



## SYMPOSIUM

### Parasite Rates of Discovery, Global Species Richness and Host Specificity

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**Synopsis** If every metazoan species has at least one host-specific parasite, as several local scale studies have suggested, then half of all species could be parasites. However, host specificity varies significantly depending on host phylogeny, body size, habitat, and geographic distribution. The best studied hosts tend to be vertebrates, larger animals, and/or widespread, and thus have a higher number of parasites and host-specific parasites. Thus, host specificity for these well-known taxa cannot be simply extrapolated to other taxa, notably invertebrates, small sized, and more endemic species, which comprise the major portion of yet to be discovered species. At present, parasites of animals comprise about 5% of named species. This article analyzed the rate of description of several largely parasitic taxa within crustaceans (copepods, amphipods, isopods, pentastomids, cirripeds), marine helminths (nematodes, acanthocephalans, flukes), gastropod molluscs, insects (ticks, fleas, biting flies, strepsipterans), and microsporidia. The period of highest discovery has been most recent for the marine helminths and microsporids. The number of people describing parasites has been increasing since the 1960s, as it has for all other taxa. However, the number of species being described per decade relative to the number of authors has been decreasing except for the helminths. The results indicate that more than half of all parasites have been described, and two-thirds of host taxa, although the proportion varies between taxa. It is highly unlikely that the number of named species of parasites will ever approach that of their hosts. This contrast between the proportion that parasites comprise of local and global faunas suggests that parasites are less host specific and more widespread than local scale studies suggest.

### Introduction

For thousands of years people have been naming species because they need to communicate information about species they consider important, whether as food, pests, or other reasons. The number of named species is a measure of how much we know about biodiversity. If science has documented only a small fraction of all species on Earth then current knowledge is a poor sample for estimating the effects of climate change and other human impacts on biodiversity (Costello 2015). Climate change is re-shuffling the geographic distributions of species (e.g., Burrows et al. 2011, 2014; Poloczanska et al. 2013; Bates et al. 2014a, b; Stuart-Smith et al. 2015; Sunday et al. 2015; Basher and Costello 2016; Molinos et al. 2016). This will include both parasites and their hosts. If parasites are highly host specific then their response to climate change may reflect that of their

hosts. However, if not so host specific, then parasites may have more flexibility in responding to climate change (Marcogliese 2016), which may provide new host opportunities for them. This article reviews difficulties in determining host specificity of parasites and places it in the context of how many parasite species have been described, and have yet to be discovered.

Increasing evidence indicates that most species on Earth have already been named and virtually all will be this century because of increasing research effort (Costello et al. 2013c). Recent analyses of current knowledge of species richness on Earth show that the number of people describing new species to science has been increasing at a faster rate than the number of new species (Costello et al. 2012, 2013a). This is not explained by the recent trend

for more than one or two authors to co-author a species name, is the case if all or only first authors are counted; and the proportion of authors who name only one or most species has been constant for the past century indicating no change in the proportion of part-time and full-time taxonomists (Costello et al. 2013a, 2014a, 2014b). The increase in number of taxonomic authors has been greater in Asia and South America, and there has been an increase in taxonomic publications in all major geographic regions (Costello et al. 2013a). Thus, two lines of evidence, numbers of authors of new species and publications, indicate increased taxonomic effort since the 1960s, as with other areas of science. That the relative catch of new species per taxonomist has been decreasing since around 1911 (Costello et al. 2012) suggests most species have been discovered. However, the proportion varies between taxa.

Biogeography is critical in understanding global species richness. Examples of high local species richness (alpha diversity) may not translate to high global species richness (gamma diversity) if those species are very widespread (i.e., low beta diversity). Thus, the most microscopic species are not as species rich as once surmised because they are more widespread than macroscopic species (Costello et al. 2013b). Thus, estimates of millions of species of fungi and nematodes (Appeltans et al. 2012; Fisher et al. 2015) are implausible (Costello 2015). However, parasites may present a different situation. If every host has several unique parasite species, then parasites should outnumber their hosts (Walther et al. 1995; May 1988; 1994). Based on local estimates of parasite diversity, several authors have proposed that a far smaller proportion of parasites have been named than their hosts (reviewed by Rohde 2002, 2016). Some have estimated that there may be hundreds of thousands of helminth parasites alone (Dobson et al. 2008, Poulin 2014). This article reviews the number of described species of parasites and provides revised estimates of how many may exist. It updates previous estimates for helminths (Hugot et al. 2001) and all parasites (Poulin 2008).

