al., 2019). These collections are administered within public and private museums, universities and research centres, and hold tens of millions of specimens as skins or whole animals in liquid preservative (Holmes et al., 2016). For example, just four major US collections hold 8 million liquid-preserved fish specimens (Harmon et al., 2019), and these four institutions represent only a tiny fraction of the 1,500 natural history collections that exist in the United States, and of the 5,000 that exist globally (Page et al., 2015). Many hosts other than fishes are typically held whole in liquid preservative, including amphibians, reptiles and invertebrates; 4 million reptile and amphibian specimens are available at just 13 major natural history collections, along with more than 74 million marine invertebrates (Holmes et al., 2016). All of these specimens are potential sources of parasitological information, encompassing a staggeringly large number of host taxa, parasite taxa, geographical regions and habitat types. Every specimen held in a natural history collection is preserved alongside meta-data on its time and location of collection, making each animal a snapshot in time and space. By carefully selecting these snapshots, parasite ecologists can reassemble time series of parasitological change. Natural history collections typically do not charge any fees for use of their specimens and

the only tools needed to take advantage of these resources are (a) knowledge of the parasitological examination techniques that might be used on any specimen of the taxon and (b) sufficient expertise for well-resolved taxonomic identifications of parasites and hosts.

Our two research groups have worked extensively with biological natural history collections over the past 15 years. Here, we establish a framework for the historical ecology of parasitism as a new sub-discipline, distinct from archaeo-parasitology (Reinhard, 1992) and palaeo-parasitology (Faulkner & Reinhard, 2014) in that—like the broader field of historical ecology (sensu Beller et al., 2017; McClenachan et al., 2015)—it focuses on the most recent few hundred years of Earth's history (Figure 2). The historical ecology of parasitism has received little recognition and research attention because until recently there were few validated tools capable of quantifying parasites over the past few hundred years. Here, we present some collections-based research tools, give a few key examples of how they can illuminate the recent ecological history of parasites, identify pitfalls and workarounds, and suggest promising areas for research. We focus primarily on metazoan parasites of wildlife, which comprise tens of thousands of species (Carlson, Dallas, et al., 2020), including worms, arthropods and myxozoans, but we also briefly discuss techniques for the detection of those smaller parasites that are usually undetectable with visual techniques, such as viruses, bacteria, fungi and protozoa. Given the dearth of alternative data streams, natural history specimens may represent one of the only research avenues available for answering questions like: is the world wormier than it used to be?

2 | CASE STUDIES

Although the historical ecology of parasitism is a young sub-discipline, it has already produced several substantive ecological insights. We review two here.

2.1 | Quantifying long-term change in parasite abundance

Until recently, science had few data to weigh the question of whether the oceans have faced a 'rising tide' of parasitic infection over the past century (Harvell et al., 2004). Some meta-analytic studies had suggested dramatic changes in parasite burden in the past few decades (Tracy et al., 2019; Ward & Lafferty, 2004)—even a 253-fold increase in the abundance of a common nematode parasite infecting many marine fish species (Fiorenza, Wendt, et al., 2020). But few studies had reached beyond a few decades into the past and fewer still had done this for more than one parasite species at a time (Figure 2a).

In the first study that used collections-based research to reconstruct a timeline of parasite abundance for a multi-parasite assemblage (which we refer to below as the 'parasites of the past' project), Welicky et al. (2021) reported 90 years of change (1930–2019) in parasite burden for 12 parasite taxa infecting English sole *Parophrys*

vetulus in Puget Sound, Washington, USA. Data were obtained by semi-destructive parasitological dissection of liquid-preserved fishes held in natural history collections. Of the 12 parasite taxa tracked, nine did not change in abundance over time, two (an acanthocephalan and a trematode) decreased and one (another trematode) increased

(Figure 3). This simple time series of parasite abundance revealed a surprising result: yes, some parasites may increase in abundance over time, but others are in decline. Instead of a 'rising tide' of marine disease, should we instead be worried about the conservation status of parasites (Carlson, Dallas, et al., 2020; Carlson, Hopkins, & Bell, 2020)?

