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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, parasite diversity per host species and host specificity of parasites, we cannot rely on this logical yet simple approach.

When quantitative methods cannot be used to extrapolate the total number of living species in a taxon, asking experts for their opinion has become the method of last resort. Expert opinion has been widely used in the past to generate predicted total numbers of species, either for specific taxa or for the entire planet (see Appeltans et al., 2012 and references therein). Sometimes experts are consulted only to estimate one particular parameter that is then used in a more rigorous method of diversity extrapolation, but on other occasions they are asked to make the diversity estimate themselves based on knowledge of their focal taxonomic group. The problem with the use of expert opinion to estimate the number of parasite species in any given taxon is that estimates obtained this way are subject to an anchoring effect, one of the most common effects in experimental psychology. Anchoring effects refer to the phenomenon that occurs when people consider a particular value for an unknown quantity before they themselves estimate what that quantity should be: the estimates they provide remain close to the original value they considered (Tversky and Kahneman, 1974; Epley and Gilovich, 2001; LeBoeuf and Shafir, 2006). The estimates remain 'anchored' close to the original value seen by the subject due to not only the subconscious priming influence of that original value, but also due to a deliberate adjustment made to the estimate to avoid entering an area of increasing uncertainty as one moves away from the anchor. The anchoring influence of seeing a number before rendering a quantitative estimate is particularly troubling, because it can be induced even by random numbers and also applies to opinions rendered by experts in any field (Englich et al., 2006). When asked to estimate the number of parasite species in a given taxon, experts are either given an existing number of described species or they find one themselves in the literature at their disposal (see notes behind the reasoning of experts in the Supplementary material of Appeltans et al., 2012). These no doubt act as anchors biasing any subsequent estimates.

To demonstrate how anchoring effects can invalidate estimated numbers of parasite species, I asked two simple questions of 120 experts (from 25 countries) using two different anchor values and then compared their answers. The questions focused on the proportion of all living species that are parasites, and not on the number of species in any particular parasite taxon. The experts are all active researchers working either on parasite ecology, evolution, taxonomy or systematics; all are empiricists rather than theoreticians. They were chosen from among the long list of parasitologists whose work is known to me, with a deliberate effort to include expertise on a broad range of parasite taxa. All experts have at least 5 years of working experience beyond completion of their PhD and none of them is a former student of mine. The 120 experts were randomly allocated to one of two groups of 60 people. Experts in the first group were asked (by e-mail) the following two questions, in addition to their consent to use of their responses in the present study:

(i) Would you say that parasites account for less or more than 30% of the species on Earth?
(ii) What do you think is the percentage of species on Earth that are parasitic?

Experts in the second group were asked the same two questions, except that the anchor value given in the first question was 50% instead of 30%. A definition of parasites accompanied the questions; although any definition can have many interpretations, this issue applied equally to participants in both groups. After answers were received, the strength of the anchoring effect was computed as the difference between the mean estimates of the two groups given in reply to the second question, divided by the difference between the two anchors (50 – 30 = 20). This ratio equals 1 in the hypothetical case where people are completely swayed by the anchor and zero for people who completely ignore the anchor they are given (Jacowitz and Kahneman, 1995).

The first question was used solely to set up the low and high anchors. It was assumed to exert the same influence as prior tallies of existing species do when an expert is asked to estimate the total species richness in a taxon: they provide a point of reference which may prime the subsequent estimate and subconsciously bias its magnitude. Of 50 respondents in the first group of experts, 45 believed that the proportion of parasites among living species was higher than the low anchor of 30%; of 40 respondents in the second group, 32 said that the proportion of parasites was higher than the high anchor of 50%. The second question served to test the strength of the anchoring effect and it provided clear results (Fig. 1). Experts primed by a higher anchor value estimated that parasites account for an extra 11% of the species on Earth compared with the average value given by experts primed by a lower anchor. The strength of the anchoring effect seen here was 0.55, which is comparable with anchoring effects shown by experts in other fields ranging from real estate agents to sentencing judges (Jacowitz and Kahneman, 1995). The anchoring effect seen here applies to estimates of relative parasite diversity, but it most probably also applies to estimates of absolute parasite diversity primed by existing values.