A Russian doll pattern of biological commensalism could suggest that a habitat forming species, such as a coral or large seaweed, may provide a home for several species, each of which may have its own commensal species, including parasites. A host may provide habitat for external, internal, and intracellular eukaryote and prokaryote parasites and diseases. As parasites evolve to maximize transmission between hosts, colonize new hosts, and/or survive host immune defences, they may become more host-specific through adaptation or population isolation on their

new host. Thus, we might expect high host specificity and at least as many parasite as host species. Previous studies stated that parasites comprise half of all species on Earth reviewed by Thomas et al. 2005; Poulin 2014). At present, the number of parasite species may be greatly underestimated because their rate of discovery probably lags behind that of host species. This article plots the rate of description of a range of parasite taxa, the number of authors involved, and the relative number of species per author per decade. These patterns provide the basis for considering whether there will be as many parasites as host species being named, and discussion of the problems in the use of host specificity as an indicator of species richness. It also provides new estimates of how many parasite species are named and exist.

## Methods

The 37,000 species examined here included marine, freshwater and terrestrial ectoparasites and endoparasites (Table 1). The nature of the host relationship is often poorly known, and some may be considered more commensal than parasitic in the literature, such as leucothoid amphipods which live inside the ventilation passages of sponges and tunicates, and hyperid amphipods which inhabit gelatinous zooplankton. A comprehensive analysis of all parasite taxa is not attempted and data are limited to those global lists published in the World Register of Marine Species (WoRMS) (Boxshall et al. 2016) which includes non-marine relatives of some taxa (Costello et al. 2013d), and from the Catalogue of Life for the dominantly terrestrial taxa (Roskov et al. 2016). No taxa can be considered complete considering the state of taxonomic knowledge (Costello et al. 2013a). Not all species in the analyzed taxa may be parasitic and parasitic species occur in taxa not analyzed here (Table 2).

The taxa were selected on the basis that most of their species are probably parasitic. The over 100,000 species of parasitoids (mainly hymenoptera wasps) were excluded because they kill their host and are thus predators. The Nematomorpha horsehair worms are also parasitoids because they kill their terrestrial invertebrate hosts, while the adults are free-living in freshwater and comprise 355 species (Schmidt-Rhaesa 2016). Phytophagous insects (e.g., aphids, scale insects, plant lice bugs), mites, and other animals (e.g., mammals) that feed on (but do not kill) plants were excluded because they can be considered herbivores. Thus, here parasite taxa are those in which most species parasitize animal hosts. For the purpose of presentation, the taxa were

**Table 1** The number of species in the taxa used in this analysis. The year in which 10% and 50% of these species had been named is shown as an indicator of the rate of discovery. The five lowest and highest years are in *italics* and **bold**, respectively.

	Common name	Number of species	10%	50%	Source
<b>Crustaceans</b>		<b>4390</b>			
Amphipoda (Hyperidea, Cymidae, Leucothoidae)	Pelagic and leucothoid amphipods, whale lice	509	1868	<i>1901</i>	Horton et al. (2015), De Broyer (2015), Horton and De Broyer (2013)
Isopoda (Gnathiidae, Bopyridae, Cymothoida)	Fish lice	1259	1880	1953	Boyko et al. (2008)
Copepoda, Siphonostomatoida	Copepod parasites	2244	1865	1959	Boxshall (2015a)
Rhizocephala	Parasitic barnacles	240	1872	1933	Boyko and Boxshall (2016)
Pentastomida	Tongue worms	138	1853	1961	Poore (2015)
<b>Molluscs, gastropods</b>		<b>4705</b>			
Pyramidellidae	Pyramid shells	3037	1844	1917	Bouchet (2015)
Eulimidae	parasitic snails	861	1860	1915	Marshall and Bouchet (2015)
Epitoniidae	Wentletrap (staircase) snails	807	1861	1931	Gofas (2015)
<b>Terrestrial</b>		<b>5552</b>			
Ixodidae	Ticks	869	1873	1940	Nijhof et al. (2016)
Siphonaptera	Fleas	2891	1905	1949	Medvedev et al. (2016)
Strepsiptera	Twisted-wing parasites	609	1909	1964	Kathirithamby (2016)
Microsporidia	Parasitic protist fungi	1183	<b>1919</b>	<b>1977</b>	Kirk (2016)
<b>Diptera</b>		<b>16,609</b>	1901	1954	Pape and Thompson (2016)
Ceratopogonidae	Biting midges	5639	<b>1915</b>	1962	
Culicidae	Mosquitos	3684	1903	1940	
Tabanoidea	Horse flies	4406	1848	1931	
Hippoboscidae	Louse flies	778	1878	1959	
Simuliidae	Black flies	2102	<b>1925</b>	1969	
<b>Helminths (mostly marine)</b>		<b>5528</b>			
Nematoda, Spirurina	Round worms	462	1846	1957	Vanaverbeke (2015)
Hirudinea	Leeches	161	1859	1939	Kolb (2015)
Cestoda	Tapeworms	1785	1863	1969	Artois (2015)
Acanthocephala	Spiny-headed worms	472	1901	<b>1972</b>	Gibson (2015)
Digenea	Flukes	1644	<b>1911</b>	<b>1970</b>	Cribb and Gibson (2015)
Monogenea	Parasitic flatworms	1004	<b>1928</b>	<b>1973</b>	Gibson and Artois (2015)

