

REVIEW

Global parasite and *Rattus* rodent invasions: The consequences for rodent-borne diseases

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Abstract

We summarize the current knowledge on parasitism-related invasion processes of the globally invasive *Rattus* lineages, originating from Asia, and how these invasions have impacted the local epidemiology of rodent-borne diseases. Parasites play an important role in the invasion processes and successes of their hosts through multiple biological mechanisms such as “parasite release,” “immunocompetence advantage,” “biotic resistance” and “novel weapon.” Parasites may also greatly increase the impact of invasions by spillover of parasites and other pathogens, introduced with invasive hosts, into new hosts, potentially leading to novel emerging diseases. Another potential impact is the ability of the invader to amplify local parasites by spillback. In both cases, local fauna and humans may be exposed to new health risks, which may decrease biodiversity and potentially cause increases in human morbidity and mortality. Here we review the current knowledge on these processes and propose some research priorities.

Key words: biological invasion, immunocompetence, parasite release, spillback, spillover

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INTRODUCTION

Emerging infectious diseases share several patterns and processes with free-living invasive organisms. How-

ever, host–parasite (in a broad sense including macro microparasites and microparasites) interactions are more complex due to interactions operating at the level of the individual (e.g. life-history trait, defense and virulence), population (e.g. dynamics and disease regulation), community (e.g. co-interactive networks of parasitism, competition and predation) and ecosystem (e.g. parasites in food webs, and disease spread within habitat connectivity).

Parasites play an important role in the invasion processes and successes of their hosts through multiple biological mechanisms, such as “parasite release” (Torchin *et al.* 2003), “immunocompetence advantage” (Møller & Cassey 2004), “biotic resistance” (Britton 2012), and “novel weapon” (Strauss *et al.* 2012), among others (Prenter *et al.* 2004; Bell *et al.* 2009; Dunn 2009; Kelly *et al.* 2009; Morand *et al.* 2010). Parasites may also greatly increase the impact of invasions through spillover of parasites/pathogens into new hosts, potentially leading to novel emerging diseases and/or the emergence of already known diseases in new geographic areas (Hulme 2014). A second local potential impact is the ability of the invader to amplify local parasites by spillover. Spillover and local acquisition of parasites and pathogens have important consequences for ecological systems, wildlife and domestic species (Wood *et al.* 2012). In both cases, local fauna and humans may be exposed to new or elevated health risks (Hatcher *et al.* 2012).

Few host–parasite systems permit an overall view of the consequences of biological invasions at multiple levels of biological organization, at different global scales and linking risks of emerging diseases. Invasive rodents are one of the few models that allow such a comprehensive scalable analysis to be performed. Among the numerous species within *Rattus* (66 species according to Musser & Carlton 2005), the Norway or brown rat *Rattus norvegicus* (Berkenhout, 1769), the black or roof rat *Rattus rattus* (Linnaeus, 1758), and the Asian black rat *Rattus tanezumi* Temminck, 1844 have colonized urban ecosystems globally (Aplin *et al.* 2011). A fourth invasive species, the Pacific rat *Rattus exulans* (Peale, 1848) is limited to tropical Asia-Pacific areas. Finally, other species in the group [*Rattus argentiventer* (Robinson and Kloss, 1916), *Rattus nitidus* (Hodgson, 1845) and *Rattus tiomanicus* (Miller, 1900) have shown an expansion associated with human activities but to a less geographical extent (Aplin *et al.* 2003). It is well known that, once introduced, all these species can strongly interact with indigenous fauna and flora, and can alter the

colonized ecosystems in different ways (Courchamp *et al.* 2003; Banks & Hughes 2012) and can also have economic impacts. Moreover, these species display sufficient ecological differences that they would be expected to interact differently with local small mammal communities (Courchamp *et al.* 2003; Singleton *et al.* 2007). All these *Rattus* species have radically and explosively expanded their geographic range as a consequence of human activities. Interestingly, all of these rodents originated in Asia, and they can be found in sympatry in many localities, even far from their original distribution (Bastos *et al.* 2011; Blanks & Hugues 2012; Lack *et al.* 2012) due to their synanthropic behavior (Khlyap & Warshavsky 2010; McFarlane *et al.* 2012). As these rat species are closely associated with humans, the timing of their invasion is related to current and historical global trade.

Rodents are recognized as hosts of at least 60 zoonotic diseases that represent a serious threat to human health (Meerburg *et al.* 2009; Luis *et al.* 2013; Chaisiri *et al.* 2015). Historically, Asian rodents of the genus *Rattus* have been implicated in the emergence and spread of infectious diseases of importance to human health such as plague, murine typhus, scrub typhus, leptospirosis and hantavirus hemorrhagic fever, among others (Kosoy *et al.* 2015). They can cause considerable economic loss (Stenseth *et al.* 2003; Singleton *et al.* 2010; John 2014) and have great impact on biodiversity (Atkinson 1985; Lowe *et al.* 2001; Wyatt *et al.* 2008).

