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Progress on research on rodents and rodent-borne zoonoses in South-east Asia

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Abstract. This review aims to synthesise knowledge regarding the taxonomy of South-east Asian murine rodents and the challenges associated with the identification of habitat preferences and associated rodent-borne diseases. Recent studies concerning the *Rattini* tribe have identified unclear species boundaries that would benefit from further investigation. The development of barcoding may allow more accurate identification of rodents, specifically for complex species. However, knowledge on the distribution and habitat specialisations of many common murine rodents is still scarce, particularly regarding the specific habitat preferences of most synanthropic rodent species (*Rattus tanezumi* or *Rattus exulans*). Several studies have analysed the prevalence of major rodent-borne diseases in South-east Asia and it appears that the greatest risk of rodent zoonoses are in the lowland rain-fed and irrigated landscapes, generally in and around rice fields.

Additional keywords: barcoding, habitat, phylogeny, *Rattini*, *Rattus*.

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Introduction

Rodents are recognised as hosts of at least 60 zoonotic diseases that represent a serious threat to human health (Meerburg *et al.* 2009). To better understand the potential epidemiology of an individual rodent-borne disease, first an accurate identification of the rodent host at the species level is required. For example, several studies have demonstrated that some rodent species considered as important reservoir hosts actually consist of several cryptic species (e.g. *Rattus rattus* species complex) or divergent mitochondrial (mt) DNA lineages (but see Robins *et al.* 2008; Lack *et al.* 2012), which may play different roles in the transmission of diseases. Once the rodent taxonomy has been defined, accurate identification of associated zoonotic pathogens and/or parasites is required, which requires the use of improved screening methods where possible (e.g. Ahmed *et al.* 2009; Al-Sabi and Kapel 2011). The risk to human health posed by major rodent-borne pathogens such as hantaviruses or *Yersinia pestis* (the agent of bubonic or pneumonic plague) illustrates the

need to clearly identify rodent reservoirs and reservoir complexes (Haydon *et al.* 2002). Finally, information on the ecology, particularly in relation to habitat use, is also needed in order to identify high-risk environments and to better prevent and manage disease.

To understand disease ecology and parasite transmission, it must be considered that not all hosts are equally involved in parasite transmission, with some individuals or species being responsible for a disproportionate number of transmission events (Paull *et al.* 2012). Spatial factors are another source of heterogeneity, with some habitats or landscapes promoting either enhanced transmission or enhanced parasite and/or vector persistence (Ostfeld *et al.* 2005; Lambin *et al.* 2010).

This review aims to collate the current knowledge of South-east Asian murine rodent taxonomy, diversity of associated pathogens and habitat preferences and relate this to the challenges encountered in obtaining these data. Many of the results presented here are the outcome of the recent CERoPath

project (Community Ecology of Rodents and their Pathogens in a South-east Asian changing environment), which aimed at better understanding the relationships between rodent-borne diseases, rodents and their habitats using intensive field work, molecular screening and geospatial analyses (Pagès *et al.* 2010; Blasdell *et al.* 2011; Herbreteau *et al.* 2011; Dupuy *et al.* 2012; Bordes *et al.* 2013; Pumhom *et al.* 2014, 2015; Cosson *et al.* 2014; Jiyipong *et al.* 2015).

South-east Asia is a hot spot for both emerging infectious diseases (Coker *et al.* 2011) and threatened species (Sodhi *et al.* 2004; Wilcove *et al.* 2013), with the latter thought to be a significant contributing factor to the increase in outbreaks of infectious diseases (Morand *et al.* 2014). Asian rats are known to host numerous pathogens but are still difficult to identify to species level using morphological or karyotypic criteria (Badenhorst *et al.* 2009; Chaval *et al.* 2010). Moreover, reliable species identification is hampered by our imprecise knowledge of South-east Asian rat taxonomy, the lack of clear species limits within some genera (e.g. *Rattus*, *Maxomys*, *Niviventer*) and problematic access to reference specimens (Chaval *et al.* 2010; Pagès *et al.* 2010).

The habitat preferences of South-east Asian murine rodents are poorly known due primarily to a paucity of studies (Adler 1995; Adler *et al.* 1999; Aplin *et al.* 2003; Singleton *et al.* 2003; Wells *et al.* 2006, 2007). Moreover, most studies have assessed the potential impacts of rodents on agriculture or public health, and have focused primarily on peri-urban or agricultural areas (particularly rice paddy fields; Singleton 2003; Singleton *et al.* 2003, 2010; Brown *et al.* 2005; John 2014). Several studies focusing on conservation biology have investigated rodents in forested or limestone habitats (Wells *et al.* 2007; Rickart *et al.* 2011; Latinne *et al.* 2012, 2013a), but peridomestic species commonly found in households (e.g. *Rattus exulans* or *R. tanezumi*) have not been subject to extensive ecological investigation (Bordes *et al.* 2013) despite their invasive nature and likely high contact rates with humans (Kosoy *et al.* 2015).