grouped into the primarily marine helminths, crustacean, and mollusc parasites with over 14,600 species, about 11,500 terrestrial insect and protozoan taxa, and 16,600 flies (Table 1).

The number of unaccepted species names, such as synonyms, exceeds the number of accepted names (e.g., Appeltans et al. 2012). This inflates the apparent number of known species. Thus, only the names categorized as accepted were selected for analysis in this article. Nevertheless, taxonomic research will find that some of these names will prove to be unaccepted. In the early stages of discovery authors can

discover more species than later, aided by the initial knowledge of where to find the species and their diagnostic characteristics. Thus, the number of species named per author rises in the early stages of discovery and decreases as new species become harder to find. To consider these trends, the number of species and first author of each species per decade were counted. A decade was used to minimize the occurrence of zero values. Only unique first author surnames were counted to avoid any effects of multiple-authorships in recent decades inflating counts. It was assumed that any

**Table 2** Estimates of the number of described species of parasites of animals not analyzed in the present study

Taxon	Common name	Number of named species	Source
Myxozoa	498 in worms	2180	Appeltans et al. (2012)
Phthiraptera (with Anoplura)	Sucking bugs	1500	Kim 2006 (869 species in Orrell 2016)
Heteroptera, Cimicomorpha	Bed and assassin bugs	214	Orrell 2016
Glossinidae	Tsetse flies	23	Pape and Thompson (2016)
Unionida	Freshwater pearl mussels	345	Bieler and Gofas (2016)
Tantulocaridia	Tantulocarideans	36	Boxshall (2015b)
Branchiura	Freshwater fish lice	162	Boxshall (2015c)
Dicyemida	Mesozoans	122	Catalano (2015)
Nemertina, Carcinonemertidae	Ribbon worms	21	Norenburg and Gibson (2015)
Acanthocephala non-marine		669	Hugot et al. (2001)
Cestoda non-marine	Tapeworms	4300	Caira et al. (2012)
Digenea non-marine	Flukes	4365	Appeltans et al. (2012)
Monogenea non-marine	Flukes	2500	Based on average of 70% Cestoda and 30% Digenea not-marine, and Hugot et al. (2001) estimate of 3000 in total.
Nematoda excluding Spirurina	Parasitic roundworms	10,843	Hodda (2011)
Acari, Parasitengona	Velvet mites, chiggers, water mites	11,235	Zhang et al. (2011)
Acari, other	Parasitic mites	5000	Zhang, pers. comm.
<b>Sub-total</b>		<b>43,515</b>	
Protozoa and fungi		2000 to 10,000	Lee et al. 2000, Brusca and Brusca 2003
<b>Total</b>		<b>46,000 to 54,000</b>	Numbers rounded to reflect the uncertainties

effects of different authors with the same surname within a decade were negligible and/or random over time. Following the method in Costello et al. (2013a), a simple linear correlation was run with every combination of decades to determine if there was a significant break point between an increasing number of species per author, to a decreasing number of species per author, per decade.