Our aims are to review the ecological and biological knowledge on *Rattus* invaders and the consequences of their invasion success on rodent-borne diseases and, based on this review, to emphasize gaps in knowledge and recommend some future research priorities.

PARASITES IN THE INVASION PROCESSES: CAUSES AND LIKELY CONSEQUENCES

Biotic invasions are often compared to epidemics as several important factors in disease epidemiology are common to invasion biology (Mack *et al.* 2000): the chance of establishment, the minimum population size necessary for establishment in the invaded habitat, the population growth and the fate of interacting species in the new range (Drake 2003). These factors are the core of the invasion process, which has been defined as a sequence of 3 steps: introduction, initial establishment and

spread (Williamson 1996; Kolar & Lodge 2001; Facon *et al.* 2006; Fig. 1).

The first step, introduction, is associated to the dispersal ability of the species, although introduction is mainly dependent on human activities. The second step, initial establishment, depends mainly on the fate of interaction with the local environmental characteristics. The last step, spread or population growth, clearly depends on the biological characteristics of invasive species and of the effects of competition, predation and parasitism, which may ultimately affect its evolutionary adaptation to the invaded habitats (Facon *et al.* 2006).

Several hypotheses for parasite or disease-related mechanisms have been proposed to explain the success of invaders over endemic species (summarized in Fig. 1 and Table 1): parasite release (i.e. enemy release), immunocompetence advantage, the apparent competition due to co-invasive parasite spillover (i.e. novel weapon) and the reallocation of energetic resources following the loss of parasites.

In the invasion process, hosts harboring a high diversity of parasites in their native locations have a four-fold advantage. First, they lose a great number of parasites and pathogens in their introduced range and are released from their control (Torchin *et al.* 2003). The main parasites missing are those that require an intermediate host for transmission (for house mice see Singleton *et al.* 2005). Second, they have evolved strong immune defenses in their natural range (Bordes & Morand 2009), which may subsequently confer a better capacity to control parasites that they may acquire by spillback in the introduced range. Third, they do not lose all their

parasites in the introduced range; any co-introduced parasites may be useful for the control of native hosts by spillover, which may have few opportunities for investment in defense, especially if living on islands (Hochberg & Møller 2001). Fourth, in the absence of parasites in the invaded localities, invasive species can reallocate energetic resources from unnecessary costly defenses into fitness (e.g. reproduction) and growth, leading ultimately to spread and establishment success through increased competitive ability (Blossey & Nötzold 1995).

The parasite release hypothesis was proposed as an ecological mechanism to explain the success of introduced species, as the introduced species may have lost their parasites when invading new habitats. The introduced species have a competitive advantage over local species because they are released from control by their natural enemies (Elton 1958; Keane & Crawley 2002; Torchin *et al.* 2003). Nevertheless, several studies indicate that most of the parasite species of an invasive species are either left in their native area, are lost or cannot establish in the invaded habitat (Dobson & May 1986; Pisanu *et al.* 2009; Dozières *et al.* 2010; Marzal *et al.* 2011). Indeed, in the case of parasites with complex lifecycles and vector-borne pathogens, the missing intermediate hosts and vectors in the new invaded habitats could lead to a decrease in parasite diversity of the introduced species. Finally, associated invasive parasite species may fail to infect new local host species as many parasites may develop only in phylogenetically-related host species (Pisanu *et al.* 2009). Mitchell and Power (2003) and Torchin *et al.* (2003) find that parasitism is significantly reduced in organisms in their intro-

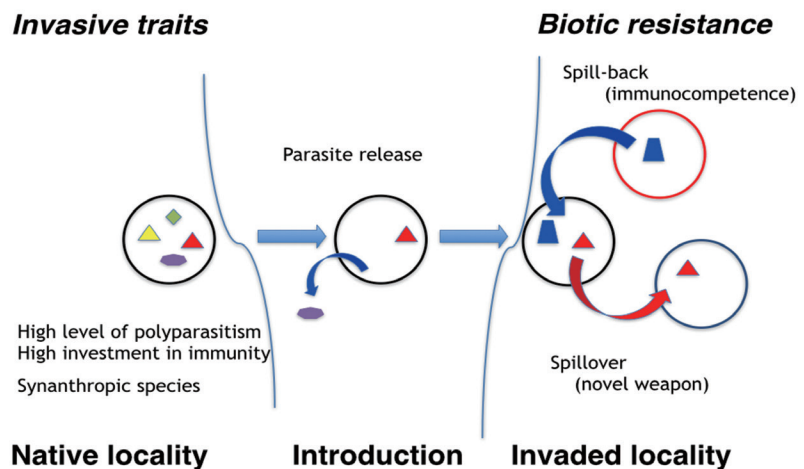


Figure 1 Parasite-related traits (native locality), mechanisms and consequences of invasion.

