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Invited Review

The state of fish parasite discovery and taxonomy: a critical assessment and a look forward

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ABSTRACT

Efforts to find and characterise new parasite species in fish hosts are crucial not just to complete our inventory of Earth's biodiversity, but also to monitor and mitigate disease threats in fisheries and aquaculture in the face of global climate change. Here, we review recent quantitative assessments of research efforts into fish parasite discovery and taxonomy. We address broad questions including: Are efforts aimed at finding new parasite species targeted at geographical hotspots of fish biodiversity, where there should be more parasite species to be found? Is the application of molecular tools to study parasite genetic diversity deployed strategically across regions of the world, or focused disproportionately on certain areas? How well coordinated is the search for new parasite species of fish among workers specialising on different higher helminth taxa? Are parasite discovery efforts in any geographical area consistent over time, or subject to idiosyncrasies due to the waxing and waning of highly prolific research careers? Is the quality of taxonomic descriptions of new species improving over time, with the incorporation of new tools to characterise species? Are taxonomic descriptions moving away from a focus on the adult stage only toward attempts to characterise the full life cycle of newly-discovered helminth species? By using empirical evidence to answer these questions, we assess the current state of research into fish parasite discovery and taxonomy. We also explore the far-reaching implications of recent research on parasite microbiomes for parasite taxonomy. We end with recommendations aimed at maximising the knowledge gained per fish sacrificed, and per dollar and time invested into research on fish parasite biodiversity.

1. Introduction

Taxonomy and systematics underpin all other research in ecology and evolution, as well as areas of applied science such as fisheries and aquaculture. Before we can learn anything else about parasites, we must first discover them, characterise them carefully in ways that will allow us to distinguish them from other species, identify their main hosts (ideally for all life stages), and determine where they fit in our growing, evolutionary-based classification of living organisms. Equipped with this knowledge, we are in a better position to identify hotspots of parasite diversity and disease emergence (Jones et al., 2008; Stephens et al., 2016), guide public health and conservation initiatives (Pérez-Ponce de León and Nadler, 2010), and tackle the key disease challenges of our changing world, such as mitigating the impacts of predicted climate change on parasite distributions (Smith, 2009; Estrada-Peña et al., 2014).

Some scientists have warned that taxonomy faces a crisis, with the number of active taxonomists and funding for the discipline both in decline (Brooks and Hoberg, 2001; Pearson et al., 2011; Cribb, 2016). In spite of these alarm bells, however, the number of new parasite species discovered and described annually has been growing steadily for decades (Cribb et al., 2014; Poulin, 2014; Poulin and Presswell, 2016). Although the eventual completion of our full inventory of parasite species on Earth still lies in the distant future, parasite taxonomy and systematics appear to be alive and well.

In particular, research on the diversity, taxonomy and systematics of fish parasites has always represented, and continues to do so, a substantial branch of fish parasitology. The numbers support this statement. A search of the *Web of Science Core Collection* for papers published between 2015 and September 2019 in eight international journals of general parasitology reveals that out of 6020 articles, 778 are specifically on parasites of fish (Table 1). Of these, 404 (51.9%) are primarily concerned with species discovery and taxonomy, systematics or phylogeny, including new species descriptions, redescriptions, taxonomic revisions, genetic charac-

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Table 1
Number (and percentage) of articles primarily concerned with species discovery and taxonomy of parasites of fish (including elasmobranchs) in eight international journals of general parasitology. See section 1 (Introduction) for further details about the types of articles considered to be focused on species discovery and taxonomy.

Journal	Total no. articles published	No. articles on fish parasites	No. articles on fish parasite taxonomy	Percent articles on fish parasite taxonomy
Acta Parasitologica	500	94	71	75.5%
International Journal for Parasitology	477	34	7	20.6%
International Journal for Parasitology – Parasites and Wildlife	309	27	6	22.2%
Journal of Helminthology	472	98	54	55.1%
Journal of Parasitology	499	91	57	62.6%
Parasitology	896	89	21	23.6%
Parasitology International	662	91	72	79.1%
Parasitology Research	2205	254	116	45.7%
Total	6020	778	404	51.9%

terisations of species, resolution of life cycles, and cryptic species identification and discrimination. Just as taxonomy and systematics dominate research on fish parasites, fish hosts dominate research on parasite taxonomy and systematics: during the same time period, 185 (54.3%) of 341 articles published in the main specialist journal in this field, *Systematic Parasitology*, investigated fish parasites. It is clear that research focused on species discovery and taxonomy is an important, if not the main, activity of fish parasitologists as a whole. Due to its central place in our scientific community, it is essential to assess how well we are conducting this research, and what could be done to improve its efficiency or quality.

Here, we offer a brief assessment of the state of fish parasite discovery, taxonomy and systematics. We use large databases compiled for helminth parasites (trematodes, cestodes, acanthocephalans and nematodes) of vertebrates to provide quantitative analyses of how well this area of research is performing. We re-examine these data specifically for fish hosts, to answer specific questions examining whether or not efforts toward finding and characterising parasite species in fish are deployed efficiently, and whether descriptions of new species reach the highest standards of quality. We also figuratively open a new can of worms by suggesting how parasite taxonomy may have to adapt in the era of microbiome research. Finally, we end with a few recommendations for future taxonomic research, with our aim being to initiate a discussion rather than to pontificate.

2. Geography of fish parasite discovery

As in other consumer-resource interactions, local parasite species richness should be strongly dependent on local host species richness, such that host richness and parasite richness are correlated across sampling localities (Hechinger and Lafferty, 2005; Thieltges et al., 2011; Kamiya et al., 2014). In other words, for any given taxon, the more host species in an area, the more parasite species we should expect to find. Therefore, to maximise the number of new parasite species discovered per unit effort, i.e. to maximise parasite discovery efficiency, the search for new parasite species should be proportionally more directed at areas of highest host diversity. However, research in ecology and systematics has long been spatially biased, and disproportionately concentrated on the regional biota near the home institutions of researchers (Martin et al., 2012; Bellard and Jeschke, 2016). For that reason, the rates of discovery and description of new parasite species in different regions may not necessarily be proportional to host richness in those regions. We already know that there is a disparity in our knowledge of parasites of fish between different parts of the world (Choudhury et al., 2016; Scholz et al., 2016). Here we ask: are efforts aimed at finding new parasite species targeted at geographical hotspots of fish biodiversity, where there should be more parasite species to be found?