## Results

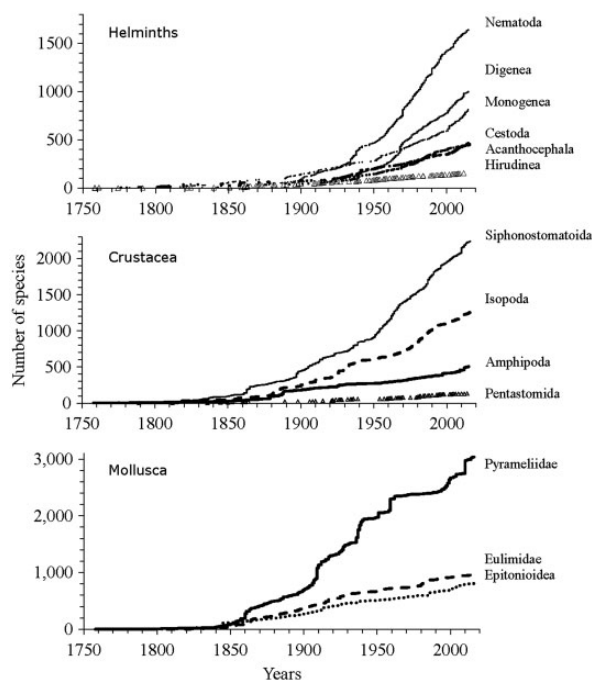
The rate of description of the mollusc and crustacean parasites took off in the 1850s to 1860s, but not until half a century later for the helminths and terrestrial parasites (Figs. 1 and 2, Table 1). The decades with most species described were between 1900–50 for molluscs, 1960–90 for crustaceans, and 1970–2000 for marine helminths (Fig. 3). For the terrestrial taxa, the peak periods of discovery were for 1900–60 for ticks, 1920–70 for fleas, 1950–60 for twisted-wing insects and 1960–2000 for microsporidians (Fig. 4). Overall, the taxa whose peak period of description was latest were dominated by the helminth endoparasites.

The number of authors involved has increased for marine helminths since 1960 and crustaceans since 1950, but has not shown any increase for molluscs (Fig. 3). Note that the number of authors for the last decade could be considered up to half of the likely total between 2010 and 2020. The ratio of number of species to the number of authors per decade has been decreasing for the molluscs and crustaceans since around 1950, but not so for helminths (Fig. 3). For molluscs, there was an increasing number of species per author until 1930 ( $r^2 = +0.871$ ) and decreasing from 1980 ( $r^2 = -0.904$  respectively). For crustaceans, the decrease began in 1940 ( $r^2 = -0.948$ ). In contrast, there was no significant trend for the helminths until 1970 ( $r^2$  range  $-0.4$  to  $+0.4$ ), and since then it has been increasing each decade ( $r^2 = +0.833, +0.905, +0.989$ ).

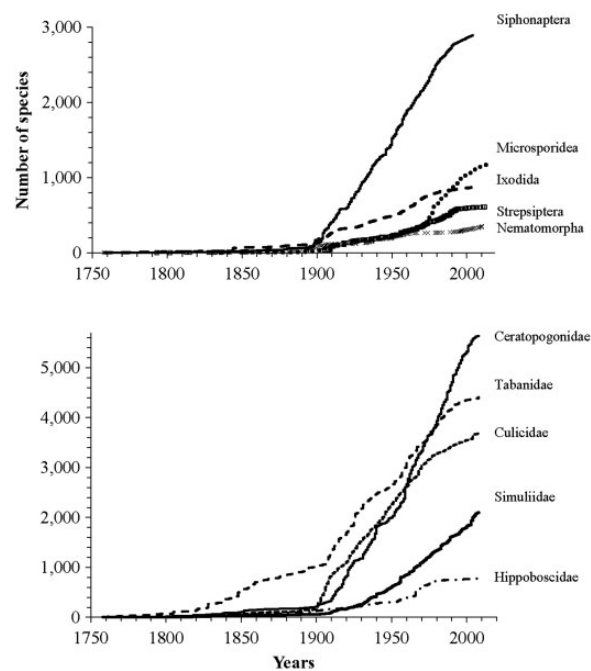
## Discussion

### Parasite host specificity

There are several reasons why current knowledge based on field observations may bias and/or overestimate parasite host specificity: (1) under sampling of hosts; (2) host removal of parasites; (3) more



**Fig. 1** The cumulative number of species of helminth (top), parasitic crustacean (middle), and parasitic molluscs (lower).

