Phylogeography helps with investigating the building of human parasite communities

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SUMMARY

Phylogeography of parasites and microbes is a recent field. Phylogeographic studies have been performed mostly to test three major hypotheses that are not mutually exclusive on the origins and distributions of human parasites and microbes: (1) the "out of Africa" pattern where parasites are supposed to have followed the dispersal and expansion of modern humans in and out of Africa, (2) the "domestication" pattern where parasites were captured in the domestication centres and dispersed through them and (3) the "globalization" pattern, in relation to historical and more recent trade routes. With some exceptions, such studies of human protozoans, helminths and ectoparasites are quite limited. The conclusion emphasizes the need to acquire more phylogeographic data in non-Occidental countries, and particularly in Asia where all the animal domestications took place.

Key words: Phylogeography, phylogenetics, 'out of Africa', animal domestication, domestication centres, globalization, human dispersal.

INTRODUCTION

Homo sapiens is certainly the most investigated species regarding its infectious diseases. More than 1,400 species are listed as human pathogens (Cleaveland *et al*. 2001; Woolhouse and Gowtage-Sequeria, 2005) and at least 60 per cent of these are zonootic (Taylor *et al*. 2001). Documenting and understanding ecological, historical and biogeographical associations between humans and parasites has been the subject of numerous studies (May, 1958; Cockburn, 1967; McNeil, 1976; Dobson and Carper, 1996; Guernier *et al*. 2004; Wolfe *et al*. 2007), in which it has been emphasized that humans have gained their parasites either through descent (i.e. inherited from a common ancestor) or by acquiring from either wild or domesticated animal species in sympatry.

Co-phylogenetic studies such as between primates and *Pneumocystis* spp. (Hugot *et al*. 2003), lice (Reed *et al*. 2007) or viruses (Switzer *et al*. 2005) have provided examples showing that parasites may have been inherited by descent from the common ancestors of *Homo sapiens* and/or close relatives. Moreover, Davies and Pedersen (2008) showed that infectious diseases are more often shared between pairs of primate species, including humans, that are phylogenetically related but also that live in the same geographical region. However, most parasite species infecting modern humans have come from domestic and wild animals through hunting or domestication (Cleaveland *et al*. 2001; Weiss, 2001; Woolhouse and Gowtage-Sequeria, 2005; Perrin *et al*. 2010).

Perrin *et al*. (2010) using the checklist of Ashford and Crew (1998) of 402 parasite species (helminths, arthropods and protozoans) in humans showed that carnivores are the most likely to share their parasite species with humans (124 parasite species – 31%), followed by ruminants and pigs (83 species – 21%), rodents (66 species – 17%) and horses and other equids (nine parasite species – 2%). Humans and canids cohabited long before dogs became domesticated, which occurred around 15,000 years ago (i.e. before other mammals). Ruminants and pigs are considered among the oldest domesticated groups after dogs, from about 6,000 to 8,000 years ago. The high number of parasites shared with rodents is explained by their being used for meat and by a long history of several species living as human commensals, feeding on food storage, waste and rubbish. Horses were domesticated between 6,000 years and 3,000 years later than dogs and cattle (Horwitz and Smith, 2000). Interestingly, elephants are not known to have donated any parasites and rarely donate zoonoses, maybe because they lived with humans at low abundance (Wolfe *et al*. 2007).

These first observations strongly suggest that interpreting geographic origins and dispersion of shared human-animal parasites needs to take into account the domestication process. Archaeological studies suggest large-scale domestication of plants and animals between 10,000–7,000 cal years BP (Gupta, 2004). Indeed, the number of parasite

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species shared between domesticated animals and humans is positively related to time since domestication (Horwitz and Smith, 2000), a pattern already observed by McNeil (1976) (see Perrin *et al*. 2010).