Jorge and Poulin (2018) tackled this question by using data on the helminth species described from vertebrate hosts in the past 50 years. Using the coordinates where each new species was found, they could determine how many new parasite species were reported from each 2° × 2° cell in a global latitude-by-longitude grid. Here, using the subset of these data for parasites of freshwater fish only, and data on the known geographical distribution of freshwater fish diversity from the latest version of the International Union for Conservation of Nature online database (IUCN, 2019; https://www.iucnredlist.org/resources/spatial-data-download), we test for spatial congruence between parasite species discovery and local host diversity across the global grid of 2° × 2° cells; see Jorge and Poulin (2018) for detailed methodology.

The results indicate a significant, but very weak, spatial covariation between local freshwater fish diversity and local rates of parasite species discovery (Fig. 1). The poor match between the two distributions indicates that there is a research deficit in parasite discovery in geographical areas corresponding to hotspots of fish diversity, in particular equatorial Africa and southeastern Asia. Areas of high host diversity have yielded disproportionately few new parasite species. The same pattern is true for parasites of marine fish (Jorge and Poulin, 2018). However, there are promising signs that taxonomic research on fish parasites may be changing to a more rational allocation of efforts across the globe. Indeed, in the past several years, the number of new helminth species of fish hosts reported from some hotspots of freshwater fish diversity such as Brazil and southeastern Asia, has been increasing rapidly (unpublished data). Often, these taxonomic studies have co-authors based in areas of lower freshwater fish diversity such as North America or Europe, indicating that experts from those areas are directing efforts toward regions of higher parasite diversity. However, other regions of relatively high fish diversity, such as equatorial Africa, have an unusually low rate of new parasite discoveries (see Jorge and Poulin, 2018). Although the same generally weak spatial match between local fish diversity and local rates of parasite species discovery also applies to marine fish, there are some encouraging exceptions (Jorge and Poulin, 2018). For example, the number of new trematodes discovered in fish from the Great Barrier Reef, Australia comes close to what we would expect from the diversity of fish species in that region, thanks to what we might call the Tom Cribb effect (Cribb et al., 2014, 2016).

Overall, the poor geographical match between parasite discovery effort and fish diversity casts doubt over some recent attempts to extrapolate global parasite biodiversity based on existing knowledge of extant helminth species (Costello, 2016). On the positive side, maps of the relative mismatch between parasite discovery and host diversity (see Jorge and Poulin, 2018) identify areas with the greatest deficit in overall effort aimed at parasite discov-

