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



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## 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).

**Table 1**  
Some studies that investigated the determinants of parasite diversity of mammals.

| Domains of hypotheses    | Determinant                                 | Parasite organisms           | Hosts                 | Effect                               | Reference               |
|--------------------------|---|------------------------------|-----------------------|--------------------------------------|-------------------------|
| Biogeography             | Latitudinal gradient                        | Helminths                    | Mammals               | No                                   | Poulin, 1995            |
|                          |   | Helminths                    | Mammals               | No                                   | Morand, 2000            |
|                          |   | Helminths                    | Mammals               | No                                   | Bordes et al., 2010     |
|                          |   | Helminths                    | Primates              | No                                   | Nunn et al., 2005       |
|                          |   | Helminths                    | Carnivores            | Positive                             | Lindenfors et al., 2007 |
|                          | Geographic area size                        | Fleas                        | Rodents               | Positive                             | Krasnov et al., 2004    |
|                          |   | Protists                     | Primates              | Negative                             | Nunn et al., 2005       |
|                          |   | Microparasites               | Rodents               | Negative                             | Bordes et al., 2011     |
|                          |   | Helminths                    | Rodents               | Positive                             | Feliu et al., 1997      |
|                          |   | Fleas                        | Rodents               | Positive                             | Krasnov et al., 2004    |
| Insular biogeography     | Host body size                              | Helminths                    | Carnivores            | Positive                             | Torres et al., 2006     |
|                          |   | Macro-, microparasites       | Carnivores            | Positive                             | Lindenfors et al., 2007 |
|                          |   | Helminths                    | Mammals               | No                                   | Morand and Poulin, 1998 |
|                          |   | Helminths                    | Rodents               | No                                   | Feliu et al., 1997,     |
|                          |   | Macro-, microparasites       | Primates              | No                                   | Nunn et al., 2003a      |
| Epidemiology             | Host density                                | Macro-, microparasites       | Ungulates             | Positive                             | Ezenwa et al., 2006     |
|                          |   | Helminths                    | Mammals               | Positive                             | Morand and Poulin, 1998 |
|                          |   | Nematodes                    | Mammals               | Positive                             | Arneberg, 2002          |
|                          |   | Fleas                        | Rodents, Insectivores | Positive                             | Stanko et al., 2002     |
|                          |   | Helminths                    | Primates              | Positive                             | Nunn et al., 2003a      |
|                          | Host longevity                              | Helminths                    | Carnivores            | Positive                             | Torres et al., 2006     |
|                          |   | Macro-, microparasites       | Carnivores            | Positive                             | Lindenfors et al., 2007 |
|                          |   | Helminths                    | Mammals               | Negative                             | Morand and Harvey, 2000 |
|                          |   | Fleas                        | Insectivores          | No                                   | Stanko et al., 2002     |
|                          |   | Helminths                    | Carnivores            | No                                   | Torres et al., 2006     |
|                          | Home range                                  | Macro-, microparasites       | Ungulates             | Positive                             | Ezenwa et al., 2006     |
|                          |   | Helminths                    | Primates              | Negative                             | Nunn et al., 2003a      |
|                          |   | Helminths                    | Ungulates             | No                                   | Ezenwa et al., 2006     |
|                          |   | Direct-transmitted parasites | Carnivores            | Negative                             | Lindenfors et al., 2007 |
|                          |   | Helminths                    | Ungulates             | No                                   | Bordes et al., 2009     |
| Group size               | Helminths                                   | Carnivores                   | Negative              | Bordes et al., 2009                  |                         |
|                          | Helminths                                   | Glires                       | Negative              | Bordes et al., 2009                  |                         |
|                          | Macro-, microparasites                      | Primates                     | No                    | Nunn et al., 2003a                   |                         |
|                          | Macro-, microparasites                      | Ungulates                    | Positive              | Ezenwa et al., 2006                  |                         |
|                          | Colony size                                 | Viruses                      | Bats                  | Negative                             | Gay et al., 2014        |
| Helminths                |   | Bats                         | No                    | Gay et al., 2014                     |                         |
| Ectoparasites            |   | Bats                         | No                    | Bordes et al. 2008; Gay et al., 2014 |                         |
| Ecology and epidemiology | Shape/fragmentation of geographic area size | Viruses                      | bats                  | Positive                             | Maganga et al, 2014     |
|                          |   | Viruses                      | Bats                  | Negative                             | Gay et al., 2014        |
|                          |   | Ectoparasites                | Bats                  | No                                   | Gay et al., 2014        |
|                          |   | Helminths                    | Bats                  | Negative                             | Gay et al., 2014        |
|                          |   | Helminths                    | Rodents               | No                                   | Bordes et al., 2007     |
| Behaviour                | Host sociality                              | Ectoparasitic arthropods     | Rodents               | Negative                             | Bordes et al., 2007     |
|                          |   | Viruses                      | Chiropteres           | No                                   | Maganga et al., 2014    |
|                          | Migration                                   | Viruses                      | Chiropteres           | No                                   | Maganga et al., 2014    |
|                          | Roosting                                    | Viruses                      | Chiropteres           | No                                   | Maganga et al., 2014    |
|                          | Diving behaviour                            | Ectoparasitic arthropods     | Mammals               | Negative                             | Felso and Rozsa, 2007   |
|                          | Ranging (defensibility)                     | Viruses                      | Primates              | Positive                             | Nunn and Dokey, 2006    |
|                          |   | Protists                     | Primates              | No                                   | Nunn and Dokey, 2006    |
|                          |   | Helminths                    | Primates              | Positive                             | Nunn and Dokey, 2006    |