The potential sources of plants and animals suitable for domestication seem not to be randomly distributed on continents, and it appears that the majority of domestic animals originated from the Middle East, Central, Southwest, and Southern Asia (Diamond, 1997; Gupta, 2004; Larson *et al*. 2005; Driscoll *et al*. 2007; Naderi *et al*. 2008). However, eight of the 15 temperate diseases investigated in the Wolfe *et al*. (2007) study reached humans from domestic animals (diphtheria, influenza A, measles, mumps, pertussis, rotavirus, smallpox and tuberculosis) and only three of the ten tropical diseases investigated originated from animal domestication, which questions the potential dispersion of zoonotic diseases.

Here, my aim is to summarize the recent advances in the phylogeographics and phylogenetics of human pathogens and to show how these studies contribute to our understanding of the building of human parasite communities. In particular, three major origins and distributions of human parasites have been tested using phylogeographic studies: (1) the "out of Africa" pattern where parasites followed the dispersal and expansion of modern humans in and out of Africa, (2) the "domestication" pattern where parasites were captured in the domestication centres and then dispersed more widely and (3) the "globalization" pattern, which reflects the distribution of parasites in relation to historical and more recent trade routes. The classification of these three mechanisms does not preclude the notion that they are not mutually exclusive as some examples reported here may show.

THE PHYLOGEOGRAPHY OF PARASITES

Even if important progress has been made in documenting the geographic distribution of parasites and pathogens, their origins and dispersion are less well known (Morand and Krasnov, 2010). Phylogeographic approaches originate in historical biogeography (Katinas *et al*. 2003) in an attempt to take account of invasive processes and the mechanisms of geographic colonization (Avise, 2000), with earlier studies related to post-glacial re-colonization in Europe. The development of phylogenetic studies may then permit exploration of these origins and dispersion of hosts and their parasites and microbes on fine geographic and temporal scales (Nieberding *et al*. 2004; Nieberding and Olivieri, 2007).

The phylogeographic method

As evolutionary processes take place in a dynamic geographical context, patterns of genetic variation are strongly structured in space and time (Hewitt, 2001). Phylogeography investigates the processes governing the geographical distributions of lineages within and among closely related species (Avise, 2000). Phylogeographic studies of pathogens and parasites are more recent than phylogenetic studies (Holmes, 2004) and most of them argue that phylogeographic studies of parasites may help explain the phylogeography of their hosts (Nieberding *et al*. 2004; Wirth *et al*. 2005; Nieberding and Olivieri, 2007). Phylogeographic studies may also help identify timing, rate and origins of parasite emergence as exemplified by *Borrelia burgdorferi* the causative agent of Lyme disease (Gatewood Hoen *et al*. 2009).

The main distinction between phylogeographic and phylogenetic analyses is the addition of spatial information so that the inferences from the former allow testing of hypotheses concerning the association of clades (branches) of phylogenetic trees (haplotypes) according to spatial distribution. There has been substantial improvement in statistical inference methods from nested clade analysis (see Templeton, 2010) to the more recent use of approximate Bayesian computation (ABC) (Knowles, 2009; Beaumont *et al*. 2010). A promising new investigative approach has been developed by Lemey *et al*. (2009), who used Bayesian modelling of character evolution, here geographical locations, for the inference of ancestral states, in this case the geographical location of ancestral nodes and migration events.

Rather like co-phylogenetic studies, co-phylogeographic studies aim to compare phylogeographic trees obtained for both hosts and their parasites in a spatial context, while aiming to use similar statistical methods based on null hypotheses (Nieberding *et al*. 2008). Quantitative tests of mechanisms that may generate co-phylogeographic scenarios, however, are still in their infancy (but see Nieberding *et al*. 2010).

"Out of Africa" pattern

There is a consensus that modern humans left Africa up to 150,000 years ago (from 60,000–150,000 years before present, ybp; Cann *et al*. 2002). Humans dispersed out of Africa toward the Middle East ~60,000–150,000 ybp and then independently to Europe and Asia (Cavalli-Sforza *et al*. 1994), and probably in two major waves to Asia (Rasmussen *et al*. 2011). Dispersals to the Americas occurred around 14,000 ybp by peoples of East Asian ancestry who crossed the Bering Straits in two major migrations (Schurr and Sherry, 2004). Finally, it is known that the islands of the Western Pacific were populated by people who originated in Taiwan around 5,500 ybp (Gray *et al*. 2009).