Table 1 Hypotheses related to disease-causes and consequences of biological invasion with potential tests

	Hypothesis	Mechanism	Test
Causes	Enemy release/parasite release	Loss of parasites, with lowering genetic diversities and/or missing vectors and intermediate hosts in invaded localities	Parasite species and host genetic comparisons in native, historical and newly invaded localities
	Immunocompetence advantage to face biotic resistance	Strong immunocompetence that copes with local parasites	Higher immunocompetence and immunogenes diversity in native compared to invaded territories; correlation between level of immunocompetence and parasite diversity
	Novel weapon (i.e. apparent competition due to parasite spillover to face biotic resistance)	Co-invasive parasites infecting susceptible hosts in the invaded localities	Higher virulence of parasites in invaded communities than in invasive host; lower or absent immunity against the parasite in the susceptible hosts compared to the invading host
Consequences	Parasite spillover	Spread of co-invasive pathogens in humans or in local reservoirs (emerging zoonoses)	Molecular and serological surveys
	Parasite spillback	Amplification of local pathogens in the newly invaded territories (outbreaks of zoonoses)	Molecular and serological surveys
	Loss of dilution effect	Spread of co-invasive parasites in low species rich invaded communities (such as islands or disturbed habitats)	Molecular and serological surveys
	Higher reproductive success and low inflammatory response in invaders as a consequence of the parasite release hypothesis	Due to costs of the inflammatory immune response and trade-off with other life history traits, invaders releasing their pathogens can invest less in inflammatory response, more in reproduction	Measuring the inflammatory response and reproductive traits of the invading species (both in native and invaded territories) and in resident hosts
	Strong humoral immunocompetence in invader species, as a consequence of immune investment and/or of using less costly immune responses	Encountering new pathogens is more effective to fight with a less costly immune branch (e.g. humoral immune system)	Measuring the humoral immune response of the invading species (both in native and invaded territories) and in resident hosts

duced range, supporting the parasite release hypothesis, which might explain the success of introduced species (Clay 2003), through reallocating the resources towards reproduction, growth or dispersal.

Among the traits that favor the establishment and spread of invasive species in new localities are those that help in coping with parasitism (i.e. immunity). The immunocompetence advantage hypothesis was proposed for introduced plants and animals and suggests that

hosts having evolved strong immune defenses are then prime candidates for successful invasion (Lee & Klasing 2004; Møller & Cassey 2004). However, the immunocompetence advantage hypothesis has not been thoroughly investigated for invasive rodents (Morand *et al.* 2010).

Species-poor communities, presenting vacant niches within communities, both for hosts and for their parasites, may also provide opportunities for the settlement

and spread of biotic invaders (Elton 1958). The vacant niches hypothesis suggests that species-poor communities do not offer biological resistance to invasion. This would explain why insular communities are so prone to invasion.

Less investigated are the consequences of invasion for the emergence or spread of diseases either by spillover (co-invasive pathogen) or by spillback (amplification of a local pathogen by the invader; Kelly *et al.* 2009; Dunn *et al.* 2012). One example of a novel weapon, among others, concerning rodents is the introduction of the grey squirrel (*Sciurus carolinensis* Gmelin, 1788), which originated from North America but was introduced to the UK and has led to local extinction of the native red squirrel (*Sciurus vulgaris* Linnaeus, 1758) because of the co-introduced squirrel poxvirus, a highly pathogenic virus for red squirrels (Tompkins *et al.* 2003).

The study of these causes and consequences of invasion necessitate investigation of immunology (genes, structure and function) of the invasive species in its native distribution and in the invaded localities, together with its sympatric congeners (with which the chances of sharing parasites are high). Spillover presents the advantage to increase the invaders' competitive ability with local communities (i.e. the novel weapon hypothesis) and to favor the ultimate spread of the invasive species (Bell *et al.* 2009; Strauss *et al.* 2012).