This contradictory result may not suggest idiosyncratic relationships between a given host group and a given parasite group, but rather confounding relationships among body mass and several ecological and life traits as emphasized by macroecological studies (Brown, 1995) and the metabolic theory of ecology (Brown et al., 2004).

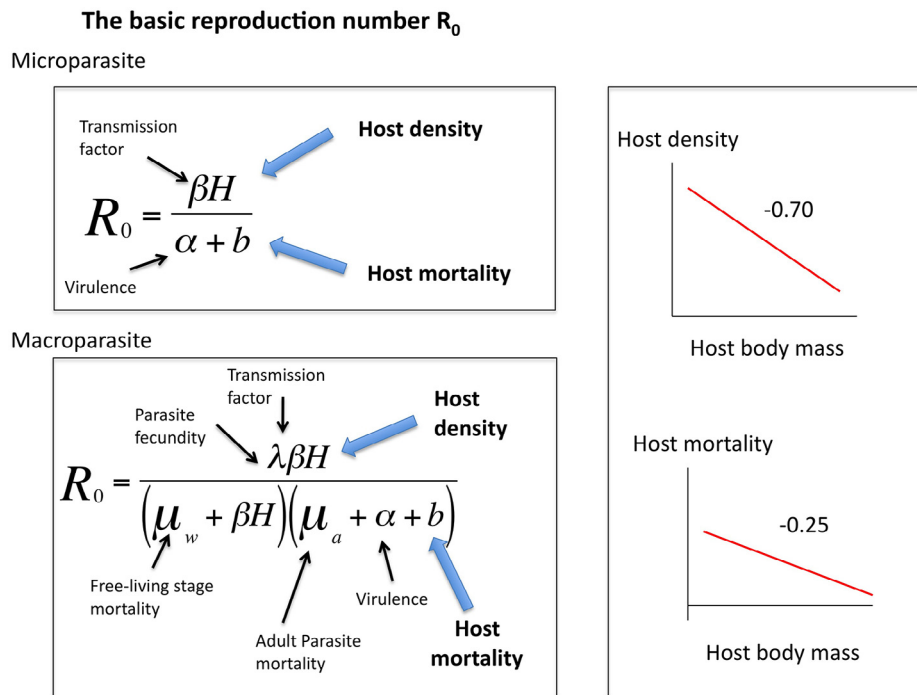
### 3.2. Epidemiological determinants

The determinants of parasite species richness in animals have been also epidemiologically linked to their ecology, such as host density and home range, and their life traits such as longevity, litter size of number of breeding seasons (Poulin and Morand, 2000; Bordes et al., 2007, 2011; Turmelle and Olival, 2009; Luis et al., 2013).

Epidemiological models are useful to estimate parasite invasiveness using the basic reproductive number  $R_0$  (Anderson and May, 1991; Diekmann and Heesterbeek, 2000; Morand and Deter, 2008). For microparasites (bacteria, viruses, protists and fungi),  $R_0$  is defined

as the number of secondary infections produced by a unique individual infected host following entrance in a population of fully susceptible/naive hosts. For macroparasites (helminths and arthropods),  $R_0$  is defined as the average number of female offspring produced throughout the lifetime of a unique female parasite introduced in a non-parasitized host population. When  $R_0$  is greater than unity, the parasite, or the infection, can successfully invade the host population. As emphasized by Poulin and Morand (2000), a new parasite species can successfully invade a multi-parasitized host population, and increase the overall parasite species richness, if  $R_0$  is greater than unity for that species in this multi-parasitized host population.