The conclusion from this little psychological experiment is clear: experts are subject to external influences, including random ones, and even their best estimates are unlikely to be totally reliable. So we are left with no solid estimates of parasite diversity and no adequate method for obtaining one. Perhaps newer approaches to extrapolate total diversity based on consistent patterns in taxonomic structure (see Mora et al., 2011) will prove useful when applied to parasites, but for now we have no reliable estimate of parasite diversity. Maybe it does not matter. After all, estimates of global parasite diversity have little practical benefit; they are almost purely of academic interest. It is difficult to argue that obtaining a precise number of parasite species would be of any great value to science. All it would mean in practice is that we would know more precisely how many more species are left to

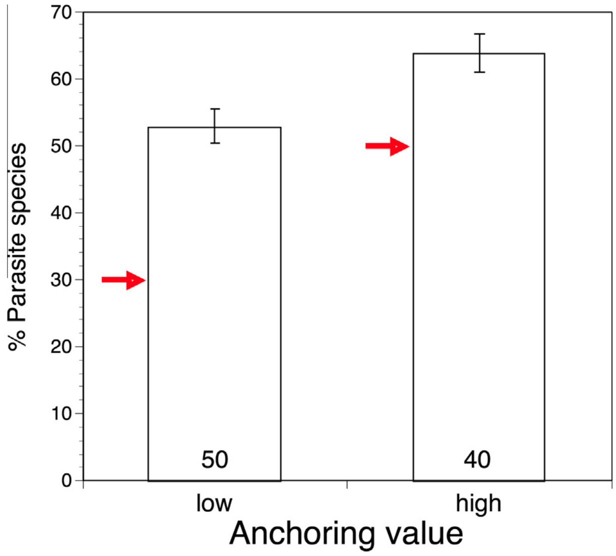

Fig. 1. Mean (±S.E.) percentage of living species that are parasites, as estimated by two groups of experts, that were first primed by either a low (30%) or high (50%) anchoring value. These anchors are shown by arrows and the numbers of respondents in each group are shown on the bars. The difference between the two groups was statistically significant ($t_{88} = 2.81$, $P = 0.006$).

be described. From cumulative numbers of described species that are still rising rapidly from year to year, we already know this number is large and perhaps that is all we need to know for the moment.

3. Are there enough taxonomists to describe all the remaining species?

If we are still a long way from completing the inventory and description of extant parasite species, the taxonomic task facing us is substantial. Do we have enough specialists to take it on and are we training enough replacements and finding them long-term positions to ensure continuity in parasite species discovery and description? Warnings of an impending global shortage of professional parasite taxonomists and systematists have been sounded over a decade ago (Brooks and Hoberg, 2000, 2001). Hard evidence that this is affecting the study of parasite biodiversity is difficult to obtain, however. For example, surveys of helminth diversity in vertebrate hosts published after the year 2000 have shown a drop in the proportion of helminth taxa identified at least to the genus level, compared with surveys published before that time (Poulin and Leung, 2010). One explanation for this trend could be a general loss of expertise in parasite taxonomy but other explanations are possible. Nevertheless, concerns for the future of species discovery and description have been expressed not only within but also outside of parasitology, as the dreaded shortage of taxonomists and systematists extends to all taxa, free-living as well as parasitic (Pearson et al., 2011).

In contrast, some authors have recently argued that there are more taxonomists describing species than ever before and that the number of new species described per taxonomist is decreasing (Joppa et al., 2011; Costello et al., 2013; Tancoigne and Dubois, 2013). For a wide range of taxa, the number of species described per year, the number of articles describing new species per year, and the number of authors describing new species per year, have all been increasing rapidly in recent decades, while at the same time the average number of new species described per taxonomist has declined more or less steadily. This decreased return in new species per taxonomic effort despite our greater access to more habitats has been interpreted as evidence that new species are becoming harder to find and that we are well past the halfway point in our compilation of the Earth's biodiversity (Costello et al., 2013).