THE *RATTUS* INVADERS: EVOLUTIONARY AND RECENT DISTRIBUTION

The *Rattini* is an evolutionarily diverse group and progress has been made in understanding the relationship and evolution of this group (Robins *et al.* 2008; Pagès *et al.* 2013). According to the phylogenetic analyses of Robins *et al.* (2008), the deepest divergence within *Rattus* occurred 3.5 Ma with the separation of the New Guinean endemic *Rattus praetor* (Thomas, 1888) and Asian lineages from a common ancestor. The *R. norvegicus* lineage diverged from other Asian lineages 2.9 Ma. Other date estimates suggest a younger age for the species ranging from 0.44 to 2.35 Ma (Song *et al.* 2014). The earliest fossils of the *R. norvegicus* lineage are of about 1.2 to 1.6 Ma (Song *et al.* 2014). The study of Robins *et al.* (2008) suggests that *R. exulans* lineage separated 2.2 Ma from the ancestor of the sister species *R. rattus* and *R. tanezumi*. These last 2 species, *R. rattus* and *R. tanezumi*, diverged 0.4 Ma from a common ancestor.

R. norvegicus originated presumably from China (Nowak 1999; Song *et al.* 2014) and expanded worldwide with more recent European trade. It significantly colonized Europe during the 18th century (Vigne & Villié 1995), and reached North America and Africa soon after (Nowak 1999; Song *et al.* 2014). Norway rats are mostly restricted to urban areas with high human density and domestic animals but few are found in wild areas, whereas in the cooler regions they can be found in grassland and marshy rural areas such as in the southern USA (Glass *et al.* 1989) or Mediterranean (Cheylan 1984) and Oceanic islands (Abdelkrim *et al.* 2005). Based on a worldwide sampling and molecular analysis, Song *et al.* (2014) suggest that the origin of the species occurred more than 1 million years ago in Southern China, and that the species started to colonize the world (Pacific Islands, Africa, North America) during the last 2 centuries from the populations that were introduced and established in Europe. Lack *et al.* (2013) have detected high gene flow among established populations in the USA, suggesting high connectivity among Norway rat populations due to the recent colonization.

R. rattus and *R. tanezumi* can be found globally and in most type of habitat. They have invaded a large range of anthropogenic and natural environments, where they are likely interacting with a large range of wild and domestic animals (Goodman 1995; Harris *et al.* 2006; Hoberg 2010; Wells *et al.* 2014a,b). The origin of the black rat is still debated. Nowak (1999) indicate a Malaysian origin, Musser and Carlton (2005) an origin from the Indian Peninsula, and Aplin *et al.* (2011) multiple lineages and geographic origins of black rats from South and Southeast Asia. Among the lineages, 4 have been described as separate species, the black rat *R. rattus* and the Asian black rat *R. tanezumi*. *R. rattus* originated in South Asia and dispersed to Europe along the Silk Road, and other trade routes that have been reported from archeological sites as early as 1500 BC from the Near-East Levant (Near East regions; Eryvynck 2002), and to Madagascar, South Arabia and East Africa with the Indo-Pacific trade (Tollenaere *et al.* 2010). It later spread worldwide with modern European trade (Aplin *et al.* 2011). Black rat populations in the USA were likely founded by a few related lineages (Lack *et al.* 2013), whereas complex invasion pathways have occurred in Africa and Madagascar, with multiple introductions from different source populations (Konečný *et al.* 2013; Brouat *et al.* 2014). *R. tanezumi* originated in South-eastern Asia and invaded several localities of South and North America, South Africa and Australia (Aplin *et al.*

2011). Both *R. rattus* and *R. tanezumi* were identified in coexistence in California (Aplin *et al.* 2011; Conroy *et al.* 2013). In mainland Southeast Asia, *R. tanezumi*, *R. norvegicus* and *R. exulans* have been found living together in households (Morand *et al.* 2015).

R. exulans originated from insular Southeast Asia, potentially from the island of Flores (Thomson *et al.* 2014), but it remains unclear how the Pacific rat invaded mainland Southeast Asia (the Indochina) and other parts of insular Southeast Asia (such as the Philippines). Pacific rat dispersal has been used to model the history of Polynesian settlement, as this animal travelled with ancestral Polynesians when they dispersed throughout the Pacific (Matisoo-Smith & Robins 2004). Archaeological records of the Pacific rats, outside their presumed original distribution, dated their presence from around 4000 BP in East Timor, 3000 BP in west Polynesia to 1000 BP in south Polynesia (Anderson 2008). New Zealand was also recently colonized by both rats and humans (Irwin *et al.* 1990). However, *R. exulans* was replaced in many localities in New Zealand by the more recent introduction of *R. rattus*, *R. norvegicus* and *Mus musculus* Linnaeus, 1758 with the European settlement in the past 200 years (Atkinson 1985; Roberts 1991b).

