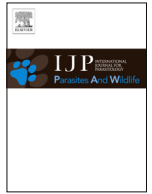




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## Parasite and viral species richness of Southeast Asian bats: Fragmentation of area distribution matters



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### ABSTRACT

Interest in bat-borne diseases and parasites has grown in the past decade over concerns for human health. However, the drivers of parasite diversity among bat host species are understudied as are the links between parasite richness and emerging risks. Thus, we aimed at exploring factors that explain macro and microparasite species richness in bats from Southeast Asia, a hotspot of emerging infectious diseases. First, we identified bat species that need increased sampling effort for pathogen discovery. Our approach highlights pathogen investigation disparities among species within the same genus, such as *Rhinolophus* and *Pteropus*. Secondly, comparative analysis using independent contrasts method allowed the identification of likely factors explaining parasite and viral diversity of bats. Our results showed a key role of bat distribution shape, an index of the fragmentation of bat distribution, on parasite diversity, linked to a decrease for both viral and endoparasite species richness. We discuss how our study may contribute to a better understanding of the link between parasite species richness and emergence.

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### 1. Introduction

Incidence of emerging infectious diseases (EIDs) has dramatically increased in recent decades (Jones et al., 2008). A majority of EIDs are zoonoses and most of them originate in wildlife (zoonotic spillover). EID events are often due to environmental alteration, including agricultural intensification and habitat modification, global trade and travel (Cunningham, 1996; Daszak et al., 2000). Several studies and reviews have suggested that the risk of disease transmission from wildlife to humans should increase with biodiversity loss and the expansion of human populations (Dobson et al., 2006; Keesing et al., 2009), as humans will get into contact with a large pool of known and unknown zoonotic pathogens from wildlife (Mahy and Brown, 2000; Murray and Daszak, 2013). Bacteria and rickettsia represent the majority of EIDs, viral and

prion pathogens cause 25.4% and other parasites 20.3% of EID events (Jones et al., 2008).

Among known reservoir species of viral EIDs, bats, which represent 20% of mammal species (Simmons, 2005), play an important role in the maintenance and spread of various viral diseases (Sulkin and Allen, 1974; Ghatak et al., 2000; McColl et al., 2000; Olival et al., 2012; Luis et al., 2013), including members of the alphaviruses, flaviviruses, paramyxoviruses, rhabdoviruses, coronaviruses and arenaviruses among others. Several notable bat-borne viruses are a public health concern in Southeast Asia (SEA) including Nipah virus, lyssaviruses and Severe Acute Respiratory Syndrome coronavirus (Mackenzie et al., 2003). While bats are increasingly viewed as a threat to human health, these mammals have important roles in ecosystems such as pollination, seed dispersal and predation on insects. They are excellent bioindicators of environmental changes as they are sensitive to a wide range of anthropogenic disturbances such as urbanization, agricultural intensification, habitat loss and fragmentation (Clarke et al., 2005; Jones et al., 2008). Understanding the ecology of these potential reservoirs of zoonotic pathogens is needed for improving

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management of bats and their habitats, ultimately ensuring the health of humans, livestock and wildlife species, while keeping their functional roles in the ecosystems (Breed et al., 2006).

The potential of human–bat interactions, either direct or indirect, may be underappreciated and greater than expected for some species. While bats rarely seek direct contact with humans, they often roost in or near human dwellings, which can lead to accidental contact or exposure to bat excreta. For example, Nipah virus has been transmitted to people who have eaten bat-contaminated date palm sap (Luby et al., 2006).

Wild animals are known to host different pathogens at the same time (Petney and Andrews, 1998; Drake and Bundy, 2000; Bordes et al., 2008; Bordes and Morand, 2011). Poly-parasitism (or multiple infections) and infection dynamics in host species are important features to understand the mechanisms of EID; the risk of disease transmission may depend on the pathogen richness found in natural reservoir species (Wolfe et al., 2005). Morse (1993) termed this pathogen diversity in wildlife hosts the ‘zoonotic pool’. In the literature, most studies emphasized the links between biodiversity loss and the risk of pathogen emergence and transmission (Keesing et al., 2009; Derne et al., 2011), whereas very few investigated the role of parasite diversity, or the size of the ‘zoonotic pool’, in the risk of emergence.