To determine whether these trends apply more specifically to parasites, I examined taxonomic publication trends using methods similar to those used by Joppa et al. (2011), Costello et al. (2013) and Tancoigne and Dubois (2013). I focused on digeneans and acanthocephalans only, as examples of a relatively diverse and a relatively species-poor taxon, respectively. The ISI Web of Science (http://thomsonreuters.com/web-of-science-core-collection/) was searched from 1980 to the present, using the search string ((trematod* or digene*) and ("new species" or "n. sp.")) for the digeneans, and the search string (acanthocephal* and ("new species" or "n. sp.")) for acanthocephalans. This search did not uncover all new species described but it provided an unbiased and representative sample of taxonomic activity during that period. Each publication was checked individually and only relevant ones were included. For each 2 year period beginning in 1980, the following data were recorded: the number of new species described, the number of articles describing new species, the number of authors describing new species, the proportion of those authors that described either only one species or ⩾5 species, the mean number of new species described per author, and the mean number of authors per new parasite described.

Some of the trends observed for digeneans and acanthocephalans are quite similar to those reported for free-living taxa (Joppa et al., 2011; Costello et al., 2013; Tancoigne and Dubois, 2013). The number of articles describing new species, the number of people authoring these articles and the number of new species described have all risen steadily over the past three decades (Fig. 2). However, the mean number of new species described per author and the mean number of authors per new species described also increased steadily over that period (Fig. 3). This is in sharp contrast to patterns reported by Costello et al. (2013) and Tancoigne and Dubois (2013). The proportion of authors that described only one species per 2 year period showed no change over time (not shown; both $P > 0.55$), matching the findings of Costello et al. (2013). However, the number of authors that described at least five species per 2 year period remained very low over the last 20 years; these authors were almost all researchers past their 50th birthday, and the names of their junior co-authors (who were trained in taxonomy by the senior author) generally disappeared from the literature in subsequent years.

Several interpretations of these patterns are possible and here I focus only on those relating to whether or not the taxonomic workforce is sufficient to keep up with the description of new species.

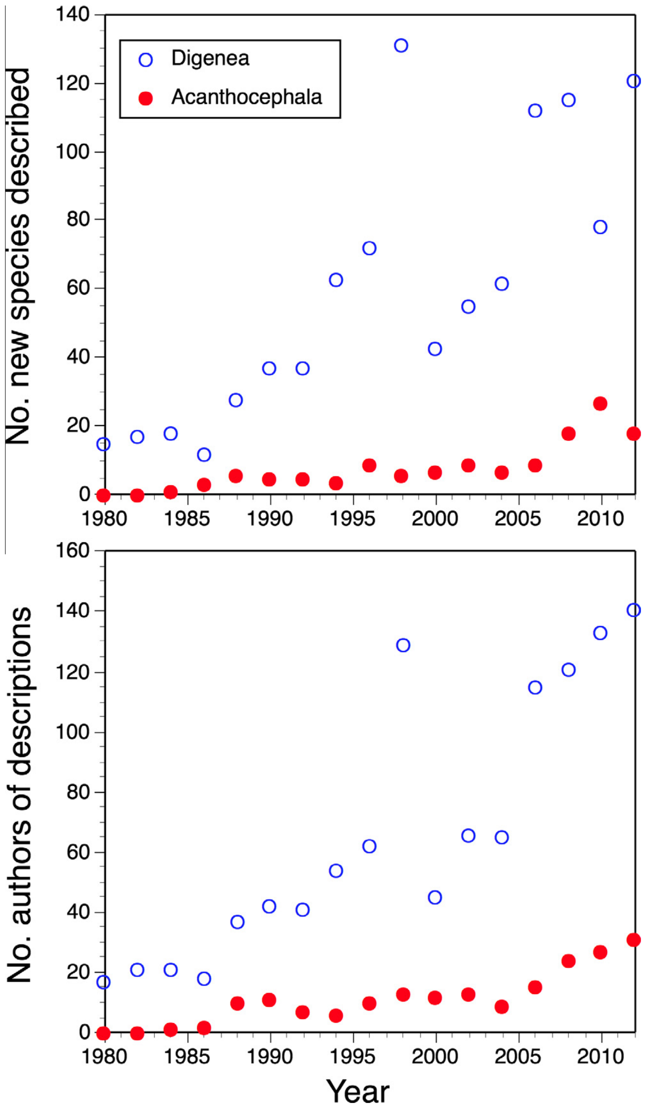

Fig. 2. Number of new species described and number of authors of species descriptions for each 2 year period from 1980 to the present. Data are from a search of ISI Web of Science and shown separately for digeneans and acanthocephalans. For both variables and both parasite groups, correlations with year are statistically significant (all $P < 0.001$).