The historical routes of invasion of the Pacific rat are then relatively clear. However, new invasions from insular Southeast Asia have recently occurred, with populations of Pacific rats established in Taiwan Island and the Ryukyu islands of Japan (Motokawa *et al.* 2001). Therefore, new invasion threats still exist for all the Pacific areas, including the South Japan islands, Australia, New Zealand, New Caledonia and French Polynesia (Russell *et al.* 2008). There is also concern about the invasion of the northern part of Indochina as *R. exulans* is currently absent from small villages in north Laos (Morand *et al.* 2015), although it is present in large cities such as Luang Prabang (Promkerd *et al.* 2008). In mainland Southeast Asia, *R. exulans* is found mostly in houses within villages (Morand *et al.* 2015). However, in insular Southeast Asia, it can be found in natural habitats, mostly forest (Roberts 1991b).

PARASITE AND DISEASE-RELATED INVASION PROCESSES IN INVASIVE *RATTUS*

Invasive *Rattus* spp. are synanthropic species; that is, living in close associations with humans although they can also be found in undisturbed habitats. They are also hosts for numerous parasites and agents of zoonotic dis-

eases in their original distributions (Palmeirim *et al.* 2014; Morand *et al.* 2015). These attributes make them good candidates for testing related parasite invasion hypotheses (Table 2).

Parasite release

One prediction of the parasite release hypothesis is that parasite species richness should be highest in its host's ancestral centre of origin, which is hypothesized to be South Asia, Southeast Asia and Southern China for invasive *Rattus* (Robins *et al.* 2008; Aplin *et al.* 2011).

At a global scale, Wells *et al.* (2014b) observed that the total numbers of parasite species were considerably higher in invaded biogeographic realms for *R. rattus* and *R. norvegicus* than in their native Oriental realm. Estimates of parasite species richness of *R. norvegicus* were higher in the Palearctic region than in the Orient, where the host genus *Rattus* originated and diversified. Neither rodent species exhibited differences in their overall parasite species richness. These observations suggest that a high number of parasite species, through spillback, have been acquired by both rat species during their colonization history.

At a regional scale, Goüy de Bellocq *et al.* (2002) investigated the helminth community structures of rodents in the Mediterranean area. They demonstrated that there was a significant decrease of helminth species richness in *R. rattus* in relation to geographical distances from invaded Mediterranean islands to the mainland. A strong positive correlation was also found between the total

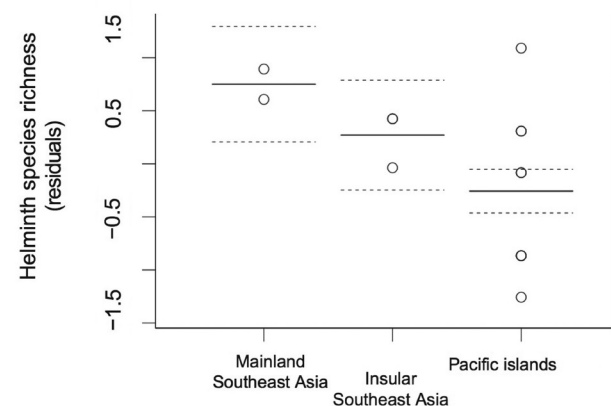


Figure 2 Helminth species richness of the Pacific rat, *Rattus exulans*, in its putative native region (insular Southeast Asia) and invaded range Mainland Southeast Asia and Pacific islands.

Table 2 Some examples of the effects and consequences of parasites on the success and impacts of invasion by *Rattus* invaders

Effect/consequence	Host–parasite system	Locality, references
Parasite release	<i>Rattus rattus</i> /helminths	Mediterranean mainland and islands, Goüy de Bellocq <i>et al.</i> (2002)
	<i>Rattus exulans</i> /helminths	New Zealand and Polynesian islands, Roberts (1991a)
Parasite spillover	<i>Rattus rattus</i> to humans and local rodents/ <i>Yersinia pestis</i> (plague)	Worldwide, Gage & Kosoy (2005)
	<i>Rattus</i> spp. to humans/ <i>Bartonella</i>	Worldwide, Bai <i>et al.</i> (2007), Hayman <i>et al.</i> (2013)
	<i>Rattus norvegicus</i> to humans/Seoul hantavirus	Worldwide, Lin <i>et al.</i> (2012)
	<i>Rattus</i> spp. to primates/ <i>Trypanosoma lewisi</i>	Brazil, Maia da Silva <i>et al.</i> (2010)
	<i>Rattus</i> spp. to <i>Acomys johannis</i> / <i>Trypanosoma lewisi</i>	Niger, Dobigny <i>et al.</i> (2011)
	<i>Rattus rattus</i> to <i>Peromyscus maniculatus</i> / <i>Trichuris muris</i>	Islands in USA, Smith & Carpenter (2006)
Parasite spillback	<i>Rattus exulans</i> / <i>Orientia</i> (scrub typhus)	Taiwan, China, Kuo <i>et al.</i> (2011)
	<i>Rattus</i> spp./livestock/ <i>Coxiella burnetii</i> (Q fever)	The Netherland, Reusken <i>et al.</i> (2011)
Novel weapon	<i>Rattus rattus</i> / <i>Rattus macleari</i> (endemic Christmas Island rat)/ <i>Trypanosoma lewisi</i>	Christmas island, Wyatt <i>et al.</i> (2008)

number of nematode species recorded in *R. rattus* populations and the size of islands. These findings are in strong accordance with the parasite release hypothesis.