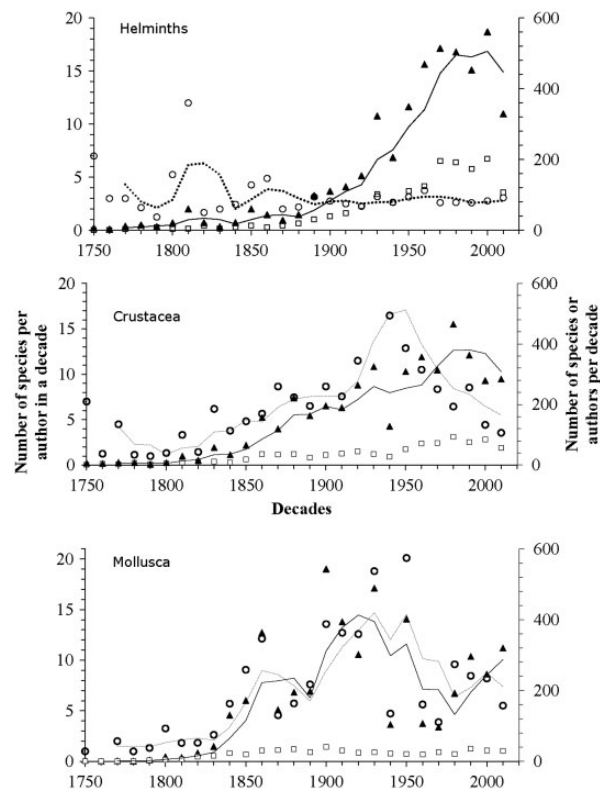


**Fig. 2** The cumulative numbers of species of terrestrial parasites (top) including biting flies (lower).

widespread and abundant hosts are more sampled; (4) environmental effects on parasite transmission success (including diet); (5) relative rates of species discovery; (6) taxonomic practice:

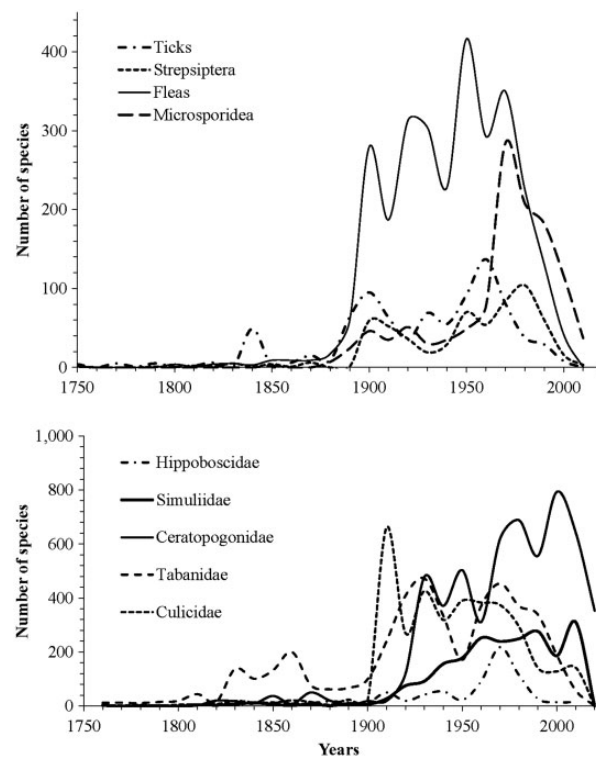
- (1) Under-sampling of hosts is a significant problem in estimating parasite species richness (Walther et al. 1995; Guégan and Kennedy 1996; Poulin 1997a, b; Poulin and Morand 2000; Medvedev and Krasnov 2006; Poulin et al. 2006; Dobson et al. 2008; Poulin 2008; Randhawa and Poulin 2010; Beveridge and Spratt 2015). In some ways, the parasite-host relationships represent a similar situation to non-parasite-habitat relationships. Under-sampling of a habitat and host will largely detect the most widespread and abundant species, which will appear more habitat and host specific than further sampling may reveal. Perhaps the best studied copepod parasites are those of farmed fish, and these are at most specific to a family of fish (Costello 1993, 2006). Other well-studied parasites, typically of humans and domestic animals, have several hosts, often with varying pathogenicity, such as for protozoans (Brusca and Brusca 2003), mites (Dowling 2006; Shatrov and Kudryashova 2006), and acanthocephalans and other helminths (Ribas and Casanova 2006).
- (2) An important difference between hosts as parasite habitat, and habitat of non-parasitic species, is that a parasite's habitat is hostile to it (Toft and Karter 1990). Hosts can actively avoid and remove parasites through grooming, use of cleaner-fish and shrimp, medicinal diets and immunologically. This will also affect the prevalence and abundance of parasites on their hosts.
- (3) In evolutionary terms, a parasite can only be highly host specific if its host is widespread, abundant or otherwise easily infected. Otherwise the parasite is likely to go extinct. Just as there are more endemic species in areas with more species, the number of host-specific parasites will be higher in species rich areas. Indeed, there are more parasites on hosts with wide geographic ranges (Price and Clancy 1983; Guégan and Kennedy 1996; Poulin 2014) and there are more host-specific parasites in species-rich faunas (Poulin 1997b; Krasnov et al. 2006). Thus potential hosts that are geographically rare, low in abundance, and in species poor faunas are not likely to have host-specific parasites. These hosts are also the species likely to have been discovered later (and thus be less well studied) and in the future (Costello et al. 2015).