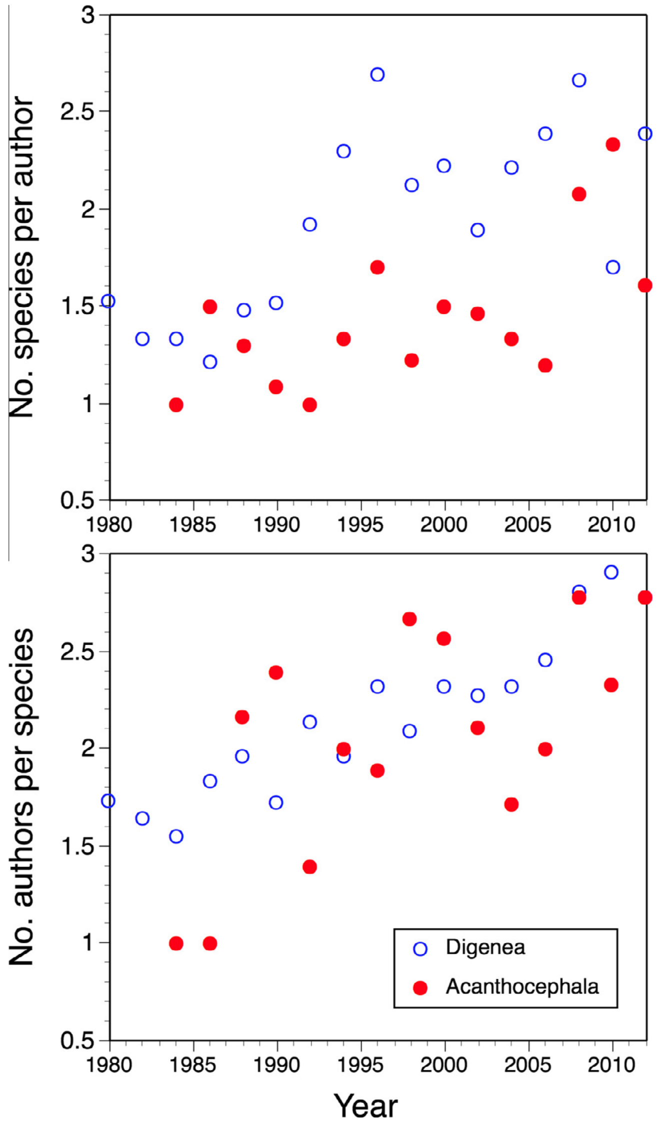

Fig. 3. Mean number of new species described per author and mean number of authors per new species described for each 2 year period from 1980 to the present. Data are from a search of ISI Web of Science and shown separately for digeneans and acanthocephalans. For both variables and both parasite groups, correlations with year are statistically significant (all $P < 0.02$).

The increase in the total number of authors of taxonomic papers, and in the average number of species described per author, is very deceptive as a measure of taxonomic expertise. The raw data indicate that in recent years, the bulk of published descriptions of new species involved a small number of key people, all renowned taxonomists in the latter part of their prolific career. Costello et al. (2013) define a taxonomist as an author of species descriptions. This may be convenient when analysing publication trends but in reality many recent multi-authored articles describing new parasite species include at best one genuine taxonomist, the other authors having made different kinds of contribution (e.g., ecologists collecting the species, molecular geneticists obtaining and analysing the sequence data). These collaborations provide the most parsimonious explanation for the rise in the mean number of authors per new parasite described (Fig. 3). The number of actual taxonomists in stable, long-term positions is apparently not increasing; if anything, it may be on the decline as feared by Brooks and Hoberg (2000, 2001). The fact that there are now more co-authors on taxonomic papers should definitely not be taken as a sign that the number of new species described per taxonomic effort is declining and that we are approaching the latter stages of our biodiversity inventory.

4. How does parasite diversity vary across host species?

Even if we do not have a complete tally of all extant parasite species, we nevertheless have sufficient knowledge of parasite diversity to answer questions about its distribution in both geographic and phylogenetic space. Identifying patterns in the distribution of parasite diversity is the first step toward elucidating the underlying processes generating these patterns. By far, the greatest efforts have been aimed at interspecific differences in parasite diversity among host species, i.e. variation in parasite species richness per host (Poulin, 1997; Poulin and Morand, 2000, 2004). Therefore let us first look at the distribution of parasite diversity using the host species as the observation unit.