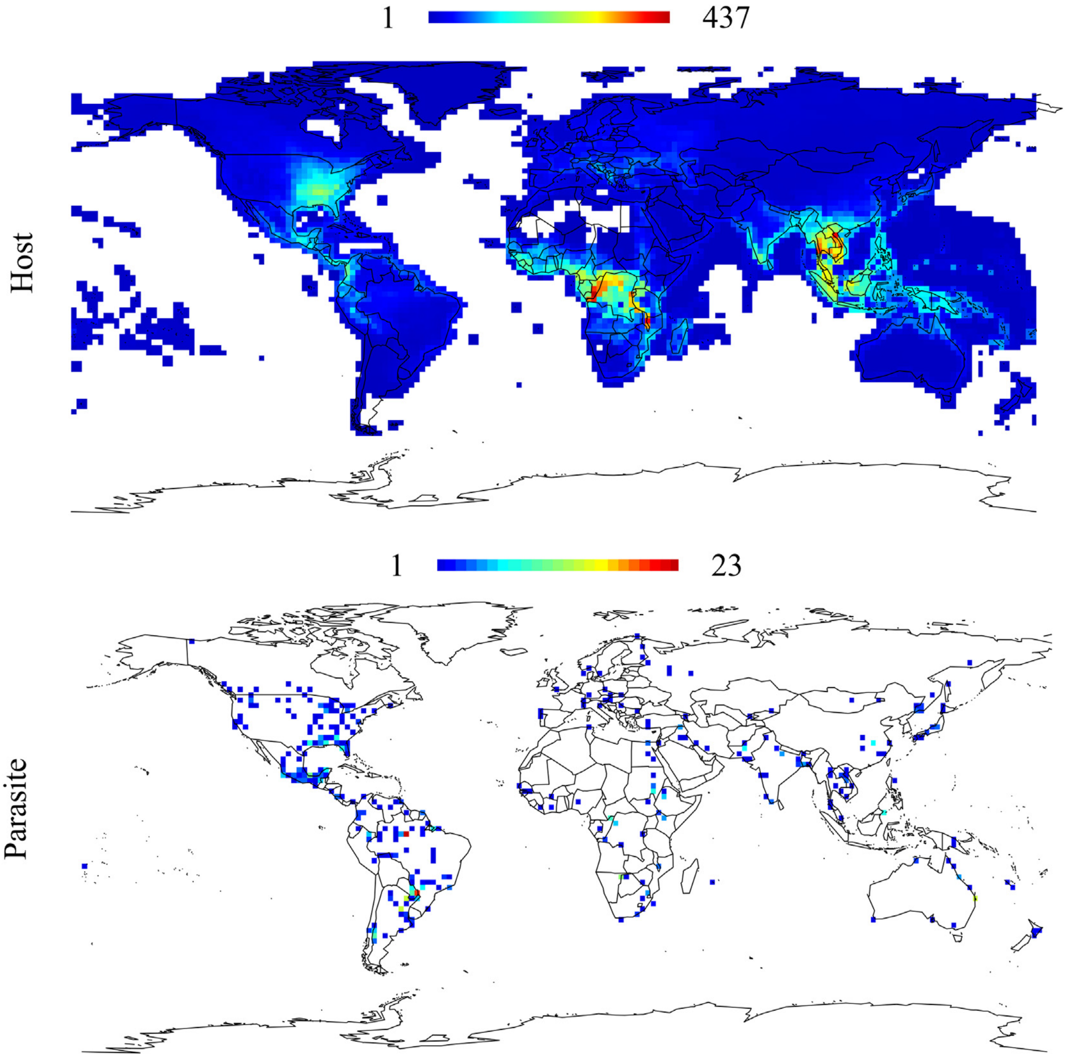

Fig. 1. Global richness maps for freshwater fish hosts and for the discoveries of their helminth parasites for the period 1970–2017. Colour gradients scale linearly with species number per cell (2° resolution). Note that the International Union for Conservation of Nature data used in the 'host' map for freshwater fishes is considered 'not comprehensive', in particular for parts of South America. Numbers of species per cell correlate positively but only weakly between the two distributional maps (*N* = 6371 cells, excluding double zeros; Spearman's correlation, rho = 0.215, *P* < 0.001). Data from Jorge and Poulin (2018).

ery and description, and these provide clear guides for a better allocation of future research effort toward parasite species prospecting.

3. Genetic research on fish parasites

Discovering new parasite species is the first step; characterising them in ways that allow clear species discrimination is the next one. Following the principles of integrative taxonomy (Dayrat, 2005; Padial et al., 2010), it is now the accepted best practise to describe new parasite species using both morphological characters and genetic data (Blasco-Costa et al., 2016; Caira, 2011; Perkins et al., 2011). Beyond taxonomy, gene sequences are now essential for other related purposes, ranging from resolving phylogenies (Olson and Tkach, 2005; Caira et al., 2014) to uncovering cryptic parasite diversity (Nadler and Pérez-Ponce de León, 2011). Here again, strategic deployment of funding and effort could streamline the process toward the full genetic characterisation of life on Earth. For instance, whereas the inventory of helminth parasites of freshwater fishes in Mexico was once thought to approach completion based on morphological species delimitation (Pérez-Ponce de León and Choudhury, 2010), the application of genetic tools has subsequently revealed a hidden diversity of parasites and rebooted the search for parasites (e.g., Pinacho-Pinacho et al., 2018).

If sequencing effort is allocated more or less in proportion to the number of parasite species requiring genetic characterisation, then a positive correlation should automatically arise between the number of parasite species in a higher taxon or in a geographical area, and the number of sequences generated for that taxon or area. However, we may expect that parasite species of medical, zoonotic or veterinary concern would receive disproportionate attention, as well as other biases due to the lack of funding or adequate facilities in certain parts of the world. The question therefore is: Is the application of molecular tools to study parasite genetic diversity deployed strategically across parasite higher taxa and across regions of the world, or focused disproportionately on certain taxa or areas?

This question has been addressed recently by Poulin et al. (2019) using two large and independent datasets on helminths of vertebrates including fish. First, data on the number of parasite species records per helminth family and per country were retrieved from the global database of host-parasite occurrences maintained by the London Natural History Museum, UK (https://www.nhm.ac.uk/research-curation/scientific-resources/taxonomy-systematics/host-parasites/database/index.jsp). These data combine information on the distribution of known parasite diversity across higher taxa and geographic regions, and information on how much effort is invested in surveys and taxonomic research on parasites of those taxa or regions. Second, data on the number of gene sequences of parasites available per helminth family and per country were extracted from the public NCBI GenBank database (https://www.ncbi.nlm.nih.gov/genbank/). This was done for the main marker genes used to characterise helminth species, investigate their population genetic structure or prospect for cryptic diversity: the cytochrome oxidase subunit 1, the 18S rRNA, and the 28S rRNA. Data on the number of gene sequences available provide a reliable estimate of the overall effort in genetic research allocated to particular helminth families or geographical regions. The relationship between the number of gene sequences versus the number of helminth records (roughly equivalent to their diversity) across all helminth families or across all geographical regions was then assessed statistically, while accounting for other confounding variables (see Poulin et al., 2019, for full analytical details).

Perhaps not surprisingly, the number of available sequences in GenBank was positively related with the number of parasite records in the London Natural History Museum database, across both helminth families and geographical regions (Poulin et al., 2019). In other words, more gene sequences have been deposited in GenBank for helminth families or geographical regions with more frequent reports of species in the literature. Therefore, generally speaking, greater effort in genetic research has been directed at higher helminth taxa or regions from which more species have been reported. However, the analyses also identified helminth families and countries that have either disproportionately more or disproportionately fewer gene sequences available than expected based on the frequency at which their species are observed and reported. As one might expect, developing countries dominate the list of regions that have received a lower effort in genetic research than warranted by the diversity of their helminth parasite fauna (Poulin et al., 2019). Helminth families of medical or veterinary relevance have received disproportionate attention in terms of genetic research. Several helminth families that use fish at some point in their life cycle (e.g. hemiurid trematodes or cystidicolid nematodes) show a clear deficit in genetic research relative to their reported diversity.

Just as with efforts to discover new parasite species, efforts to characterise them genetically are far from ideally deployed for maximal progress in parasite taxonomy or phylogenetics. This further emphasises the existence of taxonomic and geographical biases in research on parasites in general, and helminth parasites of fish in particular. The lists of helminth families and countries emerging from the analysis of Poulin et al. (2019), that show the greatest deficit in genetic research given their species richness, provide a starting point to address those biases with evidence-based investments in future research. They could be used by researchers and funders to strategically prioritise the allocation of money and effort toward understudied taxa and regions, and thereby optimise biodiversity research.

4. Fish parasite discovery across helminth taxa

Ecologists have documented that across different geographical regions, the species richness of different free-living higher taxa tends to covary spatially (e.g. Gaston, 1996; Heino, 2002; Wolters et al., 2006). In other words, regions with a high diversity of birds also tend to have high diversity of amphibians or butterflies, just as regions with a high diversity of freshwater fishes also tend to have high diversity of aquatic insects. All else being equal, the same pattern should exist for the parasites of those organisms: regions with a higher fish diversity should also have a higher known diversity of trematodes, cestodes or nematodes parasitizing those fish, relative to regions with a depauperate fish fauna. However, this will only be apparent if the same effort toward species discovery and description has been applied to all helminth taxa across different regions. It is possible, for example, that a trematode specialist sampling fish species within a particular region will find and describe many new trematode species, but either not even retrieve other taxa such as nematodes or monogeneans due to the extra time it would take, or collect them and set them aside instead of passing them on to someone with the required taxonomic expertise to describe them. This would result in a much higher known trematode richness than cestode or nematode richness for that region. If this is standard practise, we should expect a mismatch between the spatial distributions of new species discoveries and descriptions among higher helminth taxa. So, which is it? In other words, how well coordinated is the search for new parasite species of fish among workers specialising on different higher helminth taxa.