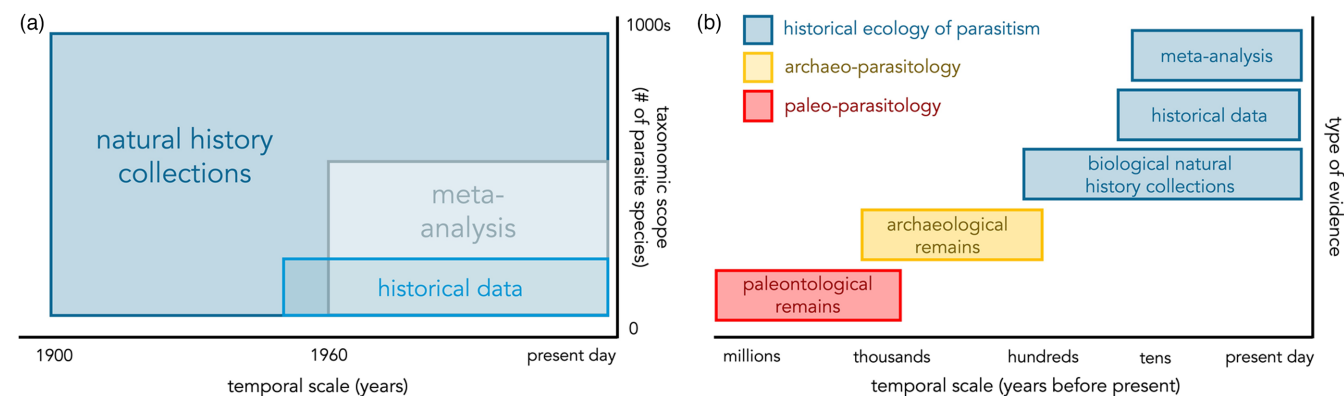


FIGURE 2 (a) The questions that ecologists can answer about the parasite burden of past ecosystems are limited by data availability. Historical datasets may provide quantitative information on parasites, but they are rare, recent and pertain to only a handful of parasite species. Meta-analysis can allow ecologists to harness replication across multiple studies on the same parasite, but can only reach back to the earliest publications documented in searchable databases (usually ~the 1960s). Natural history collections, on the other hand, hold specimens from 1900 and earlier, and given their broad representation of hosts, also contain information on a broad cross-section of parasite diversity. Adapted with permission from Fiorenza, Leslie, and Torchin (2020). (b) Across broad temporal scales, palaeo-parasitology uses palaeontological evidence (e.g. fossils, coprolites) to assess parasite burdens thousands to millions of years ago and archaeo-parasitology uses archaeological evidence (e.g. human latrines, purposeful burials) to assess parasite burdens hundreds to thousands of years ago. In contrast, historical ecology uses historical evidence (e.g. meta-analysis, historical datasets, specimens from biological natural history collections) to assess parasite burdens over the past several hundred years. Inspired by figure 1 in McClenachan et al. (2015).

