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Domesticated animals and human infectious diseases of zoonotic origins: Domestication time matters

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A B S T R A C T

The rate of emergence for emerging infectious diseases has increased dramatically over the last century, and research findings have implicated wildlife as an importance source of novel pathogens. However, the role played by domestic animals as amplifiers of pathogens emerging from the wild could also be significant, influencing the human infectious disease transmission cycle. The impact of domestic hosts on human disease emergence should therefore be ascertained. Here, using three independent datasets we showed positive relationships between the time since domestication of the major domesticated mammals and the total number of parasites or infectious diseases they shared with humans. We used network analysis, to better visualize the overall interactions between humans and domestic animals (and amongst animals) and estimate which hosts are potential sources of parasites/pathogens for humans (and for all other hosts) by investigating the network architecture. We used centrality, a measure of the connection amongst each host species (humans and domestic animals) in the network, through the sharing of parasites/pathogens, where a central host (i.e. high value of centrality) is the one that is infected by many parasites/pathogens that infect many other hosts in the network. We showed that domesticated hosts that were associated a long time ago with humans are also the central ones in the network and those that favor parasites/pathogens transmission not only to humans but also to all other domesticated animals. These results urge further investigation of the diversity and origin of the infectious diseases of domesticated animals in their domestication centres and the dispersal routes associated with human activities. Such work may help us to better understand how domesticated animals have bridged the epidemiological gap between humans and wildlife.

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1. Introduction

Amongst the species listed as human pathogens 60 per cent are presented as zoonotic (Cleaveland et al., 2001; Woolhouse and Gowtage-Sequeria, 2005). How parasite/pathogen communities of humans have been built-up in time and space has been the aim of several historical, ecological and evolutionarily studies (McNeill, 1976; Wolfe et al., 2007; Dunn et al., 2010; Gómez et al., 2013), with the assumptions that revealing the past may help to understand the present and infer future trends. Reviews emphasize that humans have gained their parasites and infectious agents either through descent (i.e. inherited from a common ancestor) or by acquiring them from either wild or domesticated animal species according to three major hypotheses (Wolfe et al., 2007; Perrin et al., 2010; Morand, 2012): the "out of Africa" source where parasites followed the dispersal and expansion of modern humans in and out of Africa; the "domestication" source where parasites were captured in domestication centres and then dispersed more widely; and the "globalization" source, which reflects the distribution of parasites in relation to historical and more recent trade routes.

The role played by domestic animals in the building of human parasite/pathogen diversity was hypothesized a long time ago by McNeill (1976), who was the first to suggest a positive relationship (although not statistically tested) between the number of parasite species shared between domesticated animals and humans and the length of time since their domestication. Here, we reinvestigated

the hypothesis of McNeill using several other data sources and more accurate information on the dates and origins of domestication (Driscoll et al., 2009). We aimed, first, to confirm statistically the relationship hypothesized by the environmental historian McNeill (1976).

Second, and in order to better explore the potential mechanisms underlying the observed relationship between parasites/pathogens shared and time since domestication, we used network analysis. Network-based approaches have been widely used in epidemiology and disease ecology to study transmission heterogeneity (Bansal et al., 2007) in particular, how network topology may determine pathogen transmission across human and wildlife populations (Salathé and Kazandjieva, 2010; Gómez et al. 2013). By using network analysis, we aimed to (1) better visualize the overall interactions between humans and domestic animals (and amongst animals) and (2) estimate which hosts are potential sources of parasites/pathogens for humans (and for all other hosts) by investigating the network topology. For this, we used centrality, a measure of the connection amongst each host species (humans and domestic animals) in the network. A central host (i.e. high value of centrality) is the one that is infected by many parasites/pathogens that infect many other hosts in the network. Following Gómez et al. (2013), we assumed that the centrality of a given host species is a good estimate of its potential to be a source of parasites/pathogens to other species (domestic animals or humans). We hypothesized that a domestic host will be central in the network, i.e. it has a high value of centrality, if it was domesticated for a long enough time to have increased opportunities to share parasites/pathogens with humans but also with other domesticated animals.

2. Materials and methods

2.1. Sources of data

Data on parasites shared between humans and domesticated animals are from a book published by Ashford and Crewe (1998); those on shared infectious diseases are from McNeill (1976). We obtained a third source of more recent data using the Global Infectious Diseases and Epidemiology Network (GIDEON) database (www.gideononline.com). GIDEON is a medical database that provides continually updated data on the regional presence and epidemic status of pathogens and it has been used in various recent studies (Fincher et al., 2008).

Data on the total number of parasites and pathogens recorded in domestic animals were obtained from the EID2 database (www.zoonosis.ac.uk/EID2) (McIntyre et al., 2014). The EID2 systematically collates information on pathogens into a single resource using evidence from the NCBI Taxonomy database, the NCBI Nucleotide database, the NCBI MeSH (Medical Subject Headings) library and PubMed. Information about pathogens is assigned using data-mining of meta-data and semi-automated literature searches together with the total number of publications, which gives an estimation of the research effort to screen parasites. The total number of parasites/microbes was obtained by searching the number of parasites and microbes reported in each mammal species, and the total number of publications that referred to the association of each of microbe/parasite with each mammal species in consideration. The number of publications is then a proxy of the research effort on microbe/parasite diversity.

2.2. Statistical analysis and control for phylogenetic inertia and research effort

We first performed linear regressions on raw values of parasites/pathogens/diseases shared between domesticated animals and

time to domestication from the three sources of data (McNeill, Ashford & Crewe, GIDEON).