Whatever the type of parasite (micro or macro), the expression for  $R_0$  includes two host features that affect parasite invasibility: the host population density and the intrinsic natural host mortality rate (Fig. 1). These host features may then be considered as likely epidemiological determinants of parasite species richness.



**Fig. 1.** Expression of the basic transmission rate ( $R_0$ ) for the case of microparasites (i.e. viruses) and macroparasites (i.e. helminths with direct transmission) (for derivations of these expressions see Morand and Deter, 2008), emphasizing the importance of two host traits, longevity and density, as likely determinants of parasite invasion and then parasite species richness. In the right panel, relationships showing that both density and longevity are in allometry with host body mass (after Brown, 1995).

Between these two epidemiological determinants, host longevity and host density that have been highlighted by epidemiological models, only host density was found as a consistent factor associated with parasite species richness of mammals (Table 1). Indeed, all comparative analyses have shown a positive relationship between host density and parasite species richness, either helminths (Arneberg, 2002; Nunn et al., 2005; Torres et al., 2006), ectoparasites (Stanko et al., 2002), or microparasites (Lindenfors et al., 2007). The lack of relationship between host longevity and parasite species richness (Stanko et al., 2002; Torres et al., 2006), or the positive or negative relationships observed (Morand and Harvey, 2000; Ezenwa et al., 2006) appear more puzzling. However, host longevity in wild can be affected by environmental adversities including parasite load and richness (but see below).

The role of home range, i.e. the area used in daily and seasonal movements, in explaining parasite species richness highlights also the importance of epidemiology in explaining parasite species richness. Negative relationships between home range size and parasite diversity have been reported for primates (Nunn et al., 2003a, 2003b), carnivores (Lindenfors et al., 2007; Bordes et al., 2009) and for glires (Bordes et al., 2009), whereas a lack of relationship was observed for ungulates (Ezenwa et al., 2006; Bordes et al., 2009). These observations contradict a simple ecological explanation that would have predicted higher parasite diversity in host species having large home ranges, similarly to the effect of geographical area size on parasite species richness. Indeed, Bordes et al. (2009) showed that host density and home range size are negatively linked. A decrease in host density associated with larger home range may reduce transmission of directly transmitted parasites and consequently may influence parasite species richness.

Group size or colony size (for bats) was also expected to positively affect parasite species richness. Again, contradictory results were reported either for group size in primates and ungulates (Nunn et al., 2003a; Ezenwa et al., 2006) and for colony size of bats (Bordes et al., 2008; Gay et al., 2014) (but see below).

### 3.3. The search of new determinants

Recently Gay et al. (2014) and Maganga et al. (2014) tested the influences of both the size and the shape of host geographic distribution, where the shape of the geographic distribution was estimated using the ratio of the total perimeter to the total geographic area. Two alternative explanations have been proposed to explain the linking host distribution shape and parasite species richness (Maganga et al., 2014). A first geographical hypothesis is that a longer border of the geographical distribution, due to distribution fragmentation, may entail higher habitat diversity, which would increase contacts with various parasites. A second hypothesis is that longer border may reflect host species vulnerability due to area fragmentation, with associated reduced host population size leading to a decrease in parasite transmission and then overall decrease of parasite species richness.

The opposite patterns found between bats from Africa (Maganga et al., 2014), with a positive relationship between viral diversity and shape of the geographical distribution, and bats from Southeast Asia (Gay et al., 2014), with a negative relationship between these two variables, suggests that several mechanisms may act.

The shape of the distribution range is the historical product of speciation, extinction and range expansion (Gaston, 1998). Host species that have experienced past expansion and contraction of their range through past climate change may then have accumulated parasite species, especially in refuges (Goüy de Bellocq et al., 2002). In this case, we may hypothesize that the genetic structure of species living in highly fragmented distribution would be high, reflecting complex historical events, and positively associated with parasite diversity (Pariselle et al., 2003; Turmelle and Olival, 2009).