Human microbes and parasites are used as markers of these human dipsersals (Dominguez-Bello and Blaser, 2011). A variety of human pathogens such as

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Table 1. Phylogeographic studies of microbes and parasites of humans

Agent	Name	Methods	Ancestor origin	Reference
Virus	Hepatitis G Virus	RNA sequencing	African origin	Muerhoff *et al*. 2005
	JC Virus	DNA sequencing	African origin	Agostini *et al*. 1997; Sugimito *et al*. 2002
	Dog Rabies virus (RABV)	Sequencing	Asian origin	Bourhy *et al*. 2008
	Variola virus (VARV)	SNPs	African origin or Asian origin followed by dispersion routes	Li *et al*. 2007
Bacteria	*Helicobacter pylori*	MLST	African origin	Falush *et al*. 2003
	Mycobacterium leprae	SNPs	Silk Road trade	Monot *et al*. 2005, 2009
	Mycobacterium tuberculosis complex	SNPs, Indels* comparative genomic hybridization	East Africa (previously *M. canetti*)	Gagneux and Small, 2007
	Salmonella enterica Typhi	SNPs	Southern Asia	Roumagnac *et al*. 2006
	Streptococcus mutans	Plasmid sequencing	African origin	Caufield *et al*. 2007
	Trepanoma pallidum	Gene sequencing	African or Asian origins? Americas (Columbus origin of modern syphilis)	Harper *et al*. 2008
	Yersinia pestis	MLVA, IS elements, SNPs	Africa (Justinian's plague Central Asia (Black Death) East Asia (third pandemic)	Achtman *et al*. 2004
Helminths	*Trichinella spiralis*	Microsatellites, mitochondrial sequencing	East Asia and Middle East origins	Rosenthal *et al*. 2008
	Taenia spp.	Sequencing, mitochondrial genes	African origin	Hoberg *et al*. 2001

MLST (Multilocus sequence typing) consists of sequencing several housekeeping gene fragments for a total concatenated length of 3–4 kb.
SNP: single nucleotide polymorphism.
* large sequence polymorphisms.

Haemophilus influenzae (Musser *et al*. 1990), human polyomavirus JCV (Agostini *et al*. 1997; Sugimito *et al*. 2002; Zheng *et al*. 2003), the human T cell lymphotropic virus I (HTLV-I) (Miura *et al*. 1994), *Mycobacterium tuberculosis* (Kremer *et al*. 1999), *Mycobacterium leprae* (Monot *et al*. 2005) the human pathogenic fungus *Histoplasma capsulatum* (Kasuga *et al*. 1999), *Streptococcus mutans* (Caufield *et al*. 2007) and *Helicobacter pylori* (Ghose *et al*. 2002; Falush *et al*. 2003; Wirth *et al*. 2004) all show geographic structures. These parasites are hypothesized to have accompanied humans during their ancient and recent dispersals, and investigation of their population structures may help us to understand human evolutionary history (Wirth *et al*. 2005). For this purpose bacteria and viruses have been the most intensively investigated organisms(Table 1).

Helicobacter pylori is a bacterium that colonizes the stomachs of most humans and can cause chronic gastric pathology. Wirth *et al*. (2004) showed that *Helicobacter pylori* can distinguish between closely related Buddhist and Muslim populations in Ladakh (India). This bacterium is also divided into several populations with distinct geographical distributions on a more global scale (Falush *et al*. 2003). Molecular studies and phylogenetic reconstructions have revealed that these populations are in fact derived from ancestral populations that arose in Africa (Linz *et al*. 2007) followed by extensive diversification in Central and East Asia. Subsequent worldwide spread can be attributed to human dispersals such as the prehistoric colonization of Polynesia and the Americas, the Neolithic introduction of farming to Europe, the Bantu expansion within Africa and the slave trade.