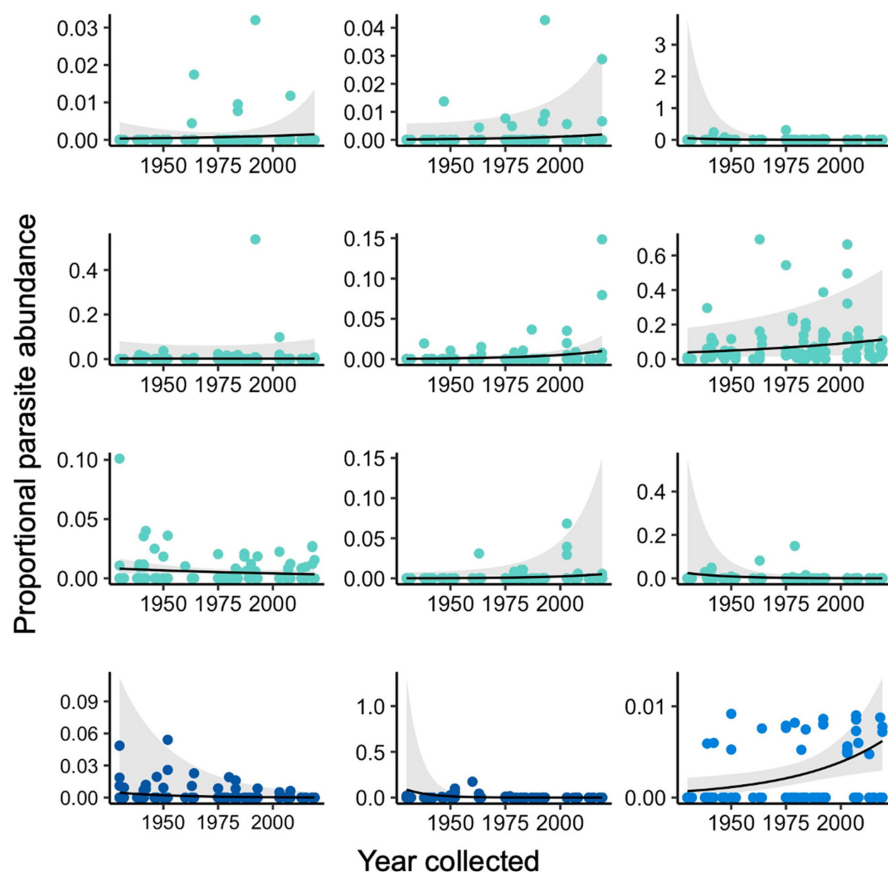


FIGURE 3 Welicky et al. (2021) dissected 109 English sole *Parophrys vetulus* from Puget Sound, USA, finding 12 common parasite taxa. The y-axis represents the abundance of parasites adjusted for fish body size (i.e. predicted number of parasites per millimetre of fish length). Solid black lines indicate the predicted fit of a GLMM, with 95% confidence interval in grey shading. Green dots indicate non-significant models; dark and light blue dots indicate parasites that significantly decreased or increased in abundance, respectively. (a) Copepoda sp., (b) *Oceanobdella pallida*, (c) Trematoda sp. 3, (d) Metacercaria sp. 1, (e) *Clavinema mariae*, (f) *Cucullanus annulatus*, (g) *Contracaecum* sp., (h) *Capillaria parophysi*, (i) Spirurida sp. 1, (j) *Echinorhynchus* sp., (k) Opecoelidae sp. 1, (l) Metacercaria sp. 2. Figure reproduced with permission from Welicky et al. (2021).

2.2 | Resolving the question of whether a parasite species is native or introduced

Nile tilapia *Oreochromis niloticus* are among the most infamous invasive species in the world. Because they are easily cultured, the species has been widely translocated from its native range in the Nile River Basin, coastal rivers of Israel, parts of West and Central Africa, and some East African lakes (Trewavas, 1983). The introduction of Nile tilapia into the Congo River Basin probably occurred in the late 1940s (Thys van den Audenaerde, 1964; Welcomme, 1988). The Congo River Basin contains a variety of native tilapia species, but for years ecologists have not known whether the parasite fauna of these species is native or was co-introduced with Nile tilapia. Because non-native parasites can have especially pernicious effects on native host species (Lymbery et al., 2014), management of these native fishes requires a better understanding of whether their parasites are native or not (Williams et al., 2013).

In the TILAPIA ('Tracing fish Introductions and Lateral Parasite transfer to Indigenous Aquatic fauna') project, Jorissen et al. (2020) explored the origins of the monogenean ectoparasites of several native tilapia species by assessing parasite presence before and after the introduction of Nile tilapia. Specimens from before introduction were liquid-preserved fish held at the Royal Museum for Central Africa (RMCA, Tervuren, Belgium). Jorissen et al.'s data collection approach was minimally destructive; by dissecting out the right-hand side gills of preserved specimens, they were able to collect monogenean parasites without much damage to specimens. Their data demonstrate that the Nile tilapia brought several of its monogenean parasite species with it when it was introduced to the Congo Basin, three of which have spilled over into native fish species since that introduction (Jorissen et al., 2020). Several other monogenean species were shared between the native and invasive hosts in historical samples, indicating that those monogeneans are native (Jorissen et al., 2020). With information on which parasites are meant to be in the region and which were co-introduced by Nile tilapia, managers are now better prepared to address the management of native tilapia species (Williams et al., 2013).

3 | HOW TO DO IT YOURSELF

Depending on the questions you seek to answer, natural history collections may contain suitable material for your research. The first step is to identify your geographical region and taxon of interest and to investigate which museums (or groups of museums) would have sufficient proximity and taxonomic representation to provide relevant data. (Typically, natural history collections will best represent ecosystems within their immediate vicinity (Cobb et al., 2019; Monfils et al., 2020, so proximal museums are a good place to start.) Once you have narrowed in on a geographical region, the way to figure out whether the material you seek exists

is to (a) explore the holdings of relevant museums by consulting their digital meta-data repositories and (b) discuss your interests directly with curators. Many museums are working to ensure that specimen label information is transcribed into publicly accessible, online databases (a process called 'digitization'; Hedrick et al., 2020; Nelson et al., 2012), including data aggregators like VertNet (www.vertnet.com), FishNet2 (<http://www.fishnet2.net>), SCAN (Symbiota Collections of Arthropods Network; scan-bugs.org), Canadensys (<http://www.canadensys.net>), the European Distributed Institute of Taxonomy (<https://cybertaxonomy.eu>), Distributed System of Scientific Collections (DiSSCo; <https://www.dissco.eu>), the Atlas of Living Australia (<https://www.ala.org.au>), the Centro de Referência em Informação Ambiental (<https://www.cria.org.br>), Arctos (<https://arctosdb.org/about/>) and Specify (<https://www.specifysoftware.org>), which feed into global data portals like GBIF (Global Biodiversity Information Facility; gbif.org) and iDigBio (Integrated Digitized Biocollections; idigbio.org). Most of these resources allow users to query hundreds of collections simultaneously. Many museums are aiming to digitize 100% of their specimens, but nonetheless, as recently as 2015 it was estimated that fewer than 10% of all specimens were documented in publicly accessible databases (Page et al., 2015), so it pays to talk with curators, who typically know their collections inside and out and may have access to metadata that are not yet publicly accessible.