On the other hand, species living in ongoing human-disturbed areas may experience drastic decreases in population size and increased extinction threat, particularly in Southeast Asia



(Schipper et al., 2008). Hence, a second hypothesis is that the increase of the fragmentation of the species distribution reflects the ongoing and recent massive fragmentation of habitats. This can be supported by showing a positive association between host extinction threat, as given by the IUCN status, and shape of host geographical distribution (defined as the ratio of the total perimeter to the total distribution). This positive association has been found in bats of Southeast Asia (Gay et al., 2014). Here, an increase of host distribution shape may reveal species vulnerability, with associated decreased population size leading to an overall decrease in parasite species richness. Finally, investigating the distribution shape draws attention on environmental factors that affect host species on the edge of their geographic distribution in the face of the ongoing global change.

Behavioural ecology has also inspired the search of new determinants such as sociality, grooming and preening behaviour (Altizer et al., 2003; Ezenwa, 2004).

Bat colony size is an example of the difficulty to disentangle the effect of population size, an epidemiological determinant, and the effect of social complexity, which reflects the structure of the social interactions between members of the colony. It is this then not surprising that no consistent trend emerges from comparative studies that have investigated this determinant by taking into account only the number of individuals in typical bat colonies (Bordes et al., 2008; Gay et al., 2014).

Bordes et al. (2007) took a different point of view and rather than using the size of host groups (rodents in their study) they used an index of social complexity. They found that the increase of social complexity is negatively correlated with ectoparasite species richness, which suggests that the evolution of sociality in rodents could be associated with behavioural traits that reduce ectoparasitism load, such as allogrooming, improve parasite avoidance, or dilute infection risks as suggested by Altizer et al. (2003).

Table 1 gives the few studies that have investigated behavioural traits as potential determinants, such as diving behaviour in mammals, roosting behaviour and migration behaviour in bats, diving behaviour, and ranging behaviour (defensibility) in primates. The contrasting results observed are reflecting either too few extensive studies or the lack of consideration of host defence (with the exception of Nunn and Dokey, 2006). Indeed, few comparative studies have tested the relationships between parasite diversity and behavioural defence in mammals in comparison with studies concerning birds or in fish (Arnal et al., 2000).

#### 4. Parasite species richness and the evolution of host-life traits

As emphasized above, host population density appears critical for the maintenance of parasite species richness. Host species living in high densities face high parasite species diversity and should have evolved adapted immune defences. However, costly immune defences have to be paid in the physiological energetic budget through trade-offs among competitive tasks (such as reproduction). Hence, parasite species richness should be linked to host fitness deterioration and to investment in immune defences through increased

energetic expenses leading to trade-offs between immunity and other life-history traits.

##### 4.1. Cumulative effects of parasite species richness

Multiple infections (i.e. simultaneous infections with multiple parasite species in a individual host), also called polyparasitism, are the rule, in natural populations (Bordes and Morand, 2009a, 2011). Deleterious effects link to higher parasitic diversion of resources and/or cumulative damages to the hosts are observed in relation to greater overall parasite loads (Bordes and Morand, 2011).

If host ecological traits affect parasite diversity (Arriero and Moller, 2008; Bordes and Morand, 2009a) and parasites impact host life-traits by diverting resources or eliciting costly immune or behavioural defences (Martin et al., 2008), then potentially strong interactions are expected between determinants and impacts of parasite diversity both at ecological and evolutionary times. The observed parasitic loads and parasite diversity in natural populations may then result from evolutionary- or ecologically-mediated interactions between host life-traits such as growth, survival, reproduction and immunity (Hanssen et al., 2004; Martin et al., 2008; van der Most et al., 2011).

##### 4.2. Parasite species richness and host immunity

White blood cell counts, spleen size, immune gene diversity have been used for investigating the impacts of parasite species richness on immune diversity (Morand and Poulin, 2000a; Nunn, 2002; Nunn et al., 2003b; Wegner et al., 2003; Ezenwa, 2004; Guernier et al., 2004; Šimková et al., 2006, 2008; Turmelle and Olival, 2009; Luis et al., 2013).

When investigating the maintenance of host genetic variation through co-evolutionary host–pathogen interactions, a first prediction suggests the existence of a link between immunogenetic diversity, such as Major Histocompatibility Complex polymorphism, with high diversity of parasites (Wegner et al., 2003; Sommer, 2005). This pattern has been confirmed in Palearctic rodents, with high MHC genetic diversity found correlated to high parasite species richness (Goüy de Bellocq et al., 2008). Several studies in fish have also shown that individual hosts harbouring higher parasite species have higher genetic diversity at the MHC genes (Wegner et al., 2003; Šimková et al., 2006). Such pattern has been recently observed in rodents from Southeast Asia at both species and individual levels (Pilosof et al., 2014).