**Fig. 3** Number of species described per decade (triangles and solid line), authors (squares), and species per decade divided by the number of authors per decade (circles and dotted line) with three point moving average lines, for the helminths (top); parasitic crustaceans (middle); and parasitic molluscs (lower).

- (4) A good evolutionary strategy for a parasite would be to have excellent dispersal (transmission) mechanisms and the ability to reproduce on several host species. Tree fungi in Britain appear to conform to this rapid dispersal strategy (Strong and Levin 1975). This would enable the parasite to survive variations in host abundance, and to extend its geographic range, for example to infest related host species in other geographic areas. Most or all parasites may have this strategy but appear to be host specific because their mode of transmission or host availability leads to their greater abundance on one particular host species. For parasites with intermediate hosts, only those hosts that feed on the intermediate parasite will appear in the host species. Yet, the parasite may be well able to survive in alternate hosts, and may do so at such low frequencies that it is overlooked. Given a change in the environment or host abundance, the parasite prevalence and abundance may vary. Thus, field data on parasite–host relationships may not reflect the actual or



**Fig. 4** The number of species described per decade for non-marine parasite taxa. Lines are three-point moving averages.

- potential niche of a parasite because it may also occur on alternative hosts which have not been sampled within the study area, or is infrequent on sampled hosts and may not be detected. Such a parasite species may also occur on alternative hosts outside the study area, although this does not seem to be the case for the highly host-specific bat flies (Dick and Patterson 2006). Due to their life-cycle, some species may be more habitat than host specific (Medvedev and Krasnov 2006).
- (5) Species that are more geographically widespread and occur in more habitats are discovered sooner (Costello et al. 2015), and more parasite species tend to occur on more widespread hosts (Krasnov et al. 2006, Poulin 2014, Morand 2015). That the most geographically widespread and least host-specific parasites are likely to be discovered first, suggests that future discoveries will be of more endemic species. Because such a small proportion of potential host species have been sampled for parasites, the present data are likely to exaggerate host specificity of as yet undescribed parasites. Thus, future sampling of previously unsampled hosts is likely to find many of the presently known parasite species, as well as some, but

relatively few, new species. To use host specificity to estimate parasite species richness would be to assume that all known hosts are as similarly infected by parasites as the yet to be studied hosts. Thus, under-sampling and current knowledge compromises the use of parasite–host specificity ratios for extrapolating species richness.

- (6) It is also likely that taxonomic rigor has increased over time. Some early taxonomists tended to give a new scientific name to a parasite found in a different host (Poulin 2008), thereby increasing apparent host specificity. While some species may be synonymized in the future, molecular methods may subdivide others into several (Poulin et al. 2006; Appeltans et al. 2012).