To answer this question, Poulin and Jorge (2019) used the same dataset as Jorge and Poulin (2018) on the helminth species described from vertebrate hosts in the past 50 years (see earlier). With data on a total of 757 helminth species described from freshwater fish and 1717 species described from marine fish, the numbers of new parasite species discovered from each 2° × 2° cell in a global latitude-by-longitude grid were tested for spatial congruence among trematodes, cestodes and nematodes. Significant positive spatial correlations between numbers of new species found in different helminth taxa would support a scenario of roughly equal taxonomic effort across geographical areas. In contrast, negative correlations, or no correlation at all, would point toward a lack of coordinated effort among taxonomists specialising on different helminth taxa.

The results support one scenario for freshwater fish and another for marine fish (see Poulin and Jorge, 2019, for full details). For parasites of freshwater fishes, whether with simple correlations or after controlling for spatial autocorrelation in the data, the number of species of, say, trematodes discovered per 2° × 2° cell covaried negatively with that for, say, nematodes (Fig. 2). The same was true for other pairs of higher taxa, i.e. trematodes versus cestodes, and cestodes versus nematodes (see Poulin and Jorge, 2019). This suggests that which helminth taxa get described from a certain region depends on who happens to work there. In contrast, for marine fish, although very weak, positive associations emerge between the numbers of new parasite species discovered for trematodes and cestodes, and for trematodes and nematodes, after controlling for spatial autocorrelation in the data (Fig. 2; see full analyses in Poulin and Jorge, 2019). These hint at some coordination of effort among taxonomists specialising on different helminth taxa, but a loose one only.

These findings show that local taxonomic expertise plays a huge role in determining which new helminth species get described from particular regions. This is not surprising, but it nevertheless highlights a significant lack of efficiency and an idiosyncratic approach to the global initiative to uncover and catalogue parasite diversity. In addition, at a time of growing ethical and conservation awareness (Waeber et al., 2017), the unnecessary killing of fish for parasite recovery should be avoided; we must maximise the information obtained from each death by ensuring all new helminth species are properly described, not just those that fall within the expertise of the sampler. The additional time required to extract and preserve all parasites from a fish is of course a problem for a specialist with no immediate interest in other taxa; however, through mutual exchanges of specimens, this could be compensated. There have also been coordinated discovery efforts involving multiple taxonomists, leading to the taxonomic processing of all parasite specimens recovered from local fish surveys (e.g., Justine et al., 2010, 2012). More trained taxonomists in paid, long-term