It is evident to anyone who has surveyed parasites among different vertebrate species that parasite diversity is not randomly distributed among host species. Parasite species richness generally shows obvious phylogenetic conservatism: two related host species tend to harbour more similar parasite faunas, of comparable richness, than two distantly related hosts. However, ecological properties play an independent role in determining whether few or many parasite species exploit a given host species. Indeed, in many taxa of hosts, interspecific variation in parasite species richness appears to follow variation in host species traits or in the characteristics of their habitats (e.g., Nunn et al., 2003; Lindenfors et al., 2007; Arriero and Møller, 2008; Bordes et al., 2009; Poulin et al., 2011). Two theoretical frameworks have provided the source of most hypotheses about this variation (see Poulin and Morand, 2004). First, host species have been considered as ‘resource islands’ available for colonisation by parasites over evolutionary time, in accordance with a broad interpretation of the island biogeography theory (MacArthur and Wilson, 1967). Thus, all else being equal, larger-bodied host species should provide greater space and other resources to parasites, encounter them at higher rates, and represent longer-lived habitat patches, than small-bodied host species (Guégan et al., 1992; Poulin, 1995). Similarly, host species having a broad geographical range should be more likely to encounter and be colonised by several parasite species over evolutionary time, as their range overlaps with that of a greater number of other hosts acting as sources of parasites than would be the case for host species with restricted spatial ranges (e.g., Gregory, 1990; Garrido-Olvera et al., 2012). Second, epidemiological theory has also provided an impetus for comparative tests of parasite species richness across host species, since its core mathematical models postulate that certain parameters representing host traits should favour parasite establishment and persistence (Anderson and May, 1979; May and Anderson, 1979). For instance, host population density is a central parameter of basic epidemiological models; extrapolating from these models, we can predict that host species occurring at high densities should have been more readily colonised by several parasite species, and have higher parasite richness, than hosts living at low population densities (Morand and Poulin, 1998; Arneberg, 2002).

Other predictors of variation in parasite richness among host species are derived from the biology of the parasites themselves and how they are acquired by hosts. For example, in the case of trophically-transmitted parasites which are transmitted through the food chain, variation among host species in either their diet breadth, their range of prey or their position in food webs can explain much of the interspecific variation in how many parasites of this type are harboured by different host species (Chen et al., 2008; Poulin and Leung, 2011; Locke et al., 2014).

The above predictors and other host-related factors have been found to correlate with the richness of parasite species per host species in many comparative studies. However, as I have pointed out in the past (see Poulin, 2004; Poulin and Morand, 2004), the significance and direction of these relationships are not fully consistent among studies and the predictive power (i.e., R^2) of the significant ones is often low. This is exactly the kind of situation where a meta-analytic approach can cut through the idiosyncrasies of individual studies to extract a general relationship. Focusing on the most widely tested predictors of interspecific variation in parasite richness per host, Kamiya et al. (2014a) have conducted a comprehensive meta-analysis of all available studies in the literature. Their analysis identified host body size, host geographical range size and host population density as key universal determinants of variation in parasite species richness among hosts, independent of the types of hosts or parasites considered. For each of these three predictors, and for whatever subsets of original studies that were analysed separately, the overall effect sizes were significantly different from zero but generally weak (Kamiya et al., 2014a), indicating that although the predictors covary significantly with parasite richness, they influence it only to a modest extent. The meta-analysis leaves some questions unanswered, of course. For instance, these three determinants of parasite richness are not independent from each other and their respective effects cannot easily be disentangled. Also, there are too few available comparative studies of other predictors of variation in parasite richness among host species, such as diet breadth or trophic level, to allow a meta-analytical synthesis of their influence.

Nevertheless, the meta-analysis of Kamiya et al. (2014a) is a major landmark in our understanding of the drivers of parasite species richness and how it varies among host species. It identifies three basic host properties (host body size, host geographical range size and host population density) as fundamental and universal correlates of parasite richness, whatever the type of organisms under consideration. It also provides global support for the predictions arising from island biogeographic theory and epidemiological theory. Finally, it gives us a means to extrapolate how many parasite species (admittedly, with some margin of error) are likely to infect a host species previously not surveyed for parasites but whose basic ecological and life history traits are known. On the basis of the recent meta-analysis of Kamiya et al. (2014a), I would say that our understanding of patterns and processes in the distribution of parasite species richness among host species now far exceeds our understanding of other aspects of parasite diversity.