Hepatitis G virus (HGV or GBV-C) is an RNA flavivirus that is widely distributed with geographically divergent isolates. Phylogenetic analyses that include sequences from chimpanzee isolates suggest an ancient African origin (Muerhoff *et al*. 2005). Loureiro *et al*. (2002) showed that HGV was introduced from Asia to America by early human dispersals.

JC virus, a member of Polyomaviridae family, is ubiquitous in human populations and primary infection occurs asymptomatically during childhood. JCV is transmitted mainly from parents to children during prolonged cohabitation, which has enabled its use for retracing human dispersals (Sugimoto *et al*. 2002). Although there is no outgroup that can be used to root JCV trees, the phylogenetic analyses of JCV DNA sequences conducted by Sugimoto *et al*. (2002)

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suggest an African origin of the virus. Phylogenetic analyses have revealed geographic structures that are compatible with the dispersal and expansion of humans (Hammer *et al*. 2001). JVC was also used to investigate the relationships between East Asian populations (Japanese and Koreans) and Native Americans (Amerinds and Na-Denes) (Zheng *et al*. 2003). Differences between European and Africa/Asian JCV sub-populations seemed to indicate that human population structures alone cannot account for diversity patterns in the virus and that some other factors must have played a role in the genetic differentiation of the virus (Wooding, 2001). Indeed, phylogenies of human populations and JCV are not concordant, indicating extensive horizontal gene transmission in the virus (Shackelton *et al*. 2006).

The *Mycobacterium tuberculosis* complex is clustered in six lineages associated with geographic locations and phylogeographic studies suggest that these associations reflect ancient human dispersals (Gagneux and Small, 2007). As emphasized by Achtman (2008), however, most analyses have focused in Europe and North America on strains isolated from infected immigrants coming from developing countries. The *M. tuberculosis* complex is supposed to be part of a highly diversified protospecies that has infected hominids since their origins and was subject to an extreme genetic bottleneck following the emergence of the modern humans and their dispersal in and out of Africa (Gutierrez *et al*. 2005). Indeed, the previously designated *M. canetti,* from Djibouti, shows a greater genetic diversity. Although the ancestral form of *M. leprae*, the agent of leprosy, is still not known, phylogeographic studies support an African origin followed by early dispersion of the modern human (Monot *et al*. 2009).

Phylogenetic studies have shown that the occurrence of *Taenia* in humans predates the domestication of cattle and swine by Neolithic farmers, suggesting that their ancestors first became infected while consuming raw meat such as partially consumed and discarded prey items of carnivores and scavengers (Hoberg *et al*. 2001). *Taenia* accompanied early human dispersion out of Africa, and swine and cattle are thought to have acquired infections with *Taenia* species during their early domestication (Hoberg *et al*. 2001).

"Domestication" pattern

Dogs were domesticated 15,000 years ago and studies on the patterns of phylogeographic variation indicate an East Asian origin (Savolainen *et al*. 2002). The study of Bourhy *et al*. (2008) on the phylogeography of dog rabies virus (RABV) showed that the RABV from terrestrial mammals comprises six major distinct phylogeographic clades. RABV is hypothesized to have an ancestry that lies with domestic dogs from the south of India and evolutionary diversification, using coalescent-based methods, is estimated to have occurred within the last 1500 years. Moreover, Bourhy *et al*. (2008) hypothesized that the dog has served as the main vector for RABV transmission to other taxa of the Canidae such as foxes and raccoons as well as several species of Herpestidae and Mephitidae.

Cattle and swine have had extensive epidemiological interactions with humans. The results of several phylogenetic studies suggest that these animals were not only the sources of parasite and microbe infections for humans, but they were also recipients of parasites and microbes from humans acquired, in the opposite direction, as a result of domestication.

Another example is *Mycobacterium bovis*, which has been shown to arise from a *M. tuberculosis* strain. This evolutionary scenario has been confirmed by genomics, in particular by the fact that *M. bovis* has a smaller chromosome than *M. tuberculosis* (Smith *et al*. 2009). The insertion of *M. bovis* strains within West African strains of *M. tuberculosis* suggests an African origin of *M. bovis*. Unfortunately, investigations of both domesticated and wild Asian buffaloes are lacking.