In this review we first present recent results using molecular data to test the limits of the current taxonomy of the *Rattini* tribe. We aimed to establish where species boundaries are unclear and identify where further investigations are needed to provide a more rigorous systematic framework for epidemiological surveys. Second, we summarise recent findings on the habitat distribution and specialisation of the most common murine rodent species. Third, we present current knowledge on the association between rodents and the major rodent-borne diseases encountered in South-east Asia. We aimed specifically to identify synanthropic rodents and to establish their habitat specialisation, because these species are commonly hosts of significant rodent-borne diseases. Finally, we summarise recent analyses on rodent-borne diseases and the habitats that are more prone to hosting them (Herbreteau *et al.* 2012; Bordes *et al.* 2013; Chaisiri *et al.* 2015).

Which reservoir rodents? Identifying rodent species, with a focus on the *Rattini* tribe

South-east Asia is a hot spot for rodent diversification (Steppan *et al.* 2003; Robins *et al.* 2010; Fabre *et al.* 2013; Latinne *et al.* 2013b; Thomson *et al.* 2014). Within the Murinae, the *Rattini*

tribe (Lecompte *et al.* 2008) encompasses 35 genera and 167 rat species (Musser and Carleton 2005). Nearly all representatives of this tribe inhabit South-east Asia, a major hot spot of biodiversity (Myers *et al.* 2000; Heaney 2011) under threat (Wilcove *et al.* 2013).

Asian rodents are difficult to discriminate morphologically at a specific level and the wide range of intraspecific morphological variation has resulted in a confused taxonomy with an overabundance of synonyms (e.g. 41 synonyms for *R. norvegicus* and 83 for *R. rattus*; Musser and Carleton 2005). Although in recent years molecular-based identification and species identification have been used to try to clarify the taxonomy (Robins *et al.* 2007; Galan *et al.* 2012), much still needs to be resolved.

Pagès *et al.* (2010) sequenced two mitochondrial and one nuclear gene from 122 rodent samples collected from Laos, Cambodia and Thailand to perform a phylogenetic analysis of the *Rattini*. Among other findings, that study showed that the *Maxomys*, *Dacnomys* (here *Leopoldamys* and *Niviventer* as sister taxa) and *Rattus* divisions (here *Rattus*, *Bandicota* and *Berylmys*) were sustained (Fig. 1). These results were congruent with the Murinae phylogeny obtained by Lecompte *et al.* (2008) and with the revised taxonomy of *Rattini* divisions proposed by Musser and Carleton (2005).

The phylogeny of Pagès *et al.* (2010) was further used to explore species boundaries using DNA sequence data themselves as the primary information source by applying the method of Pons *et al.* (2006), which detects the point of transition in the rate of lineage branching of a tree from interspecific long branches to intraspecific short burgeoning branching and identifies clusters of specimens corresponding to putative species. Twenty-four putative species were identified by Pagès *et al.* (2010). This estimated number of species is in agreement with the number of species described for this part of mainland South-east Asia (Thailand, Laos, Cambodia), with some exceptions (see Musser and Carleton 2005), in particular within the *Berylmys* and *Rattus* genera or *Crunomys* diversion. However, regardless of the method used, species delimitation depends on the evolutionary history of the species group and may fail due to incomplete lineage sorting, trans-species polymorphism, hybridisation and introgression (Leliart *et al.* 2014).

Three putative species of *Berylmys* were identified in the sampling, whereas only two are mentioned in the literature within the geographic area surveyed (*Berylmys bowersi* and *B. berdmorei*). However, populations of *B. bowersi* in peninsular Thailand have previously been reported to be geographically isolated and to differ genetically from other populations (Francis 2008; Latinne *et al.* 2013a).

For the *R. rattus* species group, although five species have been described from this region (i.e. *R. andamanensis*, *R. argentiventer*, *R. tanezumi*, *R. tiomanicus*, and *R. losea*, which was not distinguished from *R. sakeratensis* in Pagès *et al.* 2010), the analysis corroborated the presence of an additional *Rattus* species (labelled 'R3' in Fig. 1). This putative species was identified previously as the *diardii* clade in the mitochondrial phylogeny of Robins *et al.* (2007) and, according to Aplin *et al.* (2011), could be a cryptic species. Pagès *et al.* (2013) used extensive sampling, morphological data and diverse genetic markers differing in rates of evolution and