Few studies have been devoted to parasites of *R. exulans* in its original distribution and its invasive distribution (Roberts 1991a,b; Hasegawa & Syafruddin 1995; Palmeirim *et al.* 2014). When investigating the data collected in Southeast Asia (mainland and insular) and Pacific islands, one can show that there is a decrease in parasite species richness, at least for nematodes, from insular Southeast Asia (its putative area of origin) compared to mainland Southeast Asia and the Pacific Islands (invaded areas; Fig. 2), which supports the Southeast Asian insular origin of *R. exulans* (Thomson *et al.* 2014), the parasite release hypothesis and parasite spillback.

Parasite spillover

The best-known example of spillover by rats is the plague, first from gerbils to *Rattus* (Schmid *et al.* 2015).

In the mid-14th century, one-third of the European human population died from plague, of which black rats were assumed to be the source. The third pandemic plague started in China and spread around the world via ships carrying rats infested with *Yersinia pestis* and imported into San Francisco in 1899 (Gage & Kosoy 2005). The invasive associated strains of *Y. pestis* further established themselves in the local rodent communities (Cully *et al.* 2010).

A second example concerns Seoul hantavirus, which causes hemorrhagic fever in humans. Seoul hantavirus originated in Asian *Rattini* rodents followed by worldwide expansion by Norway rats within the past few centuries (Lin *et al.* 2012; Plyusnina *et al.* 2012).

Bartonella strains have also been shown to evolve and diversify in Southeast Asia and further to disseminate worldwide with *R. rattus* and *R. norvegicus* (Ellis *et al.* 1999; Hayman *et al.* 2013). Another study showed that *Bartonella* genotypes identified in *R. rattus* in Bangladesh are identical to those observed from rats in Eu-

rope, Israel and the USA (Bai *et al.* 2007). Invasive *Rattus* also introduced borreliosis on the island of Madeira in Portugal (Matuschka *et al.* 1994).

Spillover cases may also include parasitic protists. For example, Dobigny *et al.* (2011) found *Trypanosoma lewisi* Gruby, 1843 in black rats in Niger and in native African *Acomys johannis* Thomas, 1912, which suggests spillover from *R. rattus* to the native rodent species.

Macroparasites like helminths also spilled over. Smith and Carpenter (2006) evaluate the spillover of helminth parasites from introduced black rats (*R. rattus*) to native deer mice [*Peromyscus maniculatus* (Wagner, 1845)] on California Channel Islands. Whereas 40 genera of helminths are known to parasitize deer mice in North America, only 5 genera occur in the Channel Islands, and one of these, the nematode *Trichuris muris* (Schrank, 1788), was introduced by the black rat. The nematode *Angiostrongylus cantonensis* (Chen, 1935), the rat lung worm, which causes eosinophilic meningo-encephalitis in humans through spillover, is thought to have originated in Southeast Asia. This nematode dispersed across several Pacific islands, Asia, Australia, Africa, some Caribbean islands and, most recently, in the Americas through the dispersal of *R. rattus* and *R. norvegicus* (Monte *et al.* 2012; Tokiwa *et al.* 2012) and the invasion of the terrestrial snail *Achatina fulica* (Férussac, 1821), which acts as an intermediate host (Thiengo *et al.* 2012).

Parasite spillback

One example of parasite spillback is the Q fever. Following its outbreak in the Netherlands in 2007–2010, the occurrence of the agent *Coxiella burnetii* in commensal rats was investigated (Meerburg & Reusken 2011; Reusken *et al.* 2011). The bacteria were detected in both brown and black rats, suggesting that rats might represent reservoirs contributing to maintenance and transmission of the bacteria (Reusken *et al.* 2011). The relative importance of rodents in the Q-fever pathway transmission deserves more investigation (Meerburg & Reusken 2011).

Another study focuses on *R. exulans*, which recently invaded localities in Taiwan, China. Kuo *et al.* (2011) demonstrate that this invasion contributed to the spread of scrub typhus, originally present on this island (Kelly *et al.* 2009).

Wells *et al.* (2014b) show that both globally invasive *R. rattus* and *R. norvegicus* have high overall parasite species diversity outside their geographical origins (i.e. the Orient). This finding suggests high levels of spill-

back of local parasites from wild or domestic animals.