Once suitable specimens have been identified, the next step is to have a discussion with the curator about what you'd like to do. We were hesitant when we first started these conversations, but quickly found that curators were very willing to discuss the use of the specimens under their care—even semi-destructive use. We speculate that there may be a few reasons for the openness we encountered. One is that some lots held in natural history collections are redundant, containing many individuals of the same species from the same time and place. The use of these lots does little to erode the future utility of the collection and even provides justification to build a certain redundancy into curated collections by stimulating the accessioning of vouchers from non-taxonomic studies. Additionally, curators are often interested in sponsoring active scientific research in their collections, as this can demonstrate the collection's value to decision-makers who allocate funding and even decide the fate of collections (Miller et al., 2020). Finally, we always try to be extremely deferential to the curators' authority; museum personnel are duty-bound to protect specimens for future generations, and we respect their decisions about what research will and will not provide net benefits to the collection. For more tips on how to design your collections-based research in partnership with museum personnel, see below (Section 4).

Once you've obtained permission to work on particular specimens, your approach will depend on your research question and the decisions you have made collaboratively with your curator-partners. In recent years, experimental and observational work has demonstrated that parasitological examination of liquid-preserved museum

specimens yields accurate information about the number and identity of parasites infecting a host at the time of its death (Figure 4). The liquid preservation protocols used by natural history collections (i.e. formalin fixation followed by freshwater rinses and long-term storage in denatured ethanol) were designed to obtain maximum fidelity of tissue morphology and tissue persistence through time, and what has been designed to work on host tissues also works, fortuitously, on parasite tissues. Fiorenza, Leslie, and Torchin (2020) performed a randomized controlled experiment in which fish were either preserved by the protocols used in natural history collections or maintained in their unpreserved state, and both groups were then subjected to semi-destructive parasitological dissection. For 24 of 27 parasite taxa, there was no difference in parasite detectability between the two treatments; for the three remaining parasite taxa, two were more detectable in the control treatment and one was more detectable in the preservation treatment, suggesting extremely minimal effects of preservation on parasite detectability and little evidence of bias (i.e. of greater detectability in control versus preservation treatments). If your research focuses exclusively on ectoparasites of liquid-preserved hosts, it may be possible to entirely avoid destructive sampling; for example, Van Steenberge et al. (2015) studied monogenean gill parasites on paratypes of the cichlid *Pseudosimochromis pleurospilus* by manually raising the operculum and washing the gills using a rinsing bottle. Of course, some ectoparasites (e.g. gnathiid isopods) can abandon the host when they sense that it is in distress, and thus are not well represented in collections; other approaches will be needed for these species (e.g. Grutter et al., 2019; Sikkell et al., 2019). Formalin fixation complicates the

process of extracting readable DNA, but it does not make sequencing entirely impossible; with new techniques, it is now possible and may soon be easy to extract the DNA of 'microparasites' (i.e. viruses, bacteria, protozoans; sensu Lafferty & Kuris, 2002; see Section 5, below). These data will be especially valuable, given that microparasites account for the majority of the 'emerging' infectious diseases.

Parasitological examination of liquid-preserved specimens is not the only option for extracting parasitological insight from natural history collections. Similarly useful information may be obtained from study skins (Eberhard, 2003) and other kinds of dry specimens. Study skins are often the only remains retained of bird and mammal specimens; although the viscera of these specimens are removed and the skin preserved via taxidermy, skins may nonetheless retain a large proportion of the ectoparasites that clung to the hair or feathers of the host in life (Figure 5; Eberhard, 2003). To date, we are unaware of any study that has explicitly compared the detectability of ectoparasites between fresh hosts and prepared study skins, which would reveal how faithful an ectoparasite count from a study skin is to a 'true' ectoparasite count. However, one study documents that strong correlations with the 'true' count of ectoparasitic chewing lice on bird hosts (obtained by completely dissolving the host tissues in potassium hydroxide, which leaves behind the chitinous exoskeletons of ectoparasites) can be obtained from both (a) washing the body of a recently killed bird with a dish soap solution ($r = 0.99$) and (b) post-mortem ruffling of feathers ($r = 0.98$). This and other work (e.g. Valdez et al., 2009) suggest that study skins may provide quantitative information on ectoparasite burden, but validation studies are still needed.