5. How does parasite diversity vary in geographical space?

In the previous section, I discussed patterns in the distribution of parasite diversity among host species, i.e. variation in parasite species richness per host. However, in biogeography and ecology, the focus is on the distribution of species diversity in geographical space (Lomolino et al., 2010), and the measurement unit of relevance becomes parasite species richness per area. Here I examine this aspect of parasite diversity, using parallels with three general patterns emerging from ecological studies of free-living taxa.

First, spatial variation in diversity of free-living organisms is broadly linked with spatial variation in resource availability. Indeed, in a comprehensive and quantitative review of the literature, spatial variability in temperature, rainfall, evapotranspiration and/or primary productivity consistently outperformed other competing factors, and combined to explain a substantial proportion of variation in plant and animal species richness across space (Hawkins et al., 2003). For any trophic relationship, we would therefore expect that if consumer diversity is driven by resource diversity in a 'bottom-up' process, then diversity at the higher trophic level is governed by diversity at the one below. For instance, across different habitat patches, there is overwhelming evidence that the species richness of herbivorous arthropods is strongly dependent on plant species richness (Siemann et al., 1998; Scherber et al., 2010; Castagneyrol and Jactel, 2012). For host–parasite systems, the expectation would therefore be that parasite species richness correlates strongly with host species richness across distinct habitat patches, at least for any realistic level of host specificity. This is exactly what has been reported by numerous empirical studies at a range of spatial scales and on a broad range of parasite taxa (e.g., Watters, 1992; Krasnov et al., 2004, 2007; Hechinger and Lafferty, 2005; Thieltges et al., 2011). The universality of this pattern has been confirmed by a recent meta-analysis, which found a strong average relationship between parasite species richness and host species richness, independent of the type of hosts or parasites considered or the scale of study (Kamiya et al., 2014b). Simply put, the more host species occur in a habitat, the more parasite species will co-occur in that habitat.

The second general pattern arising from ecological studies of free-living taxa and relevant to parasite diversity is the species–area relationship (He and Legendre, 1996; Lomolino, 2000). This well-documented macroecological rule amounts to this simple observation: the number of species in an area is a power function (or some similar function) of the size of that area. In log–log graphical space, the function becomes a straight line. The species–area relationship should extend directly to parasites: if larger areas contain more host species, and if the number of parasite species increases with the number of host species (see above; Kamiya et al., 2014b), then inevitably larger areas should contain more parasite species (Fig. 4). The strong statistical link between host species richness and parasite species richness means that whatever affects the number of host species must also affect the number of parasite species. This simple expectation, although logical, has only been explicitly tested once, as far as I know. Guilhaumon et al. (2012) found that among 16 large regions from around the world, for which there exist comprehensive data on the flea species parasitic on mammals, flea species richness scaled positively with the area of the region sampled (Fig. 5). Although significant, the

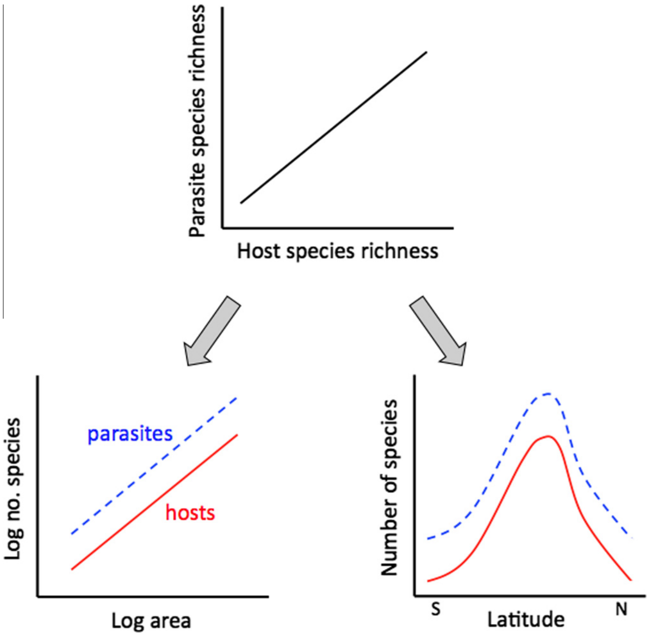

Fig. 4. Schematic summary of the inevitable extension of two well-known geographical patterns in biodiversity, the species–area relationship and the latitudinal gradient in diversity, to parasitic organisms, resulting from the strong covariance between host species richness and parasite species richness. Whatever shape the relationship between host species richness and either area or latitude takes, the corresponding function for parasite species richness will be forced to mirror it closely.