##### 4.3. Trade-offs with immunity

Concerning host metabolism, several experimental studies have linked parasitic infestations or immune stimulation to higher basal metabolic rates and costs in birds and mammals. While basal metabolic rate (BMR) scales in allometry with body mass, the reasons why some species have higher or lower metabolic rates than predicted from their body mass still remain unclear despite numerous studies (White and Seymour, 2004). BMR was expected to be positively linked to parasite loads. This was observed across mammal

**Table 2**  
Comparative studies reporting impacts of multiple infections in mammals.

| Level of impact        | Host taxa | Parasite taxa | Response to parasite species richness | Reference  |
|------------------------|-----------|---------------|---------------------------------------|--|
| Immuno-genetics        | Rodents   | Helminths     | Increased variability at MHC genes    | Goüy de Bellocq et al., 2008; Pilosof et al., 2014 |
| Demography             | Mammals   | All parasites | Male-biased mortality                 | Moore and Wilson, 2002                             |
| Demography             | Rodents   | Virus         | Litter size                           | Bordes et al., 2011                                |
| Metabolism             | Mammals   | Helminths     | Increase in basal metabolic rate      | Morand and Harvey, 2000; Bordes and Morand, 2009b  |
| Sleep duration         | Mammals   | All parasites | Increase in sleep duration            | Preston et al., 2009                               |
| Sexual size dimorphism | Mammals   | All parasites | Positive association                  | Moore and Wilson, 2002                             |

species with higher BMR positively related with helminth species richness (Morand and Harvey, 2000), but not in the case of ectoparasitic fleas (Korallo et al., 2007).

Parasite diversity was also linked to increased sleep duration in mammal taxa (Preston et al., 2009). The main explanation is a potential positive link between sleep duration and the strength of immune defences due to energy saving.

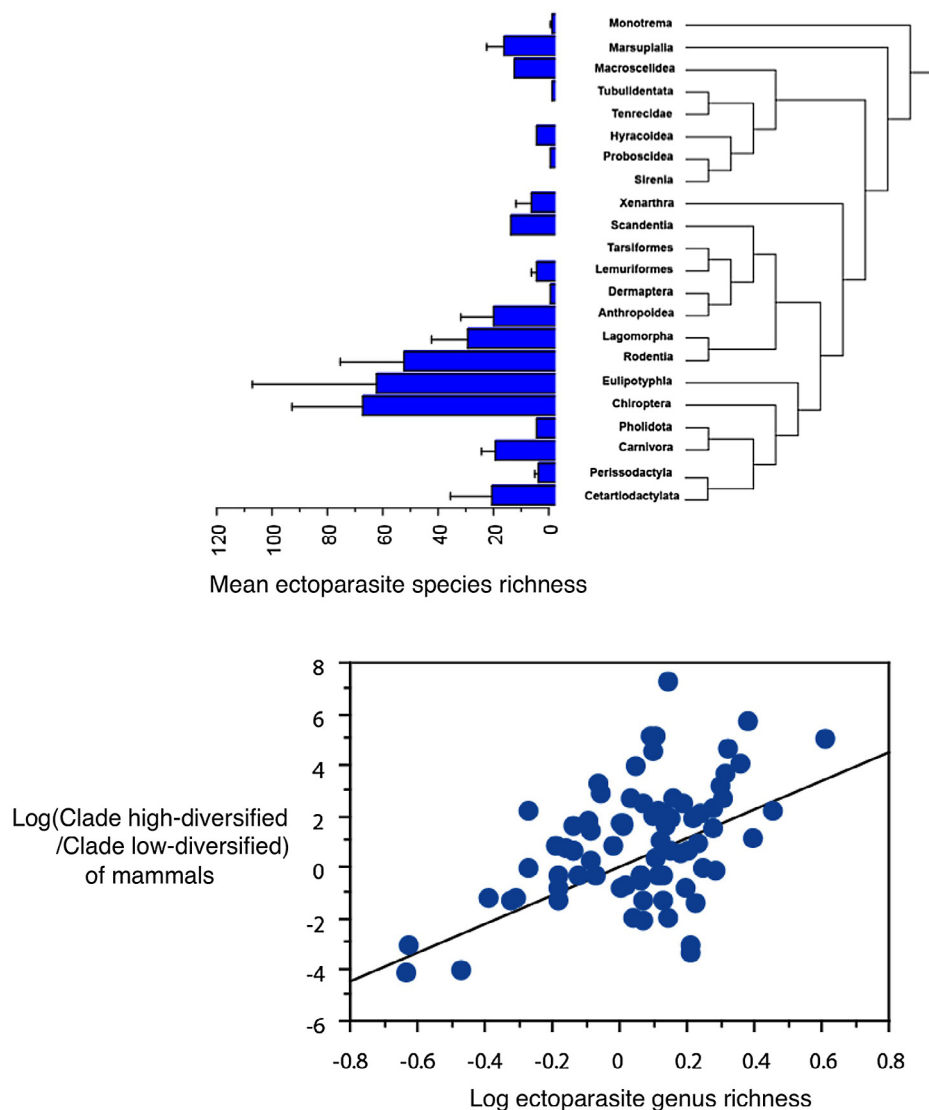
Taken together, all these results are congruent with the findings that higher helminth species richness in mammals are linked with higher white blood cell counts across species (Bordes and Morand, 2009b), but compared to others that also linked higher immune investment in host species or populations challenged by more parasite species compare to others (Šimková et al., 2008) (Table 2).