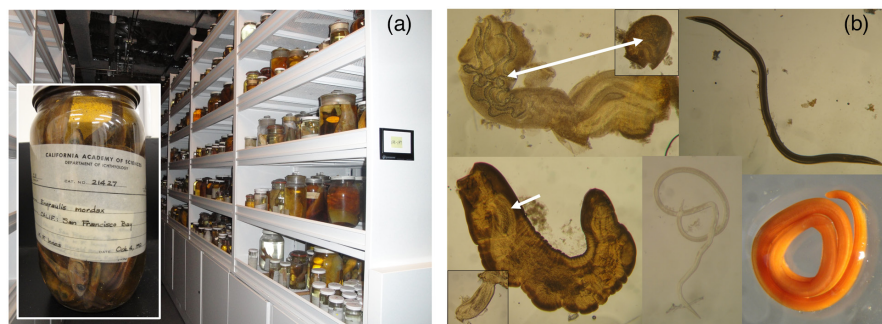


FIGURE 4 (a) Liquid-preserved specimens in the Ichthyology Collection at the California Academy of Sciences, San Francisco, CA, USA. (b) Some metazoan parasites recovered from dissections of Atlantic cod *Gadus morhua* and spiny dogfish *Squalus acanthias* at the Smithsonian Institution's National Museum of Natural History in Washington, DC, USA.

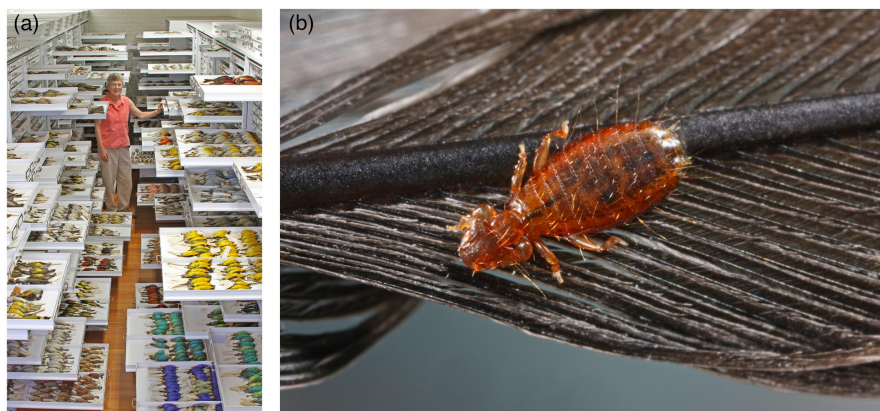


FIGURE 5 (a) Specimens in the Ornithological Collection at the Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA. Reproduced with license CC BY 2.5 from doi: <http://doi.org/10.1371/journal.pbio.1001466.g002>. (b) Feather louse on the shaft of a bird feather. Courtesy of blickwinkel/H. Bellmann/F. Hecker, Alamy Stock Photo.

Clearly, there is substantial untapped potential for deriving long, well-resolved time series of parasite burden from natural history collections. But these unique resources also entail some unique constraints and responsibilities.

4 | THE CONSTRAINTS AND RESPONSIBILITIES OF EXTRACTING PARASITOLOGICAL DATA FROM NATURAL HISTORY COLLECTIONS

4.1 | Constraints

In any empirical project set in a contemporary ecosystem, ecologists must navigate some standard challenges in sampling design: selecting appropriate samples, minimizing bias in sampling and maximizing sample size. When sampling in natural history collections, the same challenges apply, but the constraints differ.

Given unlimited resources, any species that exists today is available for ecological sampling. In contrast, only a limited subset of species, locations and times are available for examination in a natural history collection; hard limits are set by what has actually been sampled in the past, and the subset of questions that can be answered are constrained by the material available. In ecology, the scientific method often starts with a question, but when working on natural history collections, one must often instead begin with a broad area of inquiry, and allow the availability of materials to inform the selection of a question that will ultimately be addressed with data. In a non-parasitological example, McClenachan (2009) was interested in long-term change on Key West's coral reefs, and explored a document archive at the Key West Public Library. There, she discovered a tranche of trophy photos spanning 51 years (1956–2007). The photos documented fish caught by day boats and displayed on the same hanging board, and they allowed McClenachan to reconstruct mean individual size and species composition of marine fishes targeted by sport fishers on Key West's reefs (McClenachan, 2009). Not every question is answerable with collections material, so researchers need to be prepared to discard initial questions in favour of ones that turn out to be answerable.

