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Invited Review

# Parasite biodiversity revisited: frontiers and constraints

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ABSTRACT

Although parasites are widely touted as representing a large fraction of the Earth's total biodiversity, several questions remain about the magnitude of parasite diversity, our ability to discover it all and how it varies among host taxa or areas of the world. This review addresses four topical issues about parasite diversity. First, we cannot currently estimate how many parasite species there are on Earth with any accuracy, either in relative or absolute terms. Species discovery rates show no sign of slowing down and cryptic parasite species complicate matters further, rendering extrapolation methods useless. Further, expert opinion, which is also used as a means to estimate parasite diversity, is shown here to be prone to serious biases. Second, it seems likely that we may soon not have enough parasite taxonomists to keep up with the description of new species, as taxonomic expertise appears to be limited to a few individuals in the latter stages of their career. Third, we have made great strides toward explaining variation in parasite species richness among host species, by identifying basic host properties that are universal predictors of parasite richness, whatever the type of hosts or parasites. Fourth, in a geographical context, the main driver of variation in parasite species richness across different areas is simply local host species richness; as a consequence, patterns in the spatial variation of parasite species richness tend to match those already well-documented for free-living species. The real value of obtaining good estimates of global parasite diversity is questionable. Instead, our efforts should be focused on ensuring that we maintain sufficient taxonomic resources to keep up with species discovery, and apply what we know of the variation in parasite species richness among host species or across geographical areas to contribute to areas of concern in the ecology of health and in conservation biology.



## 1. Introduction

Over the years, several authors have advanced estimates of relative parasite biodiversity according to which parasites account for anywhere from one-third to over half of the species on Earth (Price, 1980; Windsor, 1998; Poulin and Morand, 2000, 2004; de Meeûs and Renaud, 2002). These estimates are based on a combination of numerical methods to extrapolate total diversity, expert opinion and guesswork. Despite the obvious uncertainty surrounding such estimates, it has become common to refer to them in the opening sentences of research articles or funding proposals, to justify a particular line of research or to emphasise the general importance of parasitism in natural systems. But how much do we really know about parasite diversity? How far along are we toward discovering all of it? Are we even capable of describing new species at a sufficient rate to aim at a full catalogue of parasite species? And are we in a position to not only venture estimates of the total magnitude of parasite diversity, but also to explain its distribution among host taxa or geographical areas?

This review summarises our current understanding of key aspects of parasite diversity and its discovery, by addressing four basic questions that have been the driving forces behind most research in this area over the past few decades. First, how many parasite species are there? I look at the methods used to answer that question and conclude that perhaps we should not even bother to try, at least not for several years. Second, are there enough parasite taxonomists to keep up with the description of new species? The available human resources must match the scale of the task ahead if we are to successfully catalogue most of parasite diversity and I examine whether or not this appears to be the case. Third, how does parasite diversity vary across host species? Not only does this matter for any attempt to estimate total parasite diversity, but it also has serious implications for conservation biology and biodiversity management and I discuss recent advances in this area. Fourth, how does parasite diversity vary in geographical space? This question is also of central importance for the preservation of biodiversity and should be considered any time protected areas

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of high diversity are established. In what follows, each section tackles one question in the light of recent evidence and arguments.

## 2. How many parasite species are there?

There would be little point in trying to estimate the diversity of any group of organisms shortly after the first few species are found and described. We need the inventory to be well under way before we can make projections of where it will stop. Two lines of evidence could indicate that for some, if not for all, groups of parasites, we probably know enough right now to attempt predictions of total diversity. The first line of evidence comes from an examination of the relationship between the body size of known species and their date of description. Typically, for small-bodied taxa such as insects, recently-described species tend to be smaller than those known for a long time, simply because the dimensions of a species affect the time and effort it will take for it to be discovered (Gaston, 1991; Gaston et al., 1995). If there is no negative relationship between body size and year of description among known species in a given taxon, we may infer that it is still poorly known, since we are not left only with the smallest species to find and describe. For several groups of metazoan parasites (monogeneans, digeneans, nematodes, copepods), we do observe a significant decrease in the body sizes of newly-described species over time (Poulin, 1996, 2002; Poulin and Morand, 2004). In some cases, this trend applies only to a subset of parasite species infecting a certain type of hosts; for instance, a negative correlation between body size and year of description was found for trematodes parasitic in mammals but not for those parasitic in either birds or fish, and it was found for copepods parasitic on fish but not for those parasitic in invertebrates (Poulin, 1996). Nevertheless, although our inventories of parasites are more complete for certain groups than others, overall these results suggest that we are well advanced in our discovery of parasite biodiversity.