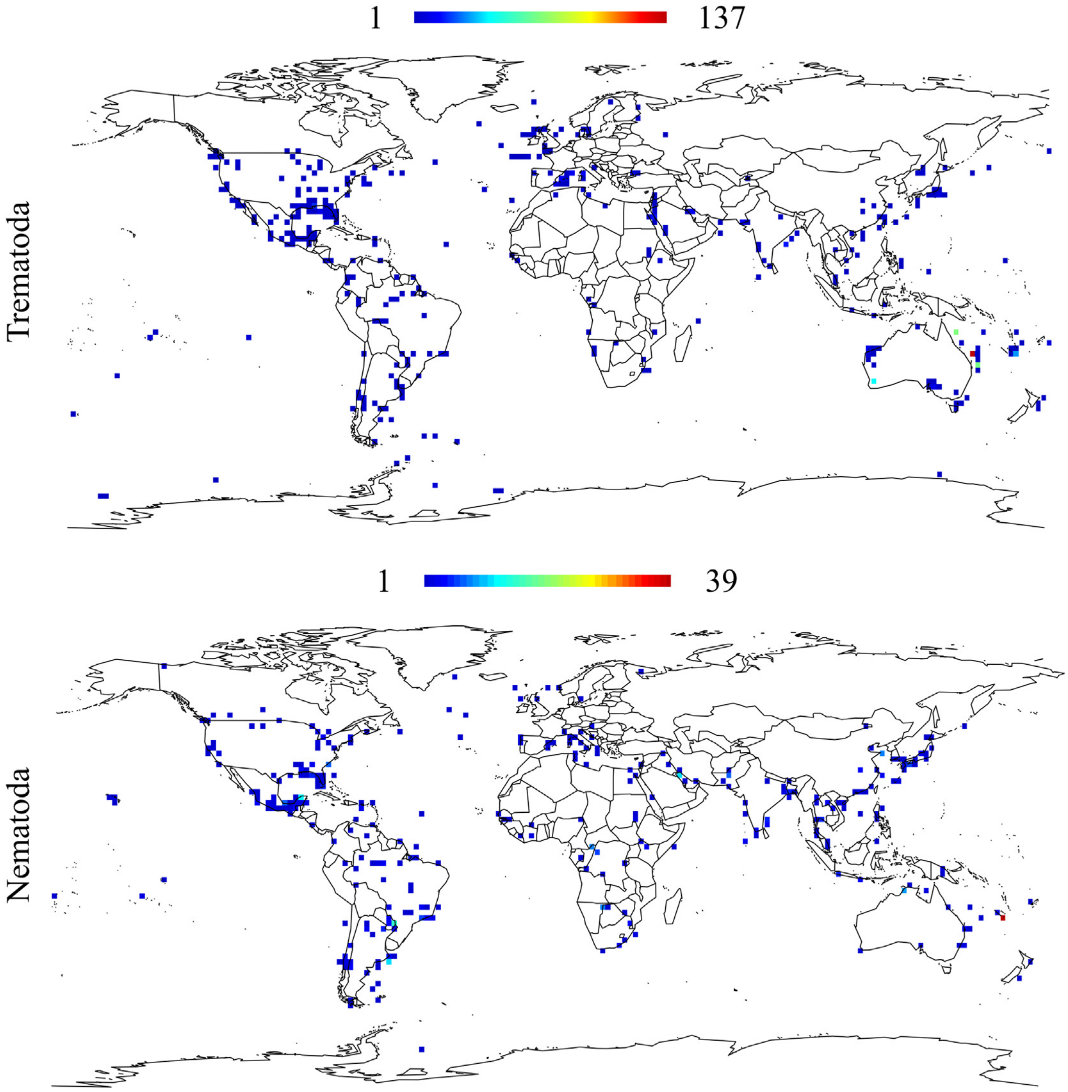

Fig. 2. Global species discovery maps for trematodes and nematodes of marine and freshwater fish hosts, for the period 1970–2017. Colour gradients scale linearly with species number per cell (2° resolution). Data from Poulin and Jorge (2019), where full analyses are also provided.

employment would greatly facilitate further coordinated efforts. Perhaps organised, evidence-based lobbying by parasitological societies toward funding agencies and research institutions would help achieve this. Additionally, taxonomic expertise should be disconnected from where the experts live, such that it can be spread more evenly across geographical areas. One way to achieve this would be to establish a public online database of helminth specimens found, preserved and shelved by workers in one part of the world, and awaiting description by qualified taxonomists based elsewhere. This would be a relatively simple step toward increasing the global efficiency of taxonomic research.

5. Temporal patterns in fish parasite discovery

Analyses of historical patterns of parasite discovery rates from a particular region often show how prolific taxonomists can almost single-handedly account for temporal peaks in new species descriptions (Beveridge and Jones, 2002; Cribb, 2004). The active research careers of these individuals are typically preceded and followed by periods of lower annual rates of new descriptions for the taxa on which they specialised. If temporal discontinuities such as these are common in parasite taxonomy on a global scale, and if focused efforts to uncover and describe parasites of particular taxa in particular regions are sporadic rather than sustained, then attempts to extrapolate total regional parasite richness from the theoretically smooth curve of cumulative numbers of known species over time are almost pointless. To further assess whether taxonomic expertise and resources are allocated optimally, we ask: are parasite discovery efforts in any geographical area consistent over time, or subject to idiosyncrasies due to the waxing and waning of highly prolific research careers?

This question was answered by Poulin and Jorge (2019) using data on the helminth species described from vertebrate hosts in the past five decades (see earlier). With data on a total of 2454 helminth species described from fish hosts (757 from freshwater fish, 1717 from marine fish), the numbers of new parasite species discovered from each 2° × 2° cell in a global latitude-by-longitude grid were tested for temporal congruence among three time periods: 1970–1985, 1986–2001, and 2002–2017. Significant positive correlations between numbers of new species found in different time periods would indicate that efforts to find and describe fish parasites in any particular region are more or less sustained over time. A lack of positive correlation would suggest that the search for new helminths in fish from given regions proceeds erratically and unpredictably over time.

For parasites of freshwater fishes, there was no evidence of positive correlations between the numbers of new helminths found per 2° × 2° cell between different time periods. In fact, these tended to be negatively correlated (see Poulin and Jorge, 2019, for full details). For marine fish, although numbers of new parasites described per cell in the oldest time period (1970–1985) correlated negatively with those found in the more recent periods, numbers of species found in the 1986–2001 period showed a positive, but very weak, association with numbers found in the 2002–2017 period, after correcting for spatial autocorrelation in the data (Poulin and Jorge, 2019). Thus, if many new helminths were described from marine fish in a particular region between 1986 and 2001, there was a slight tendency for many species to be also described from that region in the following 15 years.

Given the lack of correlations for freshwater fish parasites, and the very weak pattern observed for those of marine fish, we conclude that rates of regional species discovery are generally inconsistent over time. How many new helminth species get described in a particular region, and from what higher group, depends on who is working in that region. This can result in peaks in species discovery during certain periods, such as the high rates of trematodes described from Great Barrier Reef fishes in the past quarter of a century, i.e. the Tom Cribb effect (Cribb et al., 2014, 2016). As taxonomists with expertise on particular groups retire and get replaced (if they are replaced at all) by researchers with other expertise, the discovery and characterization of new helminth species in any given region of the world is patchy and discontinuous over time. As we suggested above, one solution would be to homogenise the taxonomic effort across all regions, by disconnecting expertise on certain taxa from where taxonomists live and tend to focus their efforts. This would ensure not only that our discovery of the Earth's parasite diversity progresses consistently over time in all regions, but also that taxonomic expertise gets allocated more strategically and not only where its bearer resides.

6. Quality of new species descriptions over time

Data on the rates of new species discoveries capture the quantity of species descriptions, not their quality, which must also be examined as part of an analysis of the state of parasite taxonomy. Over time, new tools have become available to parasite taxonomists, and these should allow greater sophistication in species description and greater rigour in species discrimination. Technological advances in molecular genetics and the growing availability of scanning electron microscopy open new windows into differences among putative species. How well have fish parasite taxonomists kept up with these advances? Has the quality of taxonomic descriptions of new helminth species improved over time, with the incorporation of new tools to characterise species?

Poulin and Presswell (2016) compiled data from new helminth descriptions published between 1980 and 2014 in two key journals with a strong focus on parasite taxonomy, including 1147 helminth species described from fish hosts (550 trematodes, 406 cestodes, and 191 nematodes). For each new species described, they scored the description with respect to several metrics of quality; here, we only focus on the number of morphological traits measured, the number of taxa to which the newly described species was compared, the number of separate line drawings provided, the number of light microscope images provided, how many scanning electron micrographs (SEMs) were provided, whether gene sequence data were provided, and whether ecological data on prevalence or intensity of infection were provided. These quality metrics were then (i) correlated against year of publication, to see whether the quality of descriptions has improved over time, and whether it has done so equally for trematodes, cestodes and nematodes; and (ii) correlated with the number of authors per description, to see whether collaborative efforts lead to better species descriptions. Only a simplified overview of the results is given here; see Poulin and Presswell (2016) for a fuller account of these analyses.