Once a question has been selected and suitable materials identified, the next task is to design a sampling strategy that minimizes bias. This is a special challenge in natural history collections, because they are produced with non-random sampling across taxonomic, geographical, temporal and trait variation (Daru et al., 2017; Gotelli et al., 2021; Meineke & Daru, 2021; Meyer et al., 2016). Most collections are shaped by the choices of collectors (Daru et al., 2017), and the individual preferences and priorities of these individuals (e.g. 'rarity-seeking syndrome' sensu Kruckeberg & Rabinowitz, 1985) can introduce bias in the kinds of species and individuals represented in the collection. For investigations of parasite burden in natural history collections, bias in taxonomic, geographical or temporal representation will tend to limit the questions that can be addressed (see above), but bias in trait representation (i.e. discrimination for or

against individuals with certain traits) could introduce distortions in parasite counts. For example, curators may avoid accessioning 'sickly' individuals (biasing parasite counts downward) or may specifically seek out these unique specimens (biasing parasite counts upward). The size distribution of collection specimens is often biased (Holmes et al., 2016), which can influence parasite counts if host body size is associated with parasite burden (Poulin, 1999). These biases can shift over the time span of a collection, as collectors' preferences change and collectors and curators themselves turn over. However, several lines of evidence suggest that these biases may introduce only negligible distortions to parasite counts. Howard et al. (2019) compared the temporal trajectory of abundance for one nematode parasite (*Clavinema mariae*) between a historical dataset (i.e. data from a research cruise in the mid-1900s, which was replicated in 2017) and a dataset on the parasite burden of fish from a natural history collection. Both datasets revealed a substantial increase in abundance over time (Howard et al., 2019). Gotelli et al. (2021) demonstrated that the abundance of various species in 17 coupled field and museum datasets were closely correlated (median r^2 of correlation between field and museum abundance = 0.43), suggesting that curators' choices about what to accession largely reflect what is available in nature. To minimize any remaining bias, researchers can choose to focus on those collections that contain the spoils of standardized government or university monitoring (e.g. contents of research trawls) and which are therefore as unbiased as the standard sampling that might be done in a purpose-designed project. We recommend deeply considering sources of bias with reference to the focal question (Meineke & Daru, 2021) in collaboration with museum personnel, who are intimately familiar with the history of the collections they manage (see Section 4.2, below).

Only so many specimens exist in natural history collections, and limitations on replication are some of the most important constraints we have encountered in our collections-based research. This is a well-recognized limitation across the field of historical ecology and ecologists working on ecosystems of the past often accept lower levels of replication than they might in a contemporary project, and instead seek certainty by other means (e.g. using multiple lines of evidence; McClenachan et al., 2012, 2016). Nonetheless, there are ways around this constraint. In the 'parasites of the past' project mentioned above (which, since Welicky et al., 2021, has expanded to include eight host species), we were limited to between 46 and 114 individuals of each host species. To increase our power to detect change in parasite burden, we pooled replication across parasite and host species; that is, instead of asking, 'has the abundance of this individual parasite species changed over time', we asked, 'has the abundance of this group of parasite species changed over time?' Low replication put limits on our ability to address individual-parasite-species-level change in abundance, but we had high power to address change in groups of parasites. For parasite diversity, richness estimators can allow researchers to estimate parasite species richness at the saturation point of the species accumulation curve, even if sampling is insufficient to reach that saturation point (Gotelli & Colwell, 2001). Finally, if replication is truly limiting, researchers can

pose questions that require only qualitative or semi-quantitative information; for example, presence/absence data are sufficient for estimating the date of a parasite species' invasion (Hartigan et al., 2010; Jorissen et al., 2020).

4.2 | Responsibilities

Specimens held in natural history collections are irreplaceable, there will never be another opportunity to collect a fish from 1945. Researchers using these precious resources therefore must assume certain responsibilities, many of which might be new to ecologists accustomed to working in contemporary ecosystems.

Any work conducted in natural history collections should be done hand-in-hand with the curators and collections managers who are the final authorities on the disposition of specimens. Ideally, collections staff should be partners who co-develop the project. For example, one of us (CLW) partnered with the Curator and Collections Manager of the Fish Collection at the University of Washington's (UW) Burke Museum of Natural History and Culture to design the 'parasites of the past' project discussed above (see Section 2). At the beginning of the project, the entire team met to discuss the research objectives, assess availability of specimens, decide on host species to target, choose lots for each host species, design a semi-destructive dissection protocol that would fulfil research objectives while minimizing damage to specimens, and choose how to preserve and where to accession the parasites recovered from dissected hosts. When it came time to analyse the data and draw conclusions, our partners at the UW Fish Collection were able to provide ecological and logistical context for these specimens, weighing in as experts in the biology of fishes and on the history of the UW Fish Collection. Similarly, the above-mentioned TILAPIA project in which one of us (MPMV) was involved as a partner, was jointly supervised by a parasitologist PI and ichthyologist co-PI (Tine Huyse and Jos Snoeks, respectively, at the RMCA). Projects will benefit greatly from the involvement of museum personnel for a number of reasons, not least of which is that collections may contain field samples in which individual specimens may not have been accounted for (Ariño, 2010), the resolution of specimen taxonomic identification may vary depending on the focus of a collection (Blagoderov et al., 2012), and a substantial proportion of specimens in existing natural history collections may be misidentified (Hedrick et al., 2020).