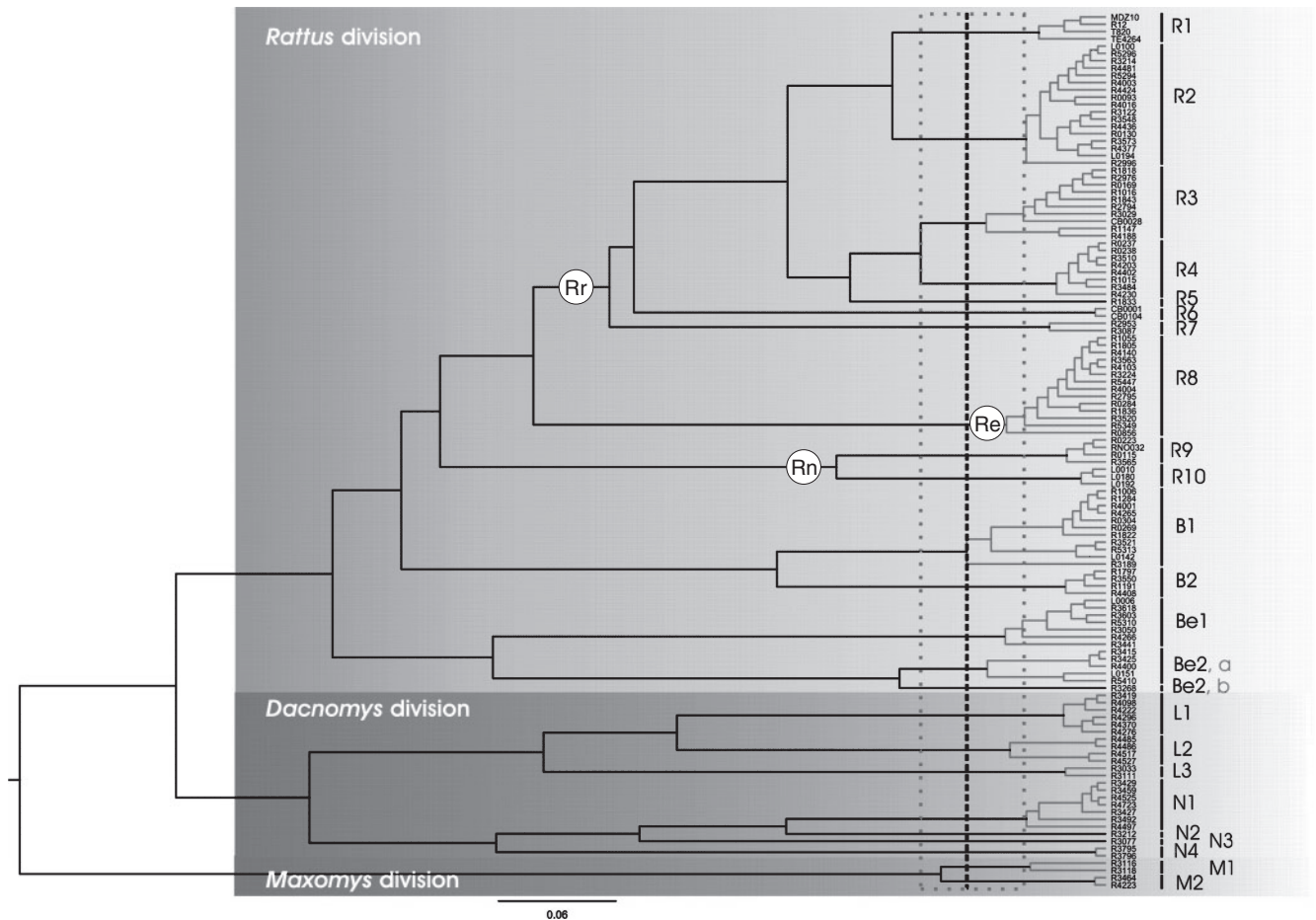


Fig. 1. *Rattini* ultrametric tree obtained with Multidivtime (freeware, available at <http://statgen.ncsu.edu/thorne/multidivtime.html>, accessed 10 March 2015) and clusters of specimens recognised as putative species by the method of Pons *et al.* (2006). Genetic clusters recognised as a putative species are highlighted and separated by longer black branches. The vertical bars group all sequences within each significant cluster, labelled R1 to M2 according to the genus to which they belong. Rr, *Rattus rattus* species group; Re, *Rattus exulans* species group; Rn, *Rattus norvegicus* species group. (R1, *R. rattus*; R2, *Rattus tanezumi*; R3, *Rattus* sp. (to be named); R4, *Rattus sakeratensis*; R5, *Rattus tiomanicus*; R6, *Rattus argentiventer*; R7, *Rattus andamanensis*; R8, *R. exulans*; R9, *R. norvegicus*; R10, *Rattus nitidus*; B1, *Bandicota indica*; B2, *Bandicota savilei*; Be1, *Berylmys berdmorei*; Be2a, *Berylmys bowersi*; Be2b, *Berylmys* sp.; L1, *Leopoldamys edwardsi*; L2, *Leopoldamys neilli*; L3, *Leopoldamys sabanus*; N1, *Niviventer fulvescens*; N2, *Niviventer* sp. 1; N3, *Niviventer* sp. 2; N4, *Niviventer langbianis* or *Chiromyscus chiropus*; M1, *Maxomys* sp.; M2, *Maxomys surifer*). Reproduced from Pagès *et al.* (2010).