In general, the quality of descriptions of new helminth species found in fish has increased over time, but not always the same way for different helminth groups. For instance, the number of line drawings provided for each new species has not increased over time in any of the three higher groups, whereas the number of taxa to which a newly described species is compared has risen over time in all groups. More interestingly, the number of morphological traits measured for each new species has increased over time for cestodes and trematodes but not for nematodes (Fig. 3); the number of light microscope images provided has increased only for cestodes; and the number of SEMs provided has increased over time for cestodes and nematodes but not for trematodes (Fig. 3). There are several possible explanations for these differences in

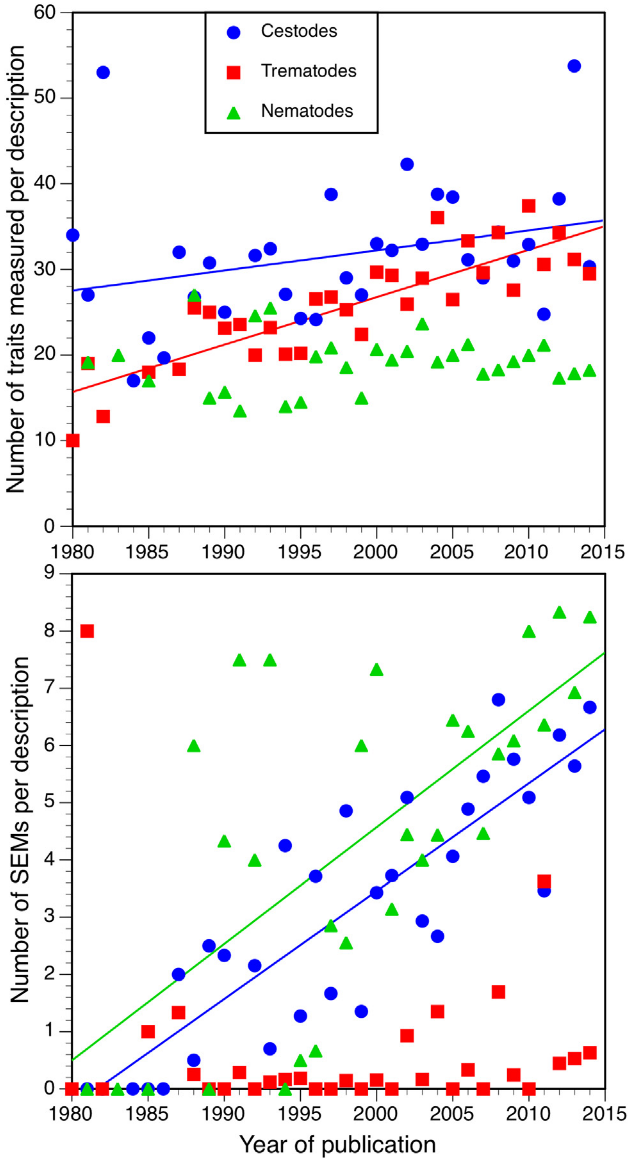

Fig. 3. Temporal trends (1980–2014) in two measures of taxonomic quality, the number of morphological traits measured and the number of scanning electron micrographs (SEMs) included, in species descriptions of cestodes (N = 406), trematodes (N = 550), and nematodes (N = 191) found in fish hosts. Data are annual mean numbers per description. Trend lines are shown only for significant relationships ($P < 0.001$). Data from Poulin and Presswell (2016).

how taxonomic quality of species descriptions has improved over time among the three groups of helminths. One possibility is that there may exist 'cultural' differences among taxonomists specialising on different taxa of helminths parasitic in fish. For example, fine external structures, such as tegumental spines, are not widely used as diagnostic species characters for trematodes, and therefore the limited use of SEMs may remain acceptable for descriptions of new trematodes, while their use for cestodes and nematodes has consistently increased over the past decades (Fig. 3). Whatever the reasons for these patterns, the bottom line is that although recent species descriptions generally score higher for most quality metrics, the improvement has been unequal among higher helminth taxa. Taxonomists studying fish parasites are not consistently making use of the full arsenal of new technologies available today for a comprehensive and multi-faceted characterization of new species.

This may reflect the relative isolation in which some taxonomists are still working. Indeed, there is evidence that collaborative efforts lead to better species descriptions. Across all years pooled, for the 1147 helminth species described from fish hosts in the dataset, a greater number of authors per species description was associated with a higher probability that SEMs are included, a higher probability that gene sequence data are provided, and to a lesser extent also a higher probability that ecological data are provided (results not shown; see Poulin and Presswell, 2016, for analysis of full dataset). The mean number of authors per species description has increased steadily over the past three decades for helminth parasites of fish hosts (Fig. 4) and those of vertebrates in general (Poulin and Presswell, 2016). Some commentators interpreted the latter trend as evidence that the number of active taxonomists is increasing (Costello et al., 2013). However, the connection between the number of authors and taxonomic quality of descriptions suggests instead that taxonomists are increasingly teaming up with experts from other disciplines, such as electron microscopy or molecular genetics, to produce more thorough and informative characterizations of new parasite species.

Overall, the data indicate that not only has the quantity of new parasite species described annually grown in recent years (Cribb et al., 2014; Poulin, 2014; Poulin and Presswell, 2016), but generally also the quality of those descriptions, thanks to an expanding toolkit to characterise species and greater collaboration among experts. The challenge now is to make sure that these trends apply more equally to all helminth taxa (see Fig. 3), to achieve the highest possible quality across all of fish parasite taxonomy.