Investigating parasitic and microbial diversity in bat species may help to identify species that are reservoir sources of a greater diversity of pathogens and to understand factors influencing this richness, particularly those related to life or ecological traits. The determinants of parasite diversity in wildlife may be linked to their biogeography (e.g., latitude, distribution area), ecology (e.g., density, migration), life-history traits (e.g., longevity and fecundity) or immunity (e.g., white blood cell counts, spleen size, immune gene diversity) (Morand and Poulin, 2000; Wegner et al., 2003; Nunn et al., 2003b; Guernier et al., 2004; Ezenwa, 2004; Bordes et al., 2007; Šimková et al., 2008; Pedersen and Gries, 2008; Turmelle and Olival, 2009; Bordes and Morand, 2011; Nunn, 2012; Luis et al., 2013). Some of these determinants can also influence the probability of contact of bats with humans and thus the potential risk of contamination and transmission; a widely distributed bat species living at high density has a greater probability of repeated contacts with humans than a species living in low density with a restricted distribution. This may be particularly true for synanthropic species that appear to be generalist in their ecology and rich in the parasite diversity they harbour (Herbreteau et al., 2012). Finally, a question rarely investigated about species richness is: “is there any correlation between microparasite (viruses, parasitic bacteria, protists, fungi) richness and macroparasite (helminths and arthropods) richness in bats?” (Bordes et al., 2008; Turmelle and Olival, 2009). The diversity of microparasites (e.g., virus and bacteria) may then depend on the diversity of macroparasites (e.g., helminths) through the activation and maintenance of different pathways of the immune system (Bordes and Morand, 2011; Ezenwa and Jolles, 2011). A positive correlation may suggest that hosts with high macroparasite diversity also harbour high viral and bacterial richness.

We focused our study on Southeast Asia (SEA), a hotspot of biodiversity and EIDs with pandemic potential (Myers et al., 2000; Jones et al., 2008; Coker et al., 2011). It is also a natural laboratory to study the evolutionary history (Guillén et al., 1997) and the impact of high human environmental pressures (Sodhi and Brook, 2006; Clements et al., 2006; Stibig et al., 2007; Wilcove et al., 2013). For our study, we defined parasite species richness (PSR) as the total number of parasite species such as microparasites as well as macroparasites identified in a given host (Poulin and Morand, 2004; Bordes et al., 2007) at the regional scale of SEA. In the present study we aimed at investigating the likely factors that may explain PSR in bats from SEA. From the literature we

compiled information on parasitic and infectious agents in SEA bats found, as well as information available on their life-history and ecological traits. Then, we tested potential factors that may explain the whole pool of parasite diversity in bats using phylogenetic comparative analyses and model selection.

We tested hypotheses related to (1) influences of the size and shape of the geographic distribution (index of the fragmentation of bat distribution, defined as the ratio of the surface of the distribution area to the edge length); (2) the size of bat colonies and the number of breeding seasons. We hypothesized that a large area should favor the accumulation of parasites and that an increase of fragmentation of bat distribution, potentially linked with increased habitat diversity, lead to an increase of the overall parasite diversity. We also hypothesized that bats species living in large colonies with a high number of breeding seasons will support a larger pool of parasite species due to large susceptible populations.

## 2. Materials and methods

### 2.1. Data on bats and their parasites

Information on bats and their parasites were compiled from the literature. Only Southeast Asian countries were selected: Brunei; Cambodia; Indonesia; Lao People’s Democratic Republic; Malaysia; Myanmar; Philippines; Singapore; Thailand; Timor; and Vietnam.

A total of 292 species bats inventoried in SEA were included in the database. Several variables were documented for each host species: distribution size; distribution shape (border edge, as a measure of the fragmentation of bat distribution area estimated by the ratio of the distribution circumference to the distribution area size); breeding seasons per year; colony size and average adult body mass (Table 1). The distribution shape ranges from 0 (cylindrical and compact distribution area) to 1 (fragmented distribution area) (Fortin et al., 2005). Information was gathered from several sources: IUCN Red List (<http://www.iucnredlist.org/>); Wilson and Reeder «Mammal Species of the World» (<http://www.bucknell.edu/msw3/>); and Harrison Institute (<http://www.sc.psu.ac.th/batdb/index.asp>). In addition, published articles were obtained through match searches using Google Scholar (<http://scholar.google.com>) and the Web of Knowledge (<http://apps.webofknowledge.com/>).

Data on parasite species richness (PSR), which is the number of parasite species described infecting a given host species, were obtained through searches on Web of Science. To identify relevant information binomial names of every Southeast Asian bat species were combined with related terms (parasite, ectoparasite, endoparasite, virus, bacteria, fungi, helminths, pathogen and disease). All resulting abstracts and available full texts were examined. We examined 964 publications from 1959 to July 2012 and identified 637 species of parasites in SEA.

In addition we used specific databases for SEA, such as the database of Armed Forces Research Institute of Medical Sciences (<http://www.afpmb.org/content/welcome-literature-retrieval-system>); the Liverpool database (<http://www.zoonosis.ac.uk/eid2>) for additional records of viral richness; and the British Natural History Museum database (<http://www.nhm.ac.uk/research-curation/research/projects/host-parasites/database/index.jsp>) for helminths.

### 2.2. Sampling effort and investigation effort

We measured sampling effort, or ascertainment bias, in two ways. First, we defined the ‘sampling effort’ as the sample size or number of individual bats tested for a given parasite or microbe screened (positive or negative). Second, the ‘investigation effort’ is the number of publications about a given parasite or microbe for a given host species, which represents the research effort for

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