

Contents lists available at [ScienceDirect](#)

International Journal for Parasitology: Parasites and Wildlife

journal homepage: www.elsevier.com/locate/ijppaw

(macro-) Evolutionary ecology of parasite diversity: From determinants of parasite species richness to host diversification



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ARTICLE INFO

Article history:

Received 30 October 2014

Revised 3 January 2015

Accepted 6 January 2015

Keywords:

Parasite diversity

Species richness

Mammals

Latitudinal gradient

Epidemiology

Macroecology

Metabolic theory

Immune defence

ABSTRACT

The present review summarized the factors or determinants that may explain parasite diversity among host species and the consequences of this parasite diversity on the evolution of host-life history traits. As host–parasite interactions are asymmetrical exploited–exploiter relationships, ecological and epidemiological theories produce hypotheses to find the potential determinants of parasite species richness, while life–history theory helps for testing potential consequences on parasite diversity on the evolution of hosts. This review referred only to studies that have specifically controlled or took into account phylogenetic information illustrated with parasites of mammals. Several points needing more investigation were identified with a special emphasis to develop the metabolic theory of epidemiology.

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1. Introduction

More than half of all organisms are parasites, with more than 10% of the metazoans living at the expense of other free-living organisms (de Meeûs and Renaud, 2002; Poulin and Morand, 2004; Dobson et al., 2008). However, we are far from having a good estimation of the number of parasite species. Although there is a dramatic decrease in the number of taxonomic experts over the last decades (Hugot et al., 2001; Pearson et al., 2011), increasing numbers of parasites and particularly protists or microbes (viruses and bacteria) have been recently described, thanks to new molecular technologies, such as next generation sequencing (Carpi et al., 2011). Estimates of parasite species richness and gaps in knowledge have been also greatly improved with the help of appropriate statistical analyses (see Walther and Moore, 2005), and Poulin (2014) has recently reviewed the recent advances in the evaluation of parasite species richness (see also Kamiya et al., 2014). The present review focuses on the following questions: why are there so many species of parasites? How does parasite diversity impact the diversification of their hosts? These pose the related questions: what are the factors or determinants that may explain parasite diversity among

host species? And, what are the consequences of this parasite diversity on the evolution of host-life history traits?

The search of the determinants of parasite species richness has been the topic of numerous studies (among many others, Poulin, 1995; Nunn et al., 2003a; Poulin and Morand, 2000, 2004), while the effects of parasite species richness on the evolution of host life-history traits (Moore and Wilson, 2002; Bordes and Morand, 2011) or host diversification (Buckling and Rainey, 2002; Nunn et al., 2004; Karvonen and Seehausen, 2012) have attracted less, but growing, attention (Morand et al., 2015).

This review presents a framework that helps at understanding causes and consequences of parasite species richness. As host–parasite interactions are asymmetrical exploited–exploiter relationships, ecological and epidemiological theories produce hypotheses to find the potential determinants of parasite species richness, while life–history theory helps for testing potential consequences of parasite diversity on the evolution of hosts. Investigating parasite species richness at the interspecific levels necessitates taking into account the evolutionary history of the hosts depicted by their phylogenies. Hence, this review will refer only to studies that have specifically controlled or taken into account phylogenetic information by using comparative method analyses (Harvey and Pagel, 1991; Morand and Poulin, 2003) illustrated with parasites of mammals. Moreover, only studies that have controlled or considered host sampling effort have been presented, as increasing parasite investigation, and hence the number of hosts investigated is known to be correlated with parasite species richness (Walther et al., 1995).

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2. Why parasite diversity matters? Asymmetry in host–parasite interactions

A framework based on evolutionary, ecological and epidemiological theories is needed to better draw hypotheses explaining parasite species richness. Such framework postulates the existence of a very asymmetrical relationship between a given host and its parasites, and therefore can be used to investigate the parasite diversity and its consequences using two theoretical domains from ecology and epidemiology.

Fundamentally, the relationships between hosts and their parasites are asymmetrical interactions. A parasite is totally dependent on its host for its reproduction and survival, and the parasite fitness is a compromise between a maximum exploitation of its host and the host responses through behavioural or immunological defences. In such a framework, the host availability and particularly the size of the host population is critical for the maintenance of the parasite. Each parasite species has to adapt to a given host species through these co-evolutionary interactions of parasite exploitation and host resistance. Direct interactions among parasite species may play little role compared to the indirect interactions through the host defence (mostly immunological defences). In this view, several comparative studies have suggested that parasite life-history traits have evolved in response to host life-traits independently of among community parasite interactions (Trouvé and Morand, 1998; Sorci et al., 2004; Morand et al., 2014).

From the exploited host side view, a given host has to deal with more than one parasite species as multiparasitism, or co-infection, is often the rule in natural systems (Bordes and Morand, 2011; Vaumourin et al., 2014). Then, a given host has to face multiple enemies.