parental inheritance (two mtDNA genes, one nuclear gene and eight microsatellite loci) to assess the reproductive isolation among *R. tanezumi*, *R. sakeratensis* and R3. Based on mtDNA data, three lineages were identified. *Rattus tanezumi* is phylogenetically isolated from the other two lineages, at a genetic distance of 5.72% from R3 and 6.84% from *R. sakeratensis*. In contrast, R3 and *sakeratensis* are closely related and separated by a shorter genetic distance (3.80%). However, only two genetic entities were identified on the basis of nuclear data: *R. sakeratensis* and another entity comprising both R3 and *R. tanezumi*. Morphometric analyses based on external measurements (lengths of head+body, tail, hind foot, ear and head) were consistent with the nuclear genetic data, because these also did not separate the *R. tanezumi* and R3 mtDNA lineages in terms of either shape or size.

The occurrence of two highly divergent mtDNA lineages (i.e. *R. tanezumi* and R3) suggests that the Asian black rat has a complex evolutionary history (Aplin *et al.* 2011). The presence

of highly divergent mtDNA lineages within a single large species may be the result of geographical structuring during Quaternary climatic oscillations, or introgression from a species yet to be identified, either of which could account for the incongruence between mtDNA and nuclear patterns in Asian black rats. Increasing the size of the sampling area would provide further insight into the evolutionary history underlying the great diversity of Asian black rats.

Based on phylogenetic, morphological and geographical evidence, Pagès *et al.* (2010) proposed to attribute names to the 24 species highlighted in their study. However, assigning the appropriate name to each species was a problematic task, particularly for the *Rattini* species, whose taxonomy is complicated by a large number of synonyms (see above). One taxonomic change that does seem well founded is the naming of the *Rattus losea*-like populations from the region comprising central and northern Thailand and the Vientiane plain of Laos. According to Aplin *et al.* (2011), these populations refer to *Rattus*

sakeratensis, a group distinguished from true *R. losea*, restricted to Cambodia, Vietnam, China and Taiwan.

Developing rodent barcoding

Field identification poses difficulties for accurate species assignment in several genera of *Rattini*, as well as for the *Mus* species. Although modern morphometrics has proved to be more efficient (Chaval *et al.* 2010), it requires well-preserved skulls that are not always available, particularly as cleaning raw skulls is time consuming when applied to large surveys.

Because few taxonomists can morphologically identify species, it has been proposed that an international consortium be developed, the Barcoding of Life (BOL), which aims at promoting and developing molecular identification of living organisms. DNA barcoding systems use a short, standardised gene region to identify species (usually the mitochondrial cytochrome *c* oxidase I (*COI*) gene) in association with morphological voucher specimens to validate the molecular identification (Hajibabaei *et al.* 2007).

Of the available DNA markers, a 648-bp region of the *COI* gene was chosen in agreement with the BOL (Pagès *et al.* 2013). For South-east Asian rodents, the *COI* gene was found to be highly relevant for species assignment because clear and robust species-specific clades were retrieved (with the notable exception of the Asian black rat complex; Pagès *et al.* 2013; and see above).

The barcoding technique has several advantages, including the requirement for small tissue pieces and the fact that it can be readily applied to museum samples. For example, Latinne *et al.* (2013a) investigated the diversity and endemism of *Rattini* in Thai limestone karsts and confirmed the existence of the species *Niviventer hinpoon* in several new localities using as reference a small DNA fragment obtained from the holotype. This work illustrates the huge opportunities ancient DNA analysis may offer to taxonomists (Willerslev and Cooper 2005; Rohland and Hofreiter 2007; for rodents, see Wyatt *et al.* 2008; Aplin *et al.* 2011).

Galan *et al.* (2012) have developed a time- and cost-effective method suitable for barcoding thousands of samples using the 454 GS FLX platform (Roche Diagnostics Corporation, Basel, Switzerland). The originality of this approach resides in the use of: (1) a high-level resolution mini-barcode of a 136-bp region of the cytochrome *b* gene suitable for identification of individuals at the specific level from tissue samples and degraded DNA (non-invasive samples, including hairs and faeces, and museum specimens); (2) combined polymerase chain reaction (PCR)-tagged primers, which enable attribution of each read to a unique sample after 454 sequencing, which could contain a mixture of different species; and (3) software associated with the GenBank database for read analysis and species identification. The relevance of this innovative approach for rodent species barcoding was validated on a reference sample (Galan *et al.* 2012) comprising 265 rodent individuals corresponding to 103 species from Asia, Africa and Europe, whose species identification was clearly established beforehand using molecular and/or morphological characters. This method identified 100% of samples at the specific level for samples collected in geographic areas where the rodent fauna is well documented by molecular data in public databanks.