The second line of evidence that could indicate that we may have found sufficient numbers of species to attempt predictions of total diversity would be a decline in the rate of species discovery. For a given and constant effort aimed at finding and describing new species, a slowing down in the rise of the cumulative number of known species over time would suggest that the remaining species are becoming more difficult to find, and therefore that we already found a substantial proportion of total diversity. The problem, of course, is that the effort and resources directed at finding and describing new species are not constant over time; they vary for a range of reasons. For example, the cumulative numbers of cestodes known from Australian vertebrates and of digeneans known from Australian fishes, instead of displaying a smooth (though incomplete) sigmoid curve over time, have both shown bumps or sharp rises that can each be attributed to the taxonomic activities of a single prolific individual and his research team (Beveridge and Jones, 2002; Cribb, 2004). Ignoring these idiosyncrasies, for most taxa of parasites, either the cumulative curve of known species is still rising steeply, or it is only beginning to show a slowing down (Poulin and Morand, 2004; Appeltans et al., 2012), suggesting that we still have some way to go before reaching an advanced stage in our inventory.

Many more issues plague our knowledge of parasite diversity. For example, many named species are probably invalid taxa, synonymous with species described earlier. Our patchy knowledge of parasite diversity is further compounded by the fact that our ignorance is geographically biased: we know disproportionately much less about parasites in the tropics than at higher latitudes (e.g., Lim, 1998). However, the biggest current concern with respect to our knowledge of parasite diversity arises from methodological advances. The now widespread application of molecular tools to the study of parasite biodiversity has opened, literally, a 'can of cryptic worms', with cryptic species popping up everywhere (Nadler and Pérez-Ponce de León, 2011). Cryptic species are, simply put, genetically distinct species that look similar morphologically, at least when we do not suspect their existence. The harder researchers look for cryptic parasite species, the more they find (Poulin, 2011). The discovery of cryptic species also affects estimates of host specificity, which is also relevant for estimates of parasite diversity (see below). In an increasing number of cases, what was once thought to be a single parasite species infecting a few host species turns out to represent a complex of cryptic species each specific to a single host species (Poulin and Keeney, 2008). Because their discovery depends almost entirely on analysis of gene sequences, the rate at which cryptic species are found will remain low until the widespread application of molecular methods in parasite systematics.

Thus any attempt at estimating total parasite biodiversity is possibly flawed by insufficient current knowledge. Keeping this in mind, we can nevertheless look at what these attempts have yielded. Some estimation methods commonly used in parasite ecology, such as non-parametric estimation (Poulin, 1998; Walther and Morand, 1998) or species accumulation curve as a function of sampling effort (Dove and Cribb, 2006), are designed for small-scale community-level studies and not for global assessments. Perhaps the most common approach for whole-taxon biodiversity estimation consists in taking the cumulative curves of known species over time and extrapolating their asymptote, which corresponds to total species richness (Dolphin and Quicke, 2001; Bebber et al., 2007). However, as stated above, rates of species discovery are currently near their maximum or still increasing for many parasite taxa, and it is not possible to estimate reliably the total number of species from a curve that has not started to decelerate (see Bebber et al., 2007). For instance, in their recent attempt at estimating the global species richness of all free-living and parasitic taxa in the oceans, Appeltans et al. (2012) relied on extrapolation from cumulative curves of known species as much as possible, but could not do so for taxa in which the rate of species discovery is still rising. This was the case for several parasite taxa, including the Cestoda, Digenea and Acanthocephala; for those groups, estimates based on expert opinion had to be used instead.

An alternative approach, inspired from the studies of Erwin (1982) and Ødegaard (2000) on arthropods, consists in applying a simple equation to estimate the global species richness separately for different groups of parasites. The equation is simply: (number of host species) * (mean number of parasite species per host species)/(host specificity, or mean number of host species used per parasite species). If we restrict this approach to groups of hosts whose diversity is relatively well known, such as the vertebrates, then we can restrict the margin of error surrounding the estimate. Using this approach, Poulin and Morand (2004) estimated that there should be at least 77,000 species of endohelminths (digeneans, cestodes, nematodes and acanthocephalans) parasitising the approximately 45,000 known species of vertebrates. This seems like a conservative estimate compared with others based on a similar methodology. For example, Dobson et al. (2008) made a rough correction for cryptic species, based mostly on their expert opinion of the existing literature on cryptic parasites, and pushed that figure up to 300,000 endohelminth species in vertebrates. For digeneans alone, Cribb et al. (2002) used the same equation for the Australian fish fauna and then used a simple extrapolation tweaked by expert opinion to estimate total digenean species richness in all fish species: their estimate was 25,000–50,000 species, compared with the 6000 or so estimated by Poulin and Morand (2004) for the same group. Clearly, this method is only as good as the original numbers that go into the equation; as long as we lack robust values for host species richness,