Researchers can help museum staff safeguard the integrity of irreplaceable specimens by proposing to examine redundant lots containing multiple individuals collected from a particular time and place (e.g. those collected with bulk techniques like trawling or seining). For example, in the TILAPIA project, the team agreed that they would dissect only a small proportion of each targeted lot (i.e. each batch of fish from a particular time and place). Protocols can also be co-designed with collections staff to be minimally invasive while providing maximum information. For example, in the 'parasites of the past' project, collections staff gave permission for destructive sampling of visceral organs, but wanted to preserve the external

morphology of each specimen examined. To find encysted parasites in the musculature of these fish, we designed a 'candling' technique in which a strong light is passed through the body wall of the fish and shadows of encysted nematodes and cestodes are detected visually. Those parasites are carefully removed with as little disturbance to fish musculature as possible. While this technique is not as exhaustive as destructive sampling, it does yield unbiased parasite counts (Fiorenza, Leslie, & Torchin, 2020) while allowing dissected specimens to be returned to the collection with almost no damage to external morphology—a worthwhile trade-off, in our view.

When we take specimens down from a shelf in a natural history collection, it can be easy to forget the labour that allowed the specimen to arrive there: the initial collection, the painstaking preservation process, the identification and cataloguing and the maintenance to physical space that keeps the specimen safe and well-preserved. Given that each specimen represents the collective effort of generations of scientists and curators and (in many cases) substantial investment of public funds, a researcher using these specimens owes it to the world to ensure data quality, reproducibility and availability. Parasite taxonomic identifications should be as highly resolved as possible and—because most of these specimens have been fixed in formalin—we often cannot rely on sequencing to achieve this. In the 'parasites of the past' project, we stained, mounted and cleared parasites to better visualize diagnostic features and we partnered with a parasite taxonomist to achieve high taxonomic resolution through strictly morphological identification (Welicky et al., 2021; Wood et al., *in review*). Derivative specimens (e.g. parasite vouchers) should be accessioned into museums where they will be made available to the public, with parasite specimens linked to host specimens in the databases of both the host's and parasite's collection so that future researchers can always trace the parasite vouchers back to the host specimen from which they originated (Thompson et al., 2021; Upham et al., 2021). Raw data and code from the project should be made available upon publication in publicly accessible, searchable databases. These moves towards data quality, reproducibility and availability are the least we can do to compensate the public for its support of the collections from which our research benefits.

5 | PROMISING AVENUES FOR RESEARCH

Hundreds of millions of preserved specimens sit in natural history collections today. The possibilities for making discoveries about past parasite burdens are therefore numerous. What are the most pressing, easiest-to-answer questions for ecologists interested in working on parasitism in ecosystems of the past?

As Earth's ecosystems face an unprecedented rate of change, basic questions about how parasites respond to these changes remain unanswered, largely for lack of long-term data. But all that is required to answer these questions are (a) a time series of environmental data and (b) a matching time series of specimens from which parasitological data are extracted. For example, in the 'parasites of the past' project, we were able to obtain temporally matched data

on sea surface temperature (and, hence, climate change; British Columbia Lightstation, [nd](#)), pollutants (Brandenberger et al., [2008](#)), nutrient enrichment (Brandenberger et al., [2008](#)) and host density (Essington et al., [2021](#); Greene et al., [2015](#)). Long-term environmental data are widely available in public databases, and can be easily matched to the temporal and spatial scope of a time series of parasitological data. These data may even help develop baselines for wildlife disease management (Cook et al., [2020](#); DiEuliis et al., [2016](#); Dunnum et al., [2017](#)).

By the same token, long time series of parasite abundance may allow us to detect parasite extinctions, extirpations and declines (Rózsa & Vas, [2015](#); Strona, [2015](#)). It may seem counterintuitive to consider parasite species as conservation targets; conservation is typically oriented towards parasite eradication or control to protect sensitive wildlife host species (Carlson, Hopkins, & Bell, [2020](#)). But parasites play important roles in ecosystems, and ecologists are increasingly recognizing that a loss of parasite biodiversity might also entail a loss of ecosystem function (Wood & Johnson, [2015](#)). Some have even gone so far as to propose conservation plans for parasites (Carlson, Hopkins, & Bell, [2020](#)), in recognition of the fact that parasitic species may in fact comprise the majority of species facing extinction (Carlson et al., [2017](#)). But although parasite species are predicted to be vulnerable, given their sensitivity to environmental change (Carlson et al., [2017](#)) and obligate dependence on hosts that may themselves be vulnerable (Lafferty, [2012](#)), few declines and extinctions have been documented (Strona, [2015](#)). Natural history collections have a central role to play in providing evidence of otherwise cryptic declines in parasite species. For example, Black ([1983](#)) examined specimens of lake trout *Salvelinus namaycush* collected from the Great Lakes before and after a trout population crash and found no swim bladder nematodes *Cystidicola stigmatura* after the crash—an apparent example of parasite extirpation due to reduction of host density below the threshold for transmission. Given the virtual absence of long-term data on parasite populations, collections-based research may be the only avenue for identifying parasite taxa that are in decline or already extinct.