Molecular identification combined with high-throughput sequencing allows fast, accurate and inexpensive species identification. As an example, the reference database for the mini-barcode has been added to the online barcoding tool RodentSEA for rodent identification (<http://www.ceropath.org>, accessed 28 February 2015). However, a major caveat of the barcoding identification method, when based on a single gene, is that it will fail to detect introgression (Pagès *et al.* 2013), which needs a combination of methods for accurate species determination (e.g. mtDNA, nuclear marker and/or morphology).

Identifying rodent habitat preferences

Environmental change, including habitat disturbance, urbanisation and biodiversity loss, affect the location and densities of parasites, hosts and vectors (Ostfeld *et al.* 2005; Gillespie and Chapman 2008; Ostfeld 2009). Because particular hosts and environments may contribute disproportionately to parasite transmission, the challenge is to identify their relative importance in order to predict disease persistence or emergence (Paull *et al.* 2012).

Recently, two concepts have emerged: (1) 'synanthropic species', namely species ecologically associated with humans; and (2) 'generalist' species, which are species living in peridomestic habitats or those that often invade disturbed habitats (McFarlane *et al.* 2012). In a comparative study performed in the Asian–Australian region, McFarlane *et al.* (2012) found that wild mammal hosts (primarily rodents and bats) of zoonotic emerging infectious diseases are 15-fold more likely to inhabit human-modified environments. That is, human-induced disturbances often increase the distribution and abundance of generalist rodent species, which are frequently important reservoirs of human pathogens.

Synanthropic rodent species with a preference for settlements and agricultural environments should be targeted for pest control, because it is these species and the diseases they carry that humans will be most commonly exposed to. Moreover, these species most likely benefit from the ongoing human modification of habitats, which led Singleton *et al.* (2010) to emphasise: 'rodent damage to agricultural production is a landscape problem that can be managed only by a widespread landscape approach'. These observations may apply worldwide because similar findings have been made in Brazil (Püttker *et al.* 2008) and eastern Africa (Makundi and Massawe 2011).

Palmeirim *et al.* (2014) evaluated the patterns of spatial distribution and specialisation of common murine rodents inhabiting South-east Asian landscapes. For this, they used the extensive geo-referenced rodent trapping database collected from Thailand, Cambodia and Laos. To illustrate the distribution of rodent species across habitat types, multivariate analysis was performed on the number of rodent individuals trapped in each of four main types of habitat: forest, agriculture on dry lands, agriculture on rain-fed or irrigated lands (i.e. paddy fields) and human settlements (isolated houses and villages). The principal component analysis (PCA) plot obtained in that analysis (Fig. 2a) showed the associations between the rodent species and habitat types. Several rodent species exhibited specialised habitat preferences: *R. norvegicus* and *R. exulans* in human settlements; *Rattus argentiventer*, *R. sakeratensis*,