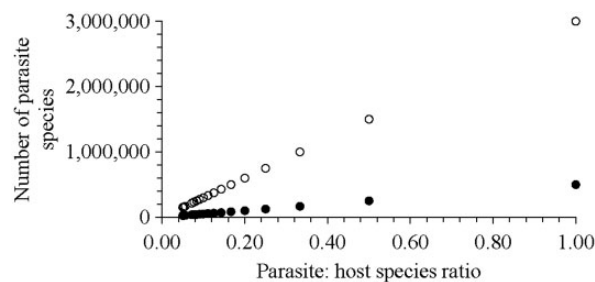
In addition to the above reasons why current knowledge of parasite host specificity is biased, the richness and abundance of parasites on host species is highly skewed (e.g., Rohde et al. 1995; Rohde 1998; Thieltges et al. 2009). Some parasites specialize in particular host taxa, but their specificity may be at the class, order, family, genus, or species level. There are more parasites in endotherms than ectotherms (Poulin and Morand 2000), and more ecto- than endo-parasites on fish (Poulin 2004). Generally, parasite species richness is greater on vertebrates than invertebrates, and on long-lived and larger host species (Poulin 1997a, 2004; Poulin and Rohde 1997; Raibaut et al. 1998; Walther and Morand 1998; Poulin and Morand 2000; Krasnov et al. 2006; Poulin et al. 2010; Morand 2015). However, vertebrates represent only 4% of all animal species globally (Costello et al. 2013b). Thus, parasite–host species ratios on vertebrates will be higher than in the majority of other taxa. Macro-invertebrates, about half of whom are insects, comprise about 80% of animal species and most have a much smaller body size and shorter life-spans than most vertebrates. The number of ectoparasite species also varies between environments and habitats; it is higher for aquatic than terrestrial animals, benthic than pelagic fish, tropical than Antarctic and deep-sea fish, and non-plankton feeding than plankton feeding fish (Rohde et al. 1995). Consequently, extrapolation from current knowledge of parasite host specificity to estimate the number of species on Earth needs to account for the variation in host specificity in different habitats, and between higher taxa, body size, and life-span. Furthermore, such estimates of global species richness should consider the bias in current knowledge, and that host specificity is likely to be less for the species yet to be described.

### Estimating global species richness

Geographic patterns of species richness are similar for parasites and their hosts; that is, where there are more host species there are more parasites (Poulin and Morand 2000; Poulin et al. 2011; Randhawa and Poulin 2010; Randhawa et al. 2015). This may reflect common factors leading to high species richness across all taxa, and/or greater host richness facilitating greater parasite richness. Thus, estimates of global species richness based on regional and/or habitat-based data need to account for varying richness patterns in other parts of the world (Poulin and Rohde 1997; Poulin 2004a). If one considers a wider definition of parasites to that used here, such as to include parasitoids, phytophagous arthropods, and fungi, then many times more taxa will be included. However, ultimately all species are associated with other species to some extent. Thus, to widen the definition will also widen the number of associated species and reduce host specificity further.

Another problem in using simple ratios to estimate species richness is mathematical. If a parasite species considered to be specific to one host is discovered to have a second, then the host-specificity ratio changes from 1:1 to 1:2 and number of estimated parasite species decreases by half, with less effect on estimates as the number of host species increases (Fig. 5). Similarly, other hyper-estimates of species richness have been derived from ratios of species in one habitat or locality, or across higher taxa, to the world (reviewed in Appeltans et al. 2012). A parasite's habitat can be narrowly defined to a host, but defining the habitat for non-commensal species is more difficult. Thus, parasites demonstrate the weakness of using simple ratios of species habitat associations to estimate global marine species richness.

Comparisons of body size distributions have also been used estimate global species richness based on the premise that there is a relationship between the average body size of a taxon and its number of species. However, this is not the case across all taxa. While there are relatively few species amongst megafauna compared to macrofauna, there are also fewer species in microscopic taxa because they are more widespread (Costello et al. 2013b). Furthermore, while very large species tend to be discovered earlier (perhaps because they have a wider geographic distribution), at a global scale body size is a minor or insignificant factor in determining when species are discovered (reviewed by Costello et al. 2015). Poulin (2014) suggested that the decrease in body size in more recently described species of parasites may indicate that most species have been discovered.



**Fig. 5** The effect of parasite to host specificity changing from 1 parasite to 1 host species, to 1 to 18, on the estimated number of parasite species if global species richness is 3 (circles) or 0.5 (dots) million species, as it may be for all and marine species, respectively (Costello et al. 2012).