Anthrax is caused by *Bacillus anthracis,* which is derived from a *Bacillus cereus* ancestor. Molecular clock estimates that the separation of *B. anthracis* from its closest outgroup occurred more than 17,000 years ago (Van Ert *et al*. 2007); this associates the radiation of *B. anthracis* with the domestication of cattle and suggests human-mediated dispersal. However, the geographic origins of anthrax have not been established largely because of the lack of studies conducted in the domestication centres.

Recent works on the phylogeny and phylogeography of measles virus (MeV) suggest a recent emergence of measles around the 11th and 12th centuries from the closely related rinderpest virus (RPV) of ruminants. This more recent origin, if it is confirmed, challenges the hypothesis of an pathogen emergence associated with the early domestication of ruminants in the Fertile Crescent or in Asia.

The history of pig domestication involves multiple centres of domestication in Asia, where pigs were first domesticated in the Neolithic period from several lineages of wild boar, and in Europe, where pigs were domesticated from distinct and presumably genetically restricted ancestors (Larson *et al*. 2005, 2007). China and Europe thus represent different domestications or breed formation processes (Megens *et al*. 2008). Pigs and wild boar are hosts to several potential zoonotic parasites, but few of them have been studied in depth phylogenetically.

Ancestors of human *Ascaris* are hypothesized to be derived from nematodes hosted by wild boar at the very start of their domestication, but there is little evidence to support this hypothesis (Criscione *et al*.

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2007). Recently, Zhou *et al*. (2011) investigated the phylogeography of *Ascaris lumbricoides* and *A. suum*. This study is not without sampling bias as it lacks inclusion of an external outgroup. Indeed, inclusion of an external outgroup would have permitted inference of the direction of host origin.

Trichinella spiralis is the second zoonotic roundworm that has been examined in a phylogeographic context. Rosenthal *et al*. (2008) investigated the diversification of *T. spiralis* using *Trichinella nativa* and *T. murrelli*, both parasites of wildlife, as outgroups. Their study suggested that European lineages of *T. spiralis* originated several thousand years ago when pigs were first domesticated there and hypothesized that, more recently, Europeans have introduced *T. spiralis* to America via infected pigs and/or rats. The lower genetic diversity observed in European lineages of *T. spiralis* compared to Asian lineages is in accordance with the lower diversity of European wild boar in comparison with Asian wild boar.

"Globalization" pattern

Human societies have been engaged in trading activities for a very long time and they not only exchanged goods but also infectious diseases (Mc Neill, 1976; Diamond, 1997). Plague, syphilis, smallpox and leprosy are strongly associated with trade but also with wars and the resulting human displacements.

Yersinia pestis is the agent of two old pandemic plagues, Justinian's plague (541–767 AD) and the Black Death (1346–1800s). The third and last pandemic was related to shipping from Hong Kong, which carried infected rats and fleas to the entire globe in 1894 (Achtman, 2008). Three centres of origin of these pandemic plagues are depicted according to phylogeographic studies, Africa, Central and East Asia. The spread of all these plagues is most likely linked with commercial trading. Unfortunately, *Y. pestis* from endemic areas in Central and East Asia has not been analysed in relation to isolates from other parts of the world (Achtman, 2008).

The comparative genomic analysis of *Mycobacterium leprae*, the agent of leprosy, suggests an African origin and its actual distribution explained by dispersal patterns of early humans and by trade routes, such as the Silk Road, which have contributed to the spread leprosy (Monot *et al*. 2005, 2009). However, in contrast to the Black Death, leprosy is thought to have originated in either Europe or the Middle East and then spread to China via the Silk Road and thereafter to the Far East (Monot *et al*. 2009).