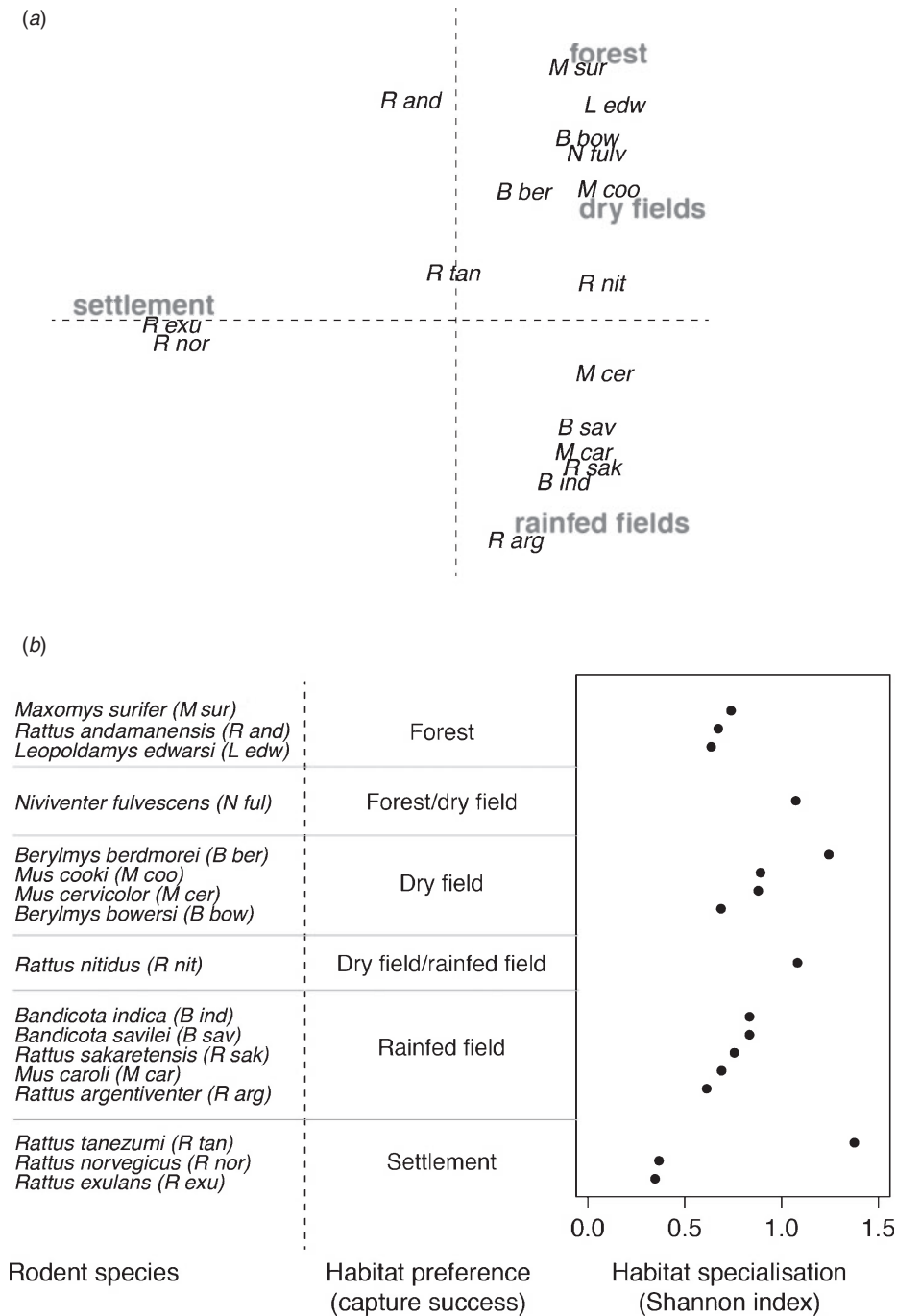


Fig. 2. (a) Distribution of rodent species according to habitat types: lowland rain-fed (paddy fields), non-flooded land (dry lands), forest and settlement (houses) on the two first axes of a principal component analysis (PCA). Dimensions 1 and 2 accounted for 80% of the variance. B ind, *Bandicota indica*; B sav, *Bandicota savilei*; Be ber, *Berylmys berdmorei*; Be bow, *Berylmys bowersi*; M sur, *Maxomys surifer*; M car, *Mus caroli*; M cer, *Mus cervicolor*; M coo, *Mus cookii*; M ful, *Niviventer fulvescens*; R arg, *Rattus argentiventer*; R exu, *Rattus exulans*; R nit, *Rattus nitidus*; R sak, *Rattus sakarensis*; R nor, *Rattus norvegicus*; R tan, *Rattus tanezumi*. Redrawn after Palmeirim *et al.* (2014). (b) Ranking of rodent species according to their habitat specialisation (Shannon index) with main habitat preference (based on capture success) corresponding to the habitat (or two habitats) in which a higher number of captures have been obtained (calculated using the data from Palmeirim *et al.* 2014).

Bandicota indica and *Mus caroli* in rain-fed fields; *Mus cookii* and *Berylmys berdmorei* in non-flooded lands; and *Maxomys surifer* and *Leopoldamys edwardsi* in forests. Some other species exhibited more generalist tendencies, including *Niviventer fulvescens*, which was found in forests or non-flooded lands, and *Rattus nitidus* found in rain-fed fields or non-flooded lands. Finally, *R. tanezumi* showed low habitat preference and was found in many habitat types, including households.

The specialisation of rodent species to the four types of habitat can be assessed using the Shannon index (Morand et al. 2015). Rodent species were ranked according to the value of the Shannon index and this was then compared with the value of their habitat type preference (i.e. for which the highest number of individual rodents of each species were trapped). The ranking of rodent species according to their habitat specialisation (using Shannon index based on data presented in Palmeirim et al. 2014) illustrated the PCA results (Fig. 2b). The level of habitat specialisation appeared to be independent of habitat preference (i.e. the habitat with the highest capture success). Whereas the synanthropic species *R. exulans* and *R. norvegicus* showed high specialisation to settlement habitat, the other synanthropic species *R. tanezumi* showed the lowest specialisation of all rodent species.

The results also provided new insights into the importance of the landscape structure on the probability of rodent presence in several habitat types in South-east Asia. The status of specialist species and/or synanthropic species for several rodent species was confirmed, although the majority of rodent species exhibited some degree of habitat specialisation. A few species showed clear preference for forested areas, such as *L. edwardsi* and *M. surifer*, at the quasi-exclusion of other habitats (i.e. agriculture lands). This pattern has been described previously for similar large-bodied rodent species, including *Leopoldamys sabanus*, *Maxomys rajah* and *Maxomys whiteheadi* by Charles and Ang (2010) in Brunei. However, most species exhibited lower habitat specificity and were found either in forested areas and dry-lands (*B. bowersi*, *N. fulvescens*) or in rain-fed fields and dry-lands (*M. cervicolor*, *B. savilei*).