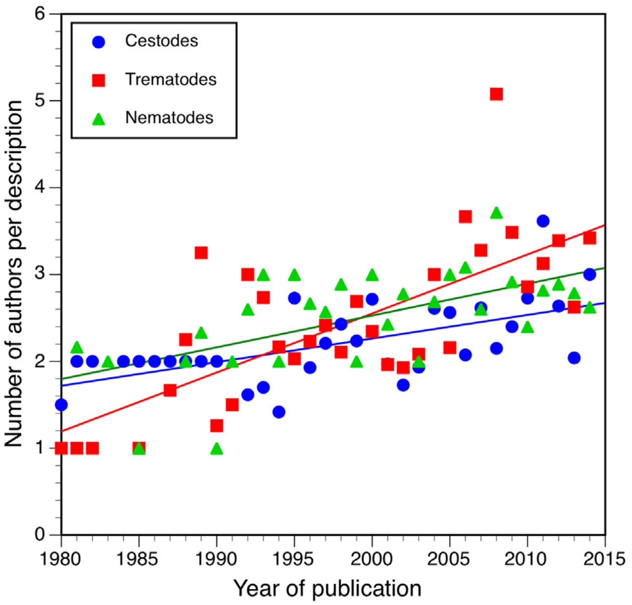

Fig. 4. Temporal trends (1980–2014) in the number of authors per species description of cestodes ($N = 406$), trematodes ($N = 550$), and nematodes ($N = 191$) found in fish hosts. Data are annual mean numbers per description. Trend lines indicate significant relationships ($P < 0.005$). Data from Poulin and Presswell (2016).

7. Taxonomy of helminths with complex life cycles

Another important factor to consider is how taxonomists deal with parasites with complex, multi-host life cycles. New helminth species have always been and still are described based on the fine details of how they look, i.e. based on their phenotype. Although somewhat influenced by external factors such as the host environment, a parasite's phenotype is mostly determined by its genotype. By convention, and also because the adult stage often presents a greater range of morphological traits useful for species discrimination, new helminth species are described based on the adult form. Yet the same genotype encodes instructions for all life stages, each presenting its own morphology. Natural selection does not act independently on each life stage; instead, the whole life cycle represents an integrated unit of selection (Benesh, 2016). Ideally, and again in accordance with the spirit and principles of integrative taxonomy (Dayrat, 2005), species descriptions should cover all life stages. This may not be practical because it would require resolving the entire life cycle and identifying all successive hosts of each new species, but it could serve as the lofty goal every new species description aims to achieve.

Resolving the life cycle of helminth species, either upon description or later, has the added benefits of strengthening the already huge contributions made by taxonomists to fish parasite ecology. For example, the inclusion of parasites into analysis of food webs requires knowledge of their life cycles if their transmission routes are to be mapped accurately onto food chains (Sukhdeo, 2010; Dunne et al., 2013; Rossiter, 2013). No solid conclusions can be drawn regarding the impact of parasites on a food web's stability or resilience without life cycle resolution. So, has the need to resolve life cycles impacted parasite taxonomy? Have taxonomic descriptions been moving away from a focus on the adult stage only toward attempts to characterise the full life cycle of newly discovered helminth species?

Again using the 1147 helminth species described from fish hosts taken from the dataset of Poulin and Presswell (2016), it is clear that information on life stages other than the adult worm in its fish definitive host, i.e. juvenile or larval stages in intermediate hosts, have rarely been, and continue to rarely be, included in new species descriptions (Fig. 5). The extra efforts required to find, describe and link other life stages with the adult stage probably represent the main obstacle toward the more frequent inclusion of full life cycle information in species descriptions. There are no easy solutions to this problem (but see Blasco-Costa and Poulin, 2017).

Therefore, for the foreseeable future, helminth species will continue to be described based only on the adult form, i.e. only on a single morphological 'snapshot' of the full ontogenetic cycle. This is a pragmatic approach, and yet the aim to achieve whole-cycle descriptions should remain on the agenda of parasite taxonomists, if only as an elusive ideal.

8. Fish parasite taxonomy in the age of microbiomes

There are new challenges on the horizon for fish parasite taxonomists. Recent research into the microbiomes of animals, i.e. the bacteria and other microbes living more or less permanently within animal cells and tissues (Bordenstein and Theis, 2015),