Novel weapon

Several studies have been able to demonstrate that a pathogen co-introduced with an invasive host pushed invaded host populations to extinction (Strauss *et al.* 2012). These studies refer to the extinction of endemic Hawaiian birds following the introduction of mosquitoes and avian malaria, and the replacement of the red squirrel by the invasive grey squirrel carrying squirrelpox virus (see Strauss *et al.* 2012 and references therein).

Wyatt *et al.* (2008) provide molecular evidence for such an effect of *T. lewisi* emerging in endemic *Rattus macleari* (Thomas, 1887) (Christmas Island rats) after the introduction of black rats. The authors demonstrate the absence of trypanosome infection in endemic rats collected prior to the introduction of black rats but the presence of the parasite after the introduction using tissue collections from museum specimens.

The invasive *Y. pestis* in USA also impacted the local rodent communities, where the induced mortality depended on susceptibility and resistance of rodent species. Some species have undergone devastating mortality, such as black-prairie dogs [*Cynomys ludovicianus* (Ord, 1815); Cully *et al.* 2010].

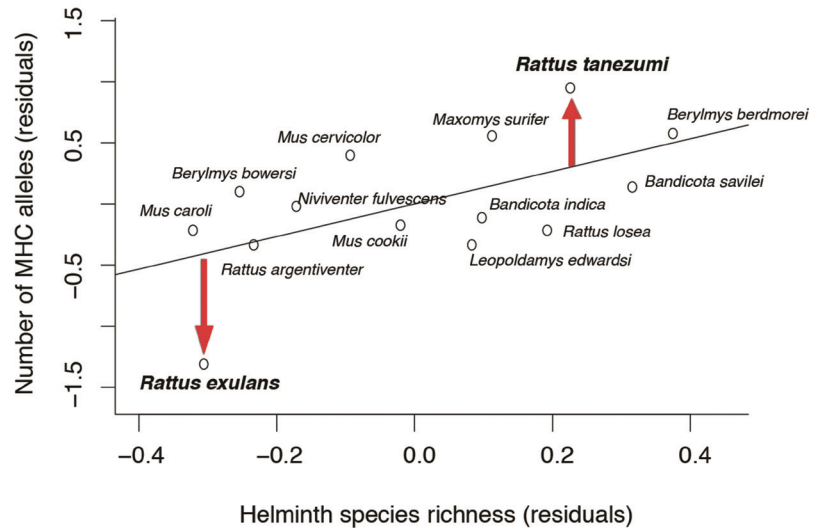
Immunogenetics and immunocompetence

Few immunoecological or immunogenetics studies have been devoted to invasive rodents and White and Perkins (2012) emphasize the gap between advances in theory and performance of empirical studies.

The relaxed parasite selection on invasive species is expected to lead to changes in the immune system (Horrocks *et al.* 2011), with reduced variability in immunogenes. Most immunogenetic studies of rodents have examined major histocompatibility complex (MHC) genes. However, invasive *Rattus* have not been the main focus of study (see Goüy de Bellocq *et al.* (2008), for which no invasive rodents were analyzed). Parasite-mediated selection maintains MHC polymorphism at both interspecific and intraspecific levels in rodents with high parasite species diversity being associated with high levels of MHC genetic diversity (Goüy de Bellocq *et al.* 2008; Pilosof *et al.* 2014).

The study of Pilosof *et al.* (2014) on MHC diversity in murine rodents from Southeast Asia may help in testing 2 predictions: (i) hosts having evolved strong immune defense in their native range, due to high parasite pressures, should show successful invasion capac-

Figure 3 Positive linear relationship between genetic diversity at the major histocompatibility complex and helminth species richness for common murine rodent species of mainland Southeast Asia. Positive residual values suggest high immunocompetence such as observed for the global invader *Rattus tanezumi*, native of Southeast Asia. Negative residual values suggest low immunocompetence, such as observed in *Rattus exulans*, which is supposedly originated from insular Southeast Asia.



ity; and (ii) invasive hosts in the invasive range should show reduced level of immune defense. Plotting allelic diversity against parasite species diversity (both controlling for sampling biases) confirmed both predictions (Fig. 3). *R. tanezumi*, from mainland Southeast Asia, showed high positive residual values of allelic diversity (controlled for parasite load) in its original range, meaning that it evolved high diversity at MHC genes that has helped it succeed as a global invader. *R. exulans*, from mainland Southeast Asia, showed high negative residual values of allelic diversity, supporting the prediction of a loss of immunogenetic diversity following its invasion in mainland Southeast Asia. However, there are no available data to test the corollaries of these predictions as *R. exulans* and *R. tanezumi* were not screened for MHC outside mainland Southeast Asia.