Identifying rodent-borne diseases in rodents

Rodents are reservoirs and hosts of many viruses, bacteria and protists of public health concern (Meerburg et al. 2009). In South-east Asia, most studies have focused on mainland countries (and principally Thailand; Herbreteau et al. 2012; Bordes et al. 2013), establishing the presence of several important zoonoses in the region. Viruses investigated have included hantaviruses (the agents of haemorrhagic fever with renal syndrome (HFRS); Blasdell et al. 2011), lymphocytic choriomeningitis virus (LCMV; Nitatpattana et al. 2000) and rabies virus (Brown et al. 1979). All these viruses can be transmitted directly between rodent hosts, although transmission of hantaviruses and LCMV likely also occurs through exposure to aerosolised infectious excretions (Monath 1975; Armstrong et al. 1995). Among the bacteria, three genera in particular have been a major focus: *Leptospira* spp., agents of leptospirosis (Thaipadungpanit et al. 2007; Ivanova et al. 2012; Cosson et al. 2014); *Bartonella* spp., agents of bartonellosis (Castle et al. 2004; Saisongkorh et al. 2009; Jiyipong et al. 2012,

2015); and *Orientia tsutsugamushi* (Coleman et al. 2003), the agent of scrub typhus. *Bartonella* spp. and *O. tsutsugamushi* are arthropod-borne agents, whereas *Leptospira* spp. are transmitted indirectly via contact with water or soils contaminated by the urine of infected rodents. Recently, *Bordetella hinzii* was also identified in rodents (Jiyipong et al. 2013). This species causes respiratory disease in poultry and has occasionally been described in humans (Gadea et al. 2000). From the three predominantly investigated protists, *Toxoplasma gondii* (Jittapalapong et al. 2011) is a significant human pathogen, whereas *Trypanosoma* spp. (Jittapalapong et al. 2008; Milocco et al. 2013; Pumhom et al. 2014) and *Babesia* spp. (Dantrakool et al. 2004) primarily infect livestock and more rarely humans.

Herbreteau et al. (2012) targeted rodent reservoirs in Thailand using published studies that screened for microparasites (viruses, bacteria and protists; Fig. 3). They proposed a simple method for prioritising and/or targeting rodents that are the dominant carriers of rodent-borne diseases by assuming that they harbour more pathogen species than expected on the basis of the relationship between pathogen richness and sampling effort. They found that microparasite richness was correlated with both rodent sample size and pathogen screening effort, and suggested that the residual variation of this correlation could help identify major rodent reservoirs and potential risky habitats. Using the residual variations of microparasite richness among rodent hosts, Herbreteau et al. (2012) showed that several rodent species harboured more pathogens than expected by the regression model (i.e. positive residual values), particularly *Rattus adamanensis*, *Bandicota savilei*, *R. argentiventer* and *R. norvegicus*. Two species appeared to harbour fewer pathogen species than expected by the regression model (i.e.

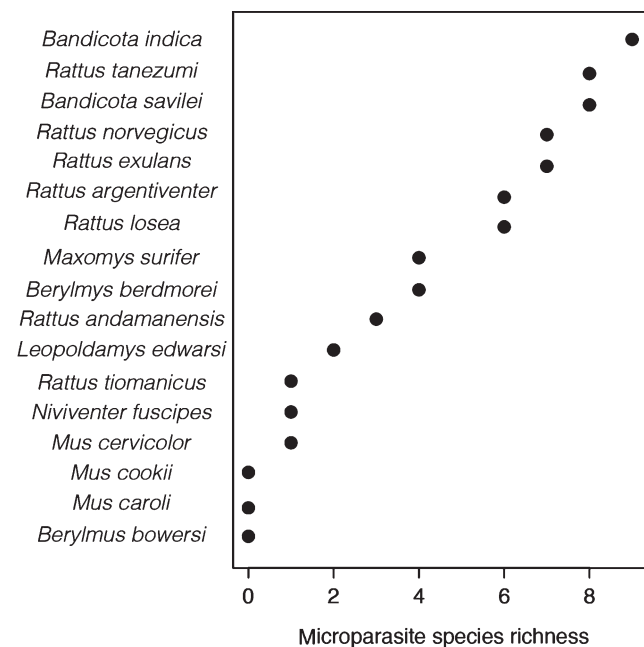


Fig. 3. Total number of known viruses, bacteria and protists causing major rodent-borne diseases in rodents from Thailand (data from Herbreteau et al. 2012).

have high negative residuals values): *Mus cervicolor* and *M. caroli*.