Due to the complex links between parasitism, energy and immune defences, more investigations are needed to connect metabolism and parasite pressures associated with high investment in immunity.

## 5. Parasite diversity and host diversification

Parasites are hypothesized to favour host species radiation (Buckling and Rainey, 2002; Nunn et al., 2004; Yoder and Nuismer, 2010; Karvonen and Seehausen, 2012). The rationale beyond this hypothesis is that parasites impose costs and then may enhance host diversification through sexual selection (Moore and Wilson, 2002; Krasnov et al., 2012). Moore and Wilson (2002) gave support to the hypothesis that parasites contribute to the relationship between sexual size dimorphism (SSD) and male-biased mortality by showing a positive relationship between male-biased parasitism and the degree of sexual selection measured by the degree of SSD. However, a study on rodent fleas found that SSD is not related to sex-biased infection (Morand et al., 2004).

Nunn et al. (2004) were the first to test the hypothesis that parasites favour host species radiation. Using a comparative method, they showed that greater parasite diversity in primate species was correlated with highly diversified primate clades. A similar finding was observed for ectoparasite species richness of mammals (Fig. 2).



**Fig. 2.** (A) Variability of ectoparasite species richness among 113 families of mammals (20 orders) (data from Kim, 1985; see Poulin and Morand, 2004). (B) Ectoparasite species richness is related to mammal diversification. The statistical analysis follows Nunn et al. (2004), where the change in the number of descendent clades is related to the change in the number of ectoparasite species, estimated using a modified version of the independent contrast method (Agapow and Isaac, 2002), for each node of the mammal phylogeny (from Binida-Emonds et al., 2007).

## 6. Conclusion/perspectives

Host–parasite interactions are characterized by a strong asymmetry with one host species facing sometimes a huge diversity of parasites (Petney and Andrews, 1998; Poulin and Morand, 2004; Steinmann et al., 2010) as multiple infections are the rule.

This review attempted to give some hypothesis-based explanations of parasite diversity and how this parasite diversity impacts the evolutionary ecology of their hosts. Although the mechanisms of parasite diversification are far from being elucidated, we have emphasized the main importance of both host density and host defence using a simple framework based on epidemiological and ecological theories.

The diversity of parasites, transmissions, impacts and interactions in natural and disturbed ecosystems are a knowledge frontier in ecological parasitology (Tompkins et al., 2010; Johnson and Hoverman, 2012). Several points need more investigation. The first one obviously concerns the mechanisms of parasite diversification (Rascalou et al., 2012; Morand et al., 2014), which will irrigate studies on community ecology of parasites with evolutionary ecology and epidemiology (Morand and Krasnov, 2008). The second domain of research concerns the role of parasite diversity in food web stability and resilience (Arias-González and Morand, 2006; Lafferty et al., 2006; Mouritsen et al., 2011), as recent findings has shown that host centrality in food web explains parasite species richness (Anderson and Sukhdeo, 2011).

More importantly, the emphasis put here on the importance of both epidemiology and life-traits urges the development of a metabolic theory of epidemiology (Bolzoni et al., 2008a, 2008b) as an extension of the metabolic theory of ecology (Allen et al., 2002; Brown et al., 2004), based on the existence of allometric relationships among body mass, host life-history, host ecological and biogeographical traits (Brown, 1995), which have been already used in epidemiological modelling (De Leo and Dobson, 1996) or to explore the evolution of parasite life-traits and parasite body size diversification (Morand and Poulin, 2000b, 2002).

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## Conflict of interest

The authors declared that there is no conflict of interest.

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