Given this framework, theories are needed to produce hypotheses that explain the richness of parasite species, and the likely explanatory determinants. These hypotheses emerge from ecological and epidemiological theories.

3. Determinants of parasite species richness

As already mentioned, sampling effort was consistently and positively correlated with parasite species richness as observed in many comparative studies (Poulin, 1995; Walther et al., 1995; Walther and Morand, 1998; Nunn et al., 2003a). Only comparative studies on mammals, and taking into account sampling effort, are then reported in Table 1. Moreover, all of them also controlled for the potential influences of phylogenetic relatedness (Morand and Poulin, 2003).

3.1. Ecological determinants

The main hypotheses to explain the richness in parasite species originate from the biogeographical ecology with explaining factors such as latitudinal gradients, host body mass or geographical range.

Considering a group such as mammals, an increasing of species richness is observed from high to low latitudes (Kaufman, 1995; Schipper et al., 2008). It was then expected that parasite species richness would follow a similar latitudinal pattern (Poulin and Morand, 2000; Bordes et al., 2010). Contradictory results were observed on the latitudinal gradient of parasite species richness (Table 1). Lindenfors et al. (2007) for helminths of carnivores found, contrary to expectations, an increase of parasite species richness towards higher latitudes. Increased flea species richness in rodents towards higher latitudes was also observed by Krasnov et al. (2004). Recently, Bordes et al. (2010) reinvestigated the relationship between latitude and helminth species richness among 239 mammal species. They did not find any latitudinal effect on helminth species richness of mammals.

However, the pattern for microparasites seems to follow the latitudinal gradient of richness. For example, Nunn et al. (2005) showed that parasite species richness increases towards lower latitudes only for protozoan parasites in Primates. Interestingly, the recent discovery of new *Plasmodium* species in tropical primates and the potential risks for humans are in favour of non-human primate origins of *Plasmodium falciparum* in lower but species-rich latitude (Rayner et al., 2011). Bordes et al. (2011) also showed that viral diversity increases towards lower latitude in rodents. These results, among other concerning studies conducted at the intraspecific level such as Guernier et al. (2004) on pathogens of humans, emphasize the importance of environmental conditions (rainfall, temperature) on the survival of free-living stages or on the diversity of the potential arthropod-borne vectors.

More than 25 different mechanisms have been proposed to explain such latitudinal gradient of species diversity of free-living organisms (Gaston, 2000), which suggests that latitude is only a proxy variable for a wide range of bioclimatic factors such as rainfall and temperature. In some ways, parasites do not differ so widely from free-living counterparts regarding their life-history traits (Morand, 1996; Trouvé and Morand, 1998; Morand et al., 2014). Endoparasites like helminths live inside the host body and arthropod ectoparasites in the fur of their hosts, which may play an important role in terms of protection against the variability of abiotic conditions, and particularly for those parasitizing warm-blooded mammals. On the other hand, parasites using intermediate invertebrate hosts as vectors may be more dependent on the external abiotic conditions. We may then expect different relationships between latitude and parasite species richness according to parasite life-history and cycles (Table 1).

One potential explanation, which remains to be tested, is that host geographical range may increase in several mammal species towards higher latitude. Species living in higher latitude have higher geographical distribution size, which may favour parasite accumulation (but see below).

Another application of the ecological theory referred to the area–species diversity relationship (Rosenzweig, 1995), which differs from the island biogeography by the ecological mechanisms involved. The application of the area–species relationship to parasites postulates that hosts having a large geographical distribution range have accumulated, and sustained, a large number of parasite species, compared to those living in small geographical distribution (see first accounts in Dritschilo et al., 1975; Price and Clancy, 1983; Morand, 2000). Most of the comparative analyses, controlling for both phylogeny and sampling effort, found a positive correlation between the size of geographical range of mammals and parasite species richness both macro- or microparasites (Feliu et al., 1997; Krasnov et al., 2004; Torres et al., 2006; Lindenfors et al., 2007) (Table 1). A host species living on a large geographical range harbours a higher diversity of parasite species than a host species living in a more restricted geographical area. This pattern has been generally explained as large geographical range offers more opportunities for a host to be parasitized by several parasite species (Morand, 2000). However, macroecology offers a more likely epidemiological explanation, as mammal species that have large distribution ranges also live in high local densities (Brown, 1995).

Larger body size has often been predicted to favour higher parasite species richness, because larger-bodied hosts are supposed to represent larger habitats for parasite colonization, using the analogy of the theory of island biogeography of MacArthur and Wilson (1967) and Kuris et al. (1980). Empirical studies that have tested this prediction have yielded contradictory results. Ezenwa et al. (2006) and Bordes et al. (2008) reported positive correlation between host body size and parasite species richness, while Feliu et al. (1997), Nunn et al. (2003a), Krasnov et al. (2004) and Korrallo et al. (2007) found no relationship between these two variables in mammals (Table 1).

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