The potential changes in parasite abundance discussed so far are primary; that is, they result from the direct effects of global change on parasite populations. What about the secondary or 'knock-on' effects of primary changes on other, co-infecting parasites? Parasites may facilitate (e.g. through immune suppression; Lello et al., [2018](#)) or inhibit (e.g. through competition for resources; Griffiths et al., [2014](#)) one another. These associations will be difficult to disentangle in a time series; that is, it would be difficult, in a time series, to distinguish a parasite that is increasing through time in response to environmental change from a parasite that is increasing through time due to facilitative interactions with a co-infecting species that is increasing through time in response to environmental change. Some proportion of the temporal changes in long time series of parasite communities are likely to be due to these co-infection dynamics (Dallas et al., [2019](#)). Manipulative experiments could help to disentangle primary from secondary (or even tertiary) effects.

Specimens in natural history collections often over-represent geographical areas that are convenient to collectors—specifically

populated, urban areas (Daru et al., [2017](#)). This bias makes some questions more difficult to answer, but creates opportunities to answer other questions. Ecologists are increasingly interested in whether fundamental ecological principles established in wildlands govern the abundance and distribution of species in cities (McHale et al., [2015](#); Pickett et al., [2001](#), [2017](#)). This question is entirely unanswered for the ecological principles governing parasite transmission, although there are hints that these processes differ between urban and rural environments (Rouffauer et al., [2017](#); Vanhove et al., [2020](#)). Careful design of before-after-control-impact studies (e.g. exploring parasite burden of hosts collected before and after urbanization in an urban and nearby non-urbanized area) can allow parasite ecologists to create century-long, large-scale natural experiments that will reveal whether and how urbanization influences parasite transmission.

Although it presents many challenges, extracting parasite DNA from specimens held in natural history collection specimens is possible (Raxworthy & Smith, [2021](#); Wood, [2018](#)). This not only opens the possibility of obtaining molecular identifications of metazoan parasites, but could also allow the historical ecology of parasitism to encompass parasites that are not readily identifiable with visual diagnosis (i.e. viruses, bacteria, fungi, protozoans). An enormous proportion of natural history collection holdings are liquid-preserved and usually formalin-fixed, including most fish, reptile and amphibian collections (Harmon et al., [2019](#)); these holdings represent a potential treasure trove of DNA sequence data on co-preserved parasites. Natural degradation and fixation (e.g. in formalin) will reduce DNA copy numbers (increasing the risk of contamination by modern DNA), break DNA into short fragments, alter nucleotide sequences and cause crosslinks leading to partial denaturation (Do & Dobrovic, [2015](#); Wood, [2018](#)), while residual formalin may inhibit reagents, like proteinase K, used in downstream molecular work (Raxworthy & Smith, [2021](#)), all of which can complicate the process of DNA extraction, amplification and sequencing. Best practices for addressing these challenges will vary depending on the specimen type, history and age (Raxworthy & Smith, [2021](#)). One solution that has proven successful is the use of primers that amplify short (<200bp) or multicopy barcode regions of the target parasite species' DNA (Wood, [2018](#)). If investigators are not specifically targeting a single parasite species or intend to survey parasites across a range of taxa, DNA metabarcoding with universal primers is an option (Wood et al., [2013](#)). Although substantial trial and error is needed to optimize protocols for a given specimen type, the field is advancing rapidly towards better, faster and cheaper sequencing options for DNA from degraded natural history specimens, making sequencing of 'microparasites' possible (Raxworthy & Smith, [2021](#)).

6 | CONCLUSIONS

Hundreds of millions of specimens sit on the shelves of natural history museums as you read these words. They hold answers to one of the most pressing questions in ecology: is parasitism on the rise? All

that remains is for ecologists to seize the opportunity to use these widely available, underutilized and inexpensive resources. When it comes to the historical ecology of parasitism, we have only begun to scratch the surface. Many low-hanging fruits remain to be picked by ecologists interested in ecosystems of the past.

AUTHOR CONTRIBUTIONS

Chelsea L. Wood and Maarten P. M. Vanhove conceived the ideas in this manuscript. Chelsea L. Wood led the writing with substantial inputs of original writing from Maarten P. M. Vanhove. Both authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST

Chelsea L. Wood and Maarten P. M. Vanhove declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data have not been archived because this article did not use data.

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