Different varieties of treponemal diseases exist, with syphilis due to the spirochete *Trepanoma pallidum* sub-species *pallidum*. A recent phylogenetic investigation has given new insights on the diversification of *T. pallidum*, which arose in Africa and Southeast Asia (*T. pallidum* subspecies *pertenue* I and II) (non-venereal infection) and spread subsequently to the Middle East/Eastern Europe, in the form of endemic syphilis, and to the Americas, in the form of New World yaws (Harper *et al*. 2008). These results support the Columbian theory of the origin of syphilis, as an American *T. pallidum* strain was reintroduced to the Old World giving rise to the progenitor of modern syphilis-causing strains.

A recent study on smallpox virus illustrates the problem of the data information. Li *et al*. (2007) show that two primary VARV clades may have diverged from an ancestral African rodent-borne variola-like virus either around 16,000 or around 68,000 ybp, depending on which historical records (East Asian or African) are used to calibrate the molecular clock. The numbers of events needing to fit the date with the two scenarios differ. A parsimony analysis has to be performed, which would likely suggest an Asian origin of smallpox with subsequent dispersion by trade routes to Africa, and from Africa to Americas by slave trade.

Limitations of phylogeographic studies

Five main limitations and potential associated pitfalls can be identified from this brief overview of phylogeographic studies on human pathogens and parasites. The first one is linked to the infectious or parasitic agent investigated in phylogenetic reconstruction. Although largely used in phylogeographic studies, viruses do not seem to be the best candidates for investigating the "out of Africa" pattern because of their high rates of mutations (Holmes, 2004). However, viruses may be of real interest for investigating recent historical events. Bacteria are also widely used, mostly to test early modern human dispersals (out of Africa) with great success (e.g. *Helicobacter pylori*). Parasites such as protozoans, helminths or arthropods rarely feature in phylogeographic studies of human parasites, although they appear to be excellent candidates for the investigation of co-speciation and co-phylogeographics (see Criscione *et al*. 2007; Nieberding and Olivieri, 2007).

The second limitation is related to the genetic markers, which will depend on the agent in question. While viruses and bacteria can be fully sequenced and comparative genomics help in investigating genomic evolution, these technological advances are used less for macroparasites. Most phylogeographic studies of macroparasites have been based on the sequencing of one (mitochondrial) or ideally several genes, both mitochondrial and nuclear (but see Criscione *et al*. 2005; Criscione, 2008). Microsatellites may have complementary significance in inferring more recent dynamics.

The third and major limitation lies in the samples themselves and the potential flaws of analyses due to sample bias. Phylogeographics need the establishment of a sampling protocol adapted to the

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hypothesis to be tested and the size of the geographic area investigated. However, most studies are not based on a specified sample protocol in relation to hypotheses under investigation and it appears that, in some studies, samples have been gathered more or less at random. Although crucial for examining dispersal (dispersion routes in the current context), the choice of the outgroup is also rarely explained and not even mentioned at all in some studies. This problem of sampling may lie in the fact that many studies simply apply a phylogenetic analysis to isolates of the organisms investigated, without any apparent awareness of the concepts and methods of phylogeographics (see Avise, 2000; Nieberding and Olivieri, 2005). Moreover, as emphasized by Beheregaray (2008) in an exhaustive review of phylogeographic studies, there is a great need to acquire more phylogeographic data outside of Occidental countries, which account for around 80% of the studies whereas Asia accounts for 15% and Africa just 7%. This is crucial for parasites and microbes of domestic animals in the domestication centres.

The fourth limitation lies in the methods used for genealogical or tree reconstruction. Most of the studies presented here have used standard phylogenetic reconstructions and few have used more recent advanced tools. Investigating recent evolutionary events takes account not only of population structure but also demography and potential genetic exchanges, as a Bayesian modelling approach may permit (Knowles, 2009).