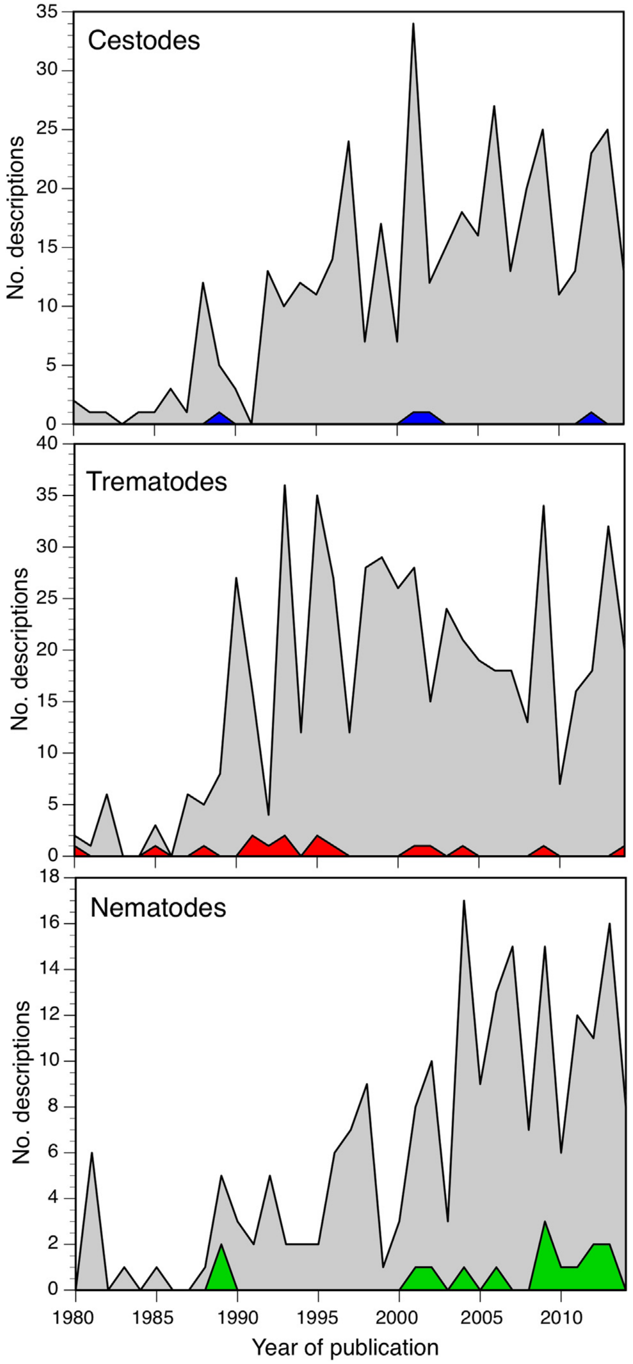

Fig. 5. Number of species descriptions per year (shaded area) and a subset of those that provided morphological data on at least one larval or juvenile stage other than the egg and identified at least one intermediate host (coloured area), for species of cestodes ($N = 406$), trematodes ($N = 550$), and nematodes ($N = 191$) found in fish hosts between 1980 and 2014. Data from Poulin and Presswell (2016).

opens up new challenges for parasite taxonomy and systematics. At present, we distinguish between closely related and morphologically similar parasite species using DNA sequences (Nadler and Pérez-Ponce de León, 2011; Blasco-Costa et al., 2016). Specimens are considered to represent different species if they differ by some percentage of base pairs for certain gene markers in the parasite's genome. Increasingly, however, biologists are recognising that a metazoan, whether it is a vertebrate or something much smaller, cannot easily be separated from the vast community of microbes it harbours, and that the animal and its microbes should be considered holistically as a single functional unit, called the holobiont (Bordenstein and Theis, 2015). The set of genes that is expressed and that can affect the phenotype of the animal come not only from the animal's genome, but also from its microbiome, with their collective genomes forming a hologenome (Zilber-Rosenberg and Rosenberg, 2008; Bordenstein and Theis, 2015).

Several helminths and other parasites have been shown to harbour their own microbiome, i.e. a set of bacteria distinct from those found in their host or the external environment, many of which are intracellular symbionts of the parasite, most of them likely transmitted vertically down parasite generations (Vaughan et al., 2012; Dheilly, 2014; Dheilly et al., 2015; Ben-Yosef et al., 2017; Sinnathamby et al., 2018). Efforts are underway to expand our knowledge of parasite microbiomes, and their role in host-parasite interactions (Dheilly et al., 2017). While not as well integrated with the parasite as are mitochondria, they nonetheless form (to some extent) a permanent, heritable partnership with it. However, even if the parasite + microbes unit is accepted as a single functional entity, i.e. a holobiont, all comparable holobionts within a host population cannot be considered as a 'holospecies'. The microbiome is probably too dynamic temporally and too variable geographically for that. Having said this, imagine that fish from two distant lakes are sampled, and that morphologically identical trematodes are recovered from their tissues. Sequences from the standard markers, such as the CO1 or the 28S rDNA genes, indicate that they diverge by less than 1% base pair difference, confirming that they represent a single species with little genetic structure. However, what if they harboured very different core microbiomes? Differences in microbiome composition between conspecific parasites from different populations may translate into important functional differences. Due to their different hologenomes, these conspecific trematodes from different populations may have distinct developmental schedules, or induce different immune responses or pathology in their hosts. They would be taxonomically the same, but functionally different.

We envisage that integrative taxonomy and systematics might need to take another step forward toward the more comprehensive characterisation of parasite species that includes their hitchhiking symbionts. In addition to morphological and genetic data, microbiome characterisation would add a new layer of information about a species. Analyses of genetic structure and phylogeography based on the traditional gene markers would benefit if they were complemented by comparisons of microbiome composition between samples, to document hologenome and possible functional divergence in addition to genetic divergence. This provocative idea may sound ridiculous and impractical. However, as technology continues to develop, as computer power and speed increase, and as multi-genome sequencing becomes simpler and cheaper, these are some of the issues that parasite taxonomists and systematists will have to address.

9. Looking ahead

This brief overview of the state of fish parasite discovery, taxonomy and systematics finds that this research area is doing relatively well. The discovery of new parasite species, their description, genetic characterisation, and placement into a phylogenetic context are core activities of fish parasitologists. More new helminth parasite species are being found and described now than ever before, the network of collaborating researchers involved in finding and characterising species seems to be growing, and the overall quality of those species descriptions is rising constantly. However, we also identify some areas where some changes could improve efficiency and progress, and for these we offer some concrete solutions:

- Focus greater species discovery efforts toward regions, now well identified, where there is a clear deficit between the helminth richness expected based on host richness and that currently known.
- Aim at the genetic characterisation of helminths from higher taxa or geographic regions, again now identified with empirical data, for which efforts in sequencing specimens are disproportionally low given their known diversity.
- Create an online public database of undescribed helminth specimens, with metadata on their host and location of origin, available to any specialists, in order not to waste collecting efforts and to disconnect taxonomic expertise from where the experts live. The costs of shipping specimens across the world pales in comparison to the cost of sampling fish de novo to obtain more specimens.
- Establish standard quality criteria for new species descriptions, specifying what information is desired (light and electron microscopy, ecological data, gene sequences, life cycle data), to ensure comparable quality across helminth taxa and drive further improvements in taxonomic quality.

These simple steps could serve to maximise returns per unit of effort toward finding and describing new helminths from fish, as well as ensuring that the quality of species descriptions increases uniformly across all helminth taxa. Finally, we may need to revisit how we characterise parasite species in light of growing knowledge of parasite microbiomes and what roles they play in parasite biology. The species concept has been debated vigorously (de Queiroz, 2007) and there is no need to rehash old arguments. However, if fish parasite taxonomists are to provide the foundation for research into the impact of parasites in fisheries and aquaculture, we may need to focus on the whole functional unit represented by the holobiont. Spatial variation in the hologenome (parasite genome + all the genomes of its symbiotic microbes) across the geographical range of a parasite species may have more relevance to its virulence or specificity, than the phylogeographic structure revealed by marker genes in the parasite's genome that are currently used to identify cryptic species. The challenges ahead augur exciting times for parasite taxonomy as it adapts to retain its central place in fish parasitology and meet the new demands of the changing research landscape.

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