Zoonotic helminths have also been extensively investigated in Asian rodents (for a review, see Chaisiri *et al.* 2015). A recent and intensive survey concerned 2478 rodent individuals trapped, with 735 (29.7%) found to be infected by the following zoonotic helminth species: *Echinostoma malayanum*, *Echinostoma ilocanum*, *Plagiorchis muris*, *Raillietina* sp., *Hymenolepis diminuta*, *Hymenolepis nana*, *Cyclodontostomum purivisi* and *Moniliformis moniliformis* (Chaisiri *et al.* 2015; Palmeirim *et al.* 2014). Infections with most of these zoonotic helminths are usually asymptomatic in humans (Hong *et al.* 1996; Chero *et al.* 2007). The three synanthropic rodents *R. tanezumi*, *R. exulans* and *R. norvegicus* were identified as reservoirs for all these pathogens. Among these rodent species, *R. tanezumi* appeared to play a major role as a reservoir host, with individuals found positive for seven of these zoonotic helminth species (Chaisiri *et al.* 2015).

Associating rodent-borne diseases with rodent habitats

Herbreteau *et al.* (2012) found that higher pathogen richness than expected from correlation with sampling effort (i.e. positive residual values) was found in non-flooded lands, forests and paddy fields. Because of the limited number of surveys that included non-flooded lands and forests, the results from these habitats should be considered with caution. However, because numerous surveys have focused on paddy rice fields and households, the findings for these habitats should be relatively robust.

Bordes *et al.* (2013) took a different approach, using information from a field spatial study that investigated the distribution of murid rodents in various habitats in three countries in South-east Asia (Dupuy *et al.* 2012) and compared this with their infection status by 10 taxa of microparasites, based on data acquired from the published literature. Microparasite species richness was calculated by rodent species on 20272 rodents belonging to 13 species (according to the identification provided by the published studies). Statistical analyses were performed to identify how microparasite diversity differs as the average distance between the trapping site of individual rodents and five categories of land cover (forest, steep agriculture land, flat agriculture land, water and built-up surfaces) varied. The analyses of Bordes *et al.* (2013) found that microparasite diversity was positively associated with flat agricultural land, meaning rice fields, the main agricultural landscape in South-east Asia (Xiao *et al.* 2006). This result suggests that rice fields may favour microparasite transmission and should be targeted for rodent-borne disease surveillance and rodent control. This is because even if only a small percentage of smallholder farmers are debilitated by rodent-borne diseases, this will impact not only on public health, but also on regional food security (Meerburg *et al.* 2009; Singleton *et al.* 2010; John 2014).

Conclusion

Thanks to the increasing application of molecular systematics, recent studies have succeeded in refining the taxonomy of one of the most difficult groups of mammals (Aplin *et al.* 2011;

Galan *et al.* 2012). Most of the species expected in the region of South-east Asia studied were confirmed using this method, but new putative species limits were also indicated, in particular within the *Berylmys*, *Maxomys* and *Rattus* genera, where future taxonomic studies should be directed. The studies presented in this review have laid the foundations to better investigate rodent-borne diseases in South-east Asia and illustrate the relevance of evolutionary studies to public health. However, to truly assess the risk to human health in the region, accurate identifications of pathogens and parasites hosted by these rodents are also needed. To enable this, the development of barcoding techniques (including the sharing of protocols and concepts), biobanking (in particular for parasites and/or pathogens hosted by rodents) and ebanking (including the accessibility and sharing of geo-referenced data, collections and tissues) is required (Morand and Clairon 2014).

Another challenge is to identify specific environmental determinants that explain higher rodent parasite burdens in human-dominated areas. Although certain associations exist between a particular disease in humans and the presence of a given host reservoir species, infection in humans is not always congruent with distribution of that host, suggesting that other factors are at work. Moreover, identifying a reservoir for a single parasite may be rather restrictive due to the circulation of multiple pathogens in natural systems. Multiple infection is the rule, but has only recently been considered as a key factor in wild ecosystems (Telfer *et al.* 2008; Bordes and Morand 2009).

A final challenge is related to the invasion or range expansion of rodents. The black rat (*R. rattus*), Norwegian rat (*R. norvegicus*), Asian house rat (*R. tanezumi*) and Pacific rat (*R. exulans*), like the house mouse (*Mus musculus domesticus*), have radically and explosively expanded their geographic range as a consequence of human activities. All these *Rattus* species originated in Asia, and can be found in sympatry in South-east Asia due to their synanthropic behaviour. These rodents have been implicated (Kuo *et al.* 2011), and still are implicated (Kosoy *et al.* 2015), in the emergence and spread of infectious diseases of public health importance, such as plague, murine typhus, scrub typhus, leptospirosis, hantavirus and haemorrhagic fever, among others. A better understanding of the range extension mechanisms and consequences would require specific investigation of the genetics (phylogeography, population genetics) and immunology (immunogenetics) of these rodent species.

Parasitic risk is global, with many parasite species harbouring zoonotic tendencies. This review demonstrates that comparative analyses can help identify rodent reservoirs and environments that present a high risk of multiple rodent-borne diseases. Because pathogen richness varies between both rodent species and habitats, the results from the studies presented herein demonstrate the need for future studies in Asian ecosystems. Such studies would greatly improve our understanding of the processes involved in the transmission ecology of rodent-borne diseases in the region.

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