Several authors have suggested that discoveries of “cryptic species”, species only distinguishable by molecular methods, may increase the number of parasitic species, especially amongst vermiform taxa with few morphological characters (e.g., Dobson et al. 2008). There is no doubt that such methods are helpful in distinguishing species and will contribute to new species discoveries. However, “cryptic” species may not significantly increase global species richness because most taxa, notably most arthropods which comprise over two-thirds of all species, can be distinguished phenotypically using morphological characters. An assessment of marine taxa found less than 1% of fish and 5% of crustaceans may be cryptic species, and overall, cryptic species may comprise 10–20% of presently known species (Appeltans et al. 2012). At least as many species names may be lost through synonymy. The proportion of cryptic species varies greatly amongst parasite genera (Poulin 2011), so a simple extrapolation from a few genera where cryptic species are found to all parasites would not be justifiable. It must also be realized that genetic differences alone do not discriminate species, so it cannot be assumed that genetic differences between populations equate to new species without phenotypic evidence (Frankham et al. 2012). Furthermore, solely using genetic methods may overlook phenotypic differences and lead to valid species being overlooked.

#### Future species discoveries

Undoubtedly, many new species of parasites and hosts will be discovered for decades to come (Costello et al. 2013c). There is likely to be increasing effort in species discovery due to more people involved as economies and scientific institutions develop around the world, and engagement with non-specialists including citizens, farmers, biologists, and ecologists. Having central open-access

taxonomic databases as used in the present article helps this effort by coordinating knowledge and expertise (Costello et al. 2013d). The question asked here is whether future discoveries of parasites will exceed those of their hosts.

This study analyzed 37,000 scientifically described species of animal parasites (Table 1), and referenced another 46,000 to 54,000 (Table 2). The number of named species is between 1.5 and 1.9 million depending if allowance is made for synonyms (Costello et al. 2013a). Thus, about 5% of all described species are parasites of animals.

Recent analyses of species discovery rates have concluded that at least two-thirds of species are known of: overall marine and terrestrial taxa; sea anemones; flowering plants; marine fish; and micro and macro-algae (reviewed by Costello et al. 2014a, b). The present assessment suggests a similar proportion of most parasite taxa may have been named, even though parasites are generally described later than non-parasite species (Costello and Wilson 2011). However, the present analysis also showed that parasite taxa are not equally well-known.

The decreases in the number of species of taxa named since 2000 may reflect delays in data entry, but this is unlikely the case prior to then. While this may in part be the case for microsporidians (Kirk, pers. comm.), it is not the case for the ticks (Nijhot, pers. comm.) and Strepsiptera (Kathirithamby pers. comm.). Thus, of terrestrial taxa, most of the ticks, fleas, twisted-wing parasites, louse flies, horse flies, and mosquitos appear to have been described (Fig. 4). Although most molluscs, crustaceans, ticks, fleas, and insects may have been named, the peak discovery period for the helminths and microsporidians contrasts with most other taxa in having begun in the 1970s. The number of species described per number of authors was decreasing in all groups except helminths (Fig. 3), as also found by Poulin (2014) for helminths. These “late-described” taxa comprise about 5000 of the 37,000 species analyzed. If the Simuliidae are included as the latest arthropod group to be described, these three taxa comprise <20% of the parasites studied here.

Recognising the uncertainties in the data, about 87,000 parasite species of animals appear to have been described (Tables 1 and 2). If split into 20% less and 80% better known groups, and multiplied by being only 1/3 and 2/3 described, respectively, this estimates about 160,000 species of animal parasites on Earth. This is about 10% of all presently named species on Earth, and it must be considered that thousands of species remain to be named in the non-parasitic taxa as well. More than a 10-fold



increase in the number of parasite species would be needed to catch-up on non-parasite richness. It appears highly unlikely that parasites will be as species rich as non-parasitic species. This indicates that current data greatly over-estimate host specificity of parasites across all species for the reasons outlined above. That about 5% of all species are parasites of animals at a global scale contrasts with local studies where parasites may comprise 40% of a species assemblage (Dobson et al. 2008). This difference between alpha and gamma diversity indicates that parasites are more widely distributed than their hosts, and that it is not possible to estimate global diversity from local data. Lower host specificity may not only provide greater flexibility of parasites to climate change, but also make predictions of changes in their distribution more difficult (Barber et al. 2016). The consequence of climate change may be more frequently pathogenic impacts of parasites as they colonize new naïve hosts rather than host's escape from parasites.

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