Moreover, as half of the genetic variability conferring resistance against parasites and pathogens is attributable to non-MHC genes, further immunogenetic studies of invasive *Rattus* should also include these (e.g. Toll-like receptors) and not only the MHC (Acevedo-Whitehouse & Cunningham 2006). Fornůsková *et al.* (2013) sequence the genes encoding Toll-like receptor 4 (Tlr4) and 7 (Tlr7) across several species within the subfamily Murinae from Southeast Asia, including *R. tanezumi* and *R. exulans*. Their results suggest the existence of parasite-mediated selection that has shaped the present species-specific variability in these rodents.

The immunogenetic studies should be accompanied by the characterization of the protective immune phe-

notype of the invader and congener rodent species. Rodents, especially rats and mice, are important models for infectious biology or for medical immunology. Despite the existing immunological toolkits for these species, we do not have information about their immunocompetence in the wild, especially along various environmental gradients. Recent studies showed that the immunocompetence of the rodents varies between captive and free-living individuals, both at intra-specific and inter-specific levels (Abolins *et al.* 2011; Tian *et al.* 2015), indicating further need for eco-immunological studies in the natural environment, including both native and invaded habitats. All empirical studies on the immunocompetence of invasive species so far have been done on bird and amphibian species (e.g. Martin *et al.* 2010; Brown *et al.* 2015). The immunocompetence of invasive species may have consequences for spillover. Using a mathematical approach taking into account historical data from a plague outbreak that occurred in Saxony in 1614–1615, Monecke *et al.* (2009) conclude that the spread of *R. norvegicus* might have contributed to the disappearance of Black Death epidemics from Europe in the 18th century. This would have occurred through the competitive advantage of *R. norvegicus* over *R. rattus* in large cities and due to its immunoresistance to *Yersinia* species.

DISCUSSION: RESEARCH NEEDED

Our review supports several non-mutually exclusive hypotheses related to the importance of parasites in the success and outcomes of invasion by the major invasive

Rattus species. However, this review also highlights a lack of knowledge, and emphasizes areas of research requiring investigation.

First, there are few studies on co-phylogeography of invasive rodents and their associated invasive parasites. Directly transmitted and specific parasites should be chosen (Nieberding *et al.* 2004; Nieberding & Olivieri 2007). Co-phylogeographic structures would help to map the historical distribution and invasion routes of rodents and their communities of parasites.

Second, investigations of parasite (macro and micro) diversity in original distributions and invaded localities (historical and recent) using molecular techniques should further help identify co-invasive parasites from spillback of local parasites.

Third, measurements of immunological parameters, immune gene diversity and immunocompetence of invading and resident hosts are almost completely lacking. A prediction is that immunocompetence and immune genes diversity should be higher in the original species distribution, especially the costly branches of immunity (e.g. inflammatory immune responses; Lee & Klasing 2004). Furthermore, the immunocompetence and immune genetic diversity should be higher than in non-invasive congeneric species in both original and invaded localities (if present).

Fourth, as the immunocompetence should be linked to parasite diversity (Ponlet *et al.* 2011), trade-offs between levels of immunocompetence and expensive life history traits are expected (Bordes *et al.* 2011; Morand 2015) as well as decreased immunocompetence with the loss of parasites and lower local biodiversity (Møller & Cassey 2004). A re-allocation of resources away from costly defenses should be particularly pronounced at the wave-front of the invasion during the range expansion stage (White & Perkins 2012).

Fifth, the risks of emergence of zoonotic diseases or outbreaks of native diseases are dependent on the types of introduced and native pathogens, as well as their ability to spillover or spillback in native and introduced hosts. However, features of invaded localities are also important determinants of outbreaks risks (native species diversity, habitat structure and connectivity; Morand *et al.* 2015). As parasite pressure (estimated by its diversity) changes (native *vs* invasive), it could explain changes in phenotypic attributes related to individual performance, behavior, and life history traits through trade-offs between costly functions and immunity. We can predict that the risk of disease spread should be higher in species-poor communities, and the risk of dis-

ease spread should be higher in human dominated habitat due to the synanthropic behavior of these invasive rodents.

CONCLUSION

Currently, trade routes are dramatically expanding as a consequence of ongoing global economic development. The economic rise of Asia and Southeast Asia, and their importance in global trade are facilitating the high risk of new invasions by these four invasive rats. Changes in habitat worldwide may also favor the spread of these invasive rodents, especially in insular Southeast Asia, Melanesia, South America and Africa. The anticipated resulting climate change is regarded as an important challenge due to its major public health implications. The effects of climate change on the ecology of rodents and rodent-borne diseases deserve further attention. Thus, addressing the above mentioned issues is of high importance, with implications for public health, the economy and conservation.

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