The final limitation relates to the dating of diversification events. This is always difficult with parasites due to the lack of fossil records against which to calibrate molecular information. Calibration depends on life cycle data (generation times) and mutation rates, but assumes that these will be roughly constant through time and lineage. For example, in the case of *T. spiralis*, the microsatellite mutations during parasite generations was calculated to estimate that Western and Asian lineages of *T. spiralis* would have diverged 18,000 years ago (Rosenthal *et al*. 2008). Such calculations have been used for several microbes and have indicated time to the most recent common ancestor (the age) is 10,000–71,000 years for *Salmonella Typhi* (Roumagnac *et al*. 2006), 13,000 years for *Y. pestis* (Achtman *et al*. 2004), 15,000–20,000 years for the *M. tuberculosis* complex (Kapur *et al*. 1994), and 40,000 years for *E. coli* O157:H7 (Zhang *et al*. 2006). These calculations should be compared with other sources of information, both historical and archaeological.

CONCLUSION

The building of human parasite communities through "out of Africa", domestication and globalization mechanisms has found its significance in evolutionary biogeography where processes are invasion, establishment and expansion (Lockwood *et al*. 2007). Phylogeography provides the tools to explore these events and their linkages (Avise, 2000). Although studies on human parasites and microbes are classified here through these three patterns, they are not mutually exclusive. A clear example is human *Taenia* species originating in Africa, which has followed human dispersal and later switched to domesticated animals. Moreover, recent trading activities may have obscured the oldest patterns, i.e. "out of Africa" and domestication centres. This brief overview of phylogeographic studies of human parasites and microbes raises two main observations, one on the small number of investigation on parasites and the second on the need to investigate parasites of domestic animals.

Parasites (helminths, ectoparasitic arthropods, fungi and even protozoans) have been poorly investigated compared to bacteria and viruses. This is quite intriguing as some species could be good candidates for testing the "out of Africa" pattern such as the fungi *Pneumocystis* spp. (Hugot *et al*. 2003) or lice (Reed *et al*. 2007) compared to viruses that may evolve too fast for depicting old dispersion events (Holmes, 2004). The pinworm, *Enterobius vermicularis,* seems to be particularly relevant as it can be found at archaeological sites and its prevalence seems to be linked with changes in settlement habits and population densities (Hugot *et al*. 1999).

There is a lack of information on the phylogeny and phylogeographics of parasites and microbes of domestic animals. The 'domestication' pattern should be completed by investigations of parasites and microbes that are specific to domesticated animals (and with relatives known in wild animals). For example, the recent molecular epidemiology of *Mycoplasma capricolum*, the causative agent of contagious caprine pleuropneumonia (CCPP) of domestic goats, showed a potential origin centre in the Middle East, which is presumably a domestication centre for the domestic goat. However, the existence of a distinct Asian cluster favours the hypothesis that this disease has been endemic in Asia for a long time (Manso-Silvan *et al*. 2011). Another example is described by Troell *et al*. (2006), who investigated the population genetic structure of the nematode *Haemonchus contortus* on a worldwide scale and showed the existence of geographic clusters. Phylogeographic investigations may depict the spreading routes of domesticated animals in Asia and in Africa. Phylogeography is a functional tool that may also help with investigations of old and recent emerging diseases (Keim and Wagner, 2009). As already emphasized by Wolfe *et al*. (2007), most studies have been based on specimens collected opportunistically from domestic animals with no systematic surveys over the spectrum of domestic and wild animals for almost any particular parasite. Among the potentially interesting organisms, Wolfe *et al*. (2007)

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cited the mite *Sarcoptes scabei* as the agent of sarcoptic mange, which affects wild mammals worldwide dramatically. Again, it is hypothesized that *S. scabei* originated in human populations and then spread to domesticated animals, which in turn, transmitted sarcoptic mange to a wide range of wild mammals (Fain, 1978).

We are still far from understanding the patterns and processes behind the building of human parasite communities. As this review emphasizes, phylogeographics is an important tool for determining the origins, distributions and dispersal patterns of human parasites and microbes. A major research effort should be initiated for zoonotic parasites and microbes that are shared with domestic animals (including the commensal rodents). As the review also highlights, we have to move our attention and effort towards Asia where almost all of the animal domestication processes took place and from where the first global commercial trade emerged, and we have to leave our Eurocentrism out of phylogeography.

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