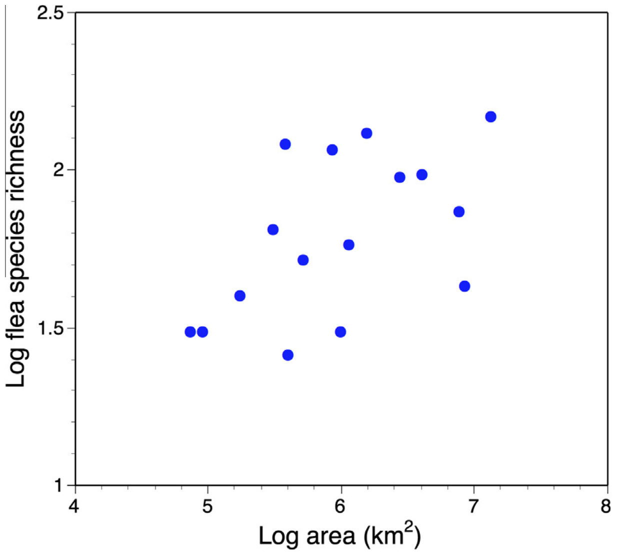

Fig. 5. Species richness of fleas ectoparasitic on mammals as a function of the area of the region sampled, across 16 large regions from around the world. The linear relationship between the two variables is statistically significant ($R^2 = 0.296$, $P = 0.029$). Data are from Guilhaumon et al. (2012).

relationship was not very strong, as the points did not fall tightly along a line. However, given that the taxonomic composition of the mammalian host fauna and the local climate varied widely among the 16 regions considered, just finding a positive relationship is telling. More importantly, although the species–area relationship for fleas was statistically weaker than that characterising their mammalian hosts across the same areas, the former mirrored the latter. Although further empirical tests of the species–area relationship using parasites would be welcome, it is probably safe to say that as a direct consequence of the strong link between parasite species richness and host species richness, the species–area relationship must apply to parasites as globally as it does to their hosts.

The third general biodiversity pattern revealed by studies of free-living taxa is the latitudinal diversity gradient (Willig et al., 2003; Hillebrand, 2004; Brown, 2014). Across the vast majority of plant and animal taxa, species richness per area increases toward the equator. Again, as a direct consequence of the coupling between parasite species richness and host species richness, the latitudinal gradient in diversity should automatically apply to parasites (Fig. 4). However, in the only test of the latitudinal gradient in parasite species richness per area that I am aware of, Guilhaumon et al. (2012) found no significant change in flea richness with decreasing latitude after correcting for area size. This may simply indicate that area size is of greater importance than latitude. Further empirical tests will be necessary before we can confirm or refute the existence of a latitudinal gradient in parasite diversity, although from first principles it seems highly likely.

As an aside, there has been much more research on patterns of parasite species richness per host species as a function of latitude. Rohde (1992) predicted that higher temperatures and higher levels of solar radiation at low latitudes should directly favour the diversification of parasite taxa through increased mutation rates and shorter generation times, at least for ectoparasites or parasites of ectothermic hosts. In contrast, the more stable conditions in the tropics have been proposed to lead to the evolution of a greater proportion of specialised species than in temperate regions, creating a latitudinal gradient in niche breadth (Vázquez and Stevens, 2004). This applies to at least some types of parasites, such as fleas parasitic on small mammals which tend to show greater host specificity at lower latitudes (Krasnov et al., 2008). Perhaps not surprisingly, as a result of these opposing forces and other confounding factors, comparative tests of parasite species richness per host as a function of latitude have yielded both support (e.g., Rohde and Heap, 1998; Lindenfors et al., 2007) and a total lack of support (e.g., Gregory et al., 1991; Poulin, 2001) for a latitudinal gradient. Meta-analytical synthesis of all available studies suggests no overall relationship between latitude and parasite species richness per host (Kamiya et al., 2014a). Since the taxonomic composition of host and parasite faunas changes dramatically with latitude, comparative studies contrasting parasite species richness between tropical and temperate hosts invariably end up comparing apples and oranges, even when controlling for phylogenetic influences on variation in host ecological and life history traits. The only way around this issue would be to focus on a globally-distributed host species and compare populations of that host from different latitudes. Guernier et al. (2004) performed such a study across human populations and found the widely expected negative relationship between latitude and parasite species richness. The burden imposed by particular parasites on human populations, measured as the per capita number of life years lost to disease, also increases toward low latitudes (Bonds et al., 2012). However, in this case there are many confounding factors that covary with latitude, including socioeconomic and cultural variables, hygiene and sanitation practices, and medical care (and the regional richness of alternative wild host species; Dunn et al., 2010). These cannot all be corrected by statistical analysis and they render the effect of latitude seen by Guernier et al. (2004) difficult to interpret and to generalise to other host species. Therefore, the special case of parasite species richness per host may not obey any latitudinal gradient, even if the more general parasite species richness per area tends to follow the pattern observed in free-living species.

In a geographical context, the strongest predictor of parasite species richness per area is host species richness: the more host species in an area, the more parasite species. Other well-documented biogeographical patterns, such as the species–area relationship or the latitudinal gradient in diversity, should ensue as almost inevitable epiphenomena. Thus, under most realistic conditions, geographical patterns in parasite species richness should mirror those for host species richness.

6. Concluding remarks

This review has provided answers to the four questions posed in the introduction. First, we still cannot estimate how many parasite species there are on Earth, with any acceptable level of accuracy, either in relative or absolute terms. On one hand, species discovery rates that show no sign of slowing down and host specificity estimates that are plagued by unknown numbers of cryptic species render existing extrapolation methods useless for many parasite taxa. On the other hand, expert opinion has been debunked as highly prone to biases. However, I argue that the actual value of obtaining estimates of parasite diversity is questionable. Second, there seems to be a real risk that we may soon not have enough parasite taxonomists to keep up with the description of new species. Although more parasite species than ever have been described in the last few years, genuine taxonomic expertise appears to be limited to a very small number of individuals in the latter stages of their career. Third, we have made great strides toward explaining variation in parasite species richness per host species, with the identification of basic host properties that are universal correlates of parasite richness, whatever the type of hosts or parasites under consideration. Fourth, in a geographical context, parasites are where the hosts are. The main driver of parasite species richness per area is simply local host species richness, and as a consequence patterns in the spatial variation of parasite species richness should match those already well-documented for free-living species.

Admittedly, the evidence and arguments considered in this review focused on the most basic facet of parasite diversity, i.e. species richness. Biological diversity can be measured using more sophisticated approaches that include information on the relative abundance, phylogenetic relationships and functional traits of species (Magurran and McGill, 2011). However, species richness remains the best studied, easiest to understand and therefore most relevant index of diversity.

In addition to joining earlier pleas (Brooks and Hoberg, 2000, 2001) for an immediate boost in the support and training of a new generation of parasite taxonomists, the main recommendation to emerge from this review of recent developments in the study of parasite diversity is to make greater use of the robust patterns we have now uncovered. The recent advances in our understanding of how and why parasite species richness varies among host species or across geographical areas can be used to inform research into areas of current concern in the ecology of health and in conservation biology. For instance, the ecological niche modelling approach, which combines data on the abiotic niche of a focal species with the biotic interactions that affect this species and its dispersal ability, can be used to determine the geographical distribution of individual species (Peterson, 2008). We should be able, using the strong relationships between host species richness and parasite species richness, to generate diversity maps for entire groups of parasites, not just individual species. These would be good starting points to identify hotspots of parasite diversity where conditions for host-switching may be ideal and from which emerging zoonotic diseases are most likely to originate (Cleaveland et al., 2001). In addition, estimates of parasite extinction rates and their geographical distribution could also be generated using the predictors of parasite species richness per host species or per area, given the tight coupling between host and parasite extinction (Moir et al., 2010; Colwell et al., 2012). These are certainly more pressing issues for the immediate future than calculating the exact number of extant parasite species on the planet.

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