Using information on mammal phylogeny (Binida-Emonds et al., 2007), we calculated the independent contrasts for each of the variables investigated with the package APE (Paradis et al., 2004) implemented in R (R Development Core Team 2012). To confirm the proper standardization of contrasts, we regressed the absolute values of standardized contrasts against their standard deviations. Contrasts were then analyzed using standard multiple regressions, with all intercepts forced through the origin. These variables were normalized using log transformation if needed. We then performed multiple linear regression on the independent contrasts (IC) of parasites/pathogens/diseases shared between domesticated animals on the four sources of data, including the EID2. To address the problem of sampling effort, we included the number of publications (obtained from www.zoonosis.ac.uk/EID2) as a covariate.

2.3. Network analysis

We used bipartite networks where nodes from hosts are interacting with nodes of pathogens/parasites, using the datasets of Ashford & Crewe and GIDEON. We projected these bipartite networks to unipartite networks using the 'tnet' package in R. These unipartite networks will represent patterns of relative interactions amongst domestic animals and humans through the occurrence of parasites/pathogens shared. Each host within a network plays a different role in pathogen sharing relative to all other nodes in the network. The role of each host within the network was examined using its centrality measurement. A central node (host) is the one that is highly connected to other nodes (hosts) and thus which is supposed to have a greater transmission potential of parasites/pathogens. We calculated the eigenvalue centrality (EC) with the 'evcent' function from the igraph package (Csardi and Nepusz, 2006) in R and we regressed the EC values to time to domestication.

3. Results

3.1. Relationships between shared parasites/pathogens and time since domestication

All three data sets showed no correlation between shared parasites/microbes/diseases and the total number of parasites/microbes/diseases identified using the EID2 (McNeill *vs* EID2, $P = 0.49$; Ashford & Crewe *vs* EID2, $P = 0.38$; GIDEON *vs* EID2, $P = 0.95$).

Research effort seemed to only slightly affect the number of diseases obtained from McNeill ($P = 0.07$), which may be explained by the use of old epidemiological sources of parasites/pathogens in this historical book. The number of parasites/pathogens shared between humans and parasites used in McNeill (1976) is affected by investigation effort, suggesting that an increase in investigation is necessary to give an accurate estimation of parasites/pathogens shared; this is also the case when using the more recent datasets (i.e., Ashford & Crewe and GIDEON).

Using several independent sources of data for parasites and infectious diseases and for domestication time (Table 1), we found positive relationships between the numbers of parasites and/or infectious diseases shared between humans and their domesticated animals and the length of time since their domestication (all $P < 0.05$, Fig. 1). Moreover, adding or removing rats from the datasets of Ashford & Crewe and GIDEON did not change the observed relationships.

Table 1

Time since domestication and the origin of the major domesticated/commensal mammals of the Old World (from Driscoll et al., 2009), including the nature of their relationship with humans. The total number of their parasites/microbes was obtained by searching the number of parasites and microbes reported in each of these mammal species, and the total number of publications that referred to the association of each of microbe/parasite with each mammal species in consideration (http://zoonosis.ac.uk/EID2). We included the rat, *Rattus rattus*, as this species was included in the book of the environmental historian McNeill (1976). We added the number of parasites/pathogens from Ashford and Crewe (1998) and GIDEON database, which allowed us to compute the number of parasites/pathogens found in humans.

Animal	Time since domestication (in years)	Origin	Nature of the relationships	Proximity with humans	Ahsford & Crewe (1998)	GIDEON	Total number of parasites/ microbes	Number of publications
Dog (*Canis familiaris*)	17,000	East Asia	Work, meat, pet	Indoor/outdoor	71	29	452	300,484
Cat (*Felis cattus*)	9700	Fertile Crescent	Pest control, meat, pet	Indoor/outdoor	54	10	293	156,375
Cattle (*Bos taurus*)	11,000	Southeast Anatolia	Work, milk, meat, leather	Indoor/outdoor	34	25	1037	347,521
Cattle (*Bos indicus*)	9000	South Asia	Work, milk, meat, skin	Indoor/outdoor	–	–	67	1651
Swine (*Sus scrofa*)	10,500	Southeast Anatolia, East Asia, Southeast Asia	Meat, leather, pet	Indoor/outdoor	34	18	2776	319,489
Sheep (*Ovis aries*)	12,000	Southeast Anatolia,	Meat, milk, wool, leather	Indoor/outdoor	84	15	536	119,508
Goat (*Capra hircus*)	11,000	Anatolia	Meat, milk, wool, leather	Indoor/outdoor	–	–	321	31,129
Horse (*Equus caballus*)	5000	Central Asia	Work, milk, meat	Indoor/outdoor	9	6	498	55,137
Donkey (*Equus asinus*)	4800	Eastern Africa	Work, meat, milk	Indoor/outdoor	–	–	86	1939
Camel (*Camellus dromedarius*)	5000	Arabia	Work, milk, meat	Outdoor	2		111	2171
Camel (*Camellus bactrianus*)	4600	East Iran	Work, milk, meat, hair	Outdoor	–		94	
(*Oryctolagus cuniculus*)	2000	Europe	Meat, fur, leather, pet	Indoor/outdoor	6	7	18	673
Rat (*Rattus rattus*)	12,000	South Asia	Meat, commensal	Indoor/outdoor	27	23	100	496,793
Human (*Homo sapiens*)	–	–	–	–	402	129	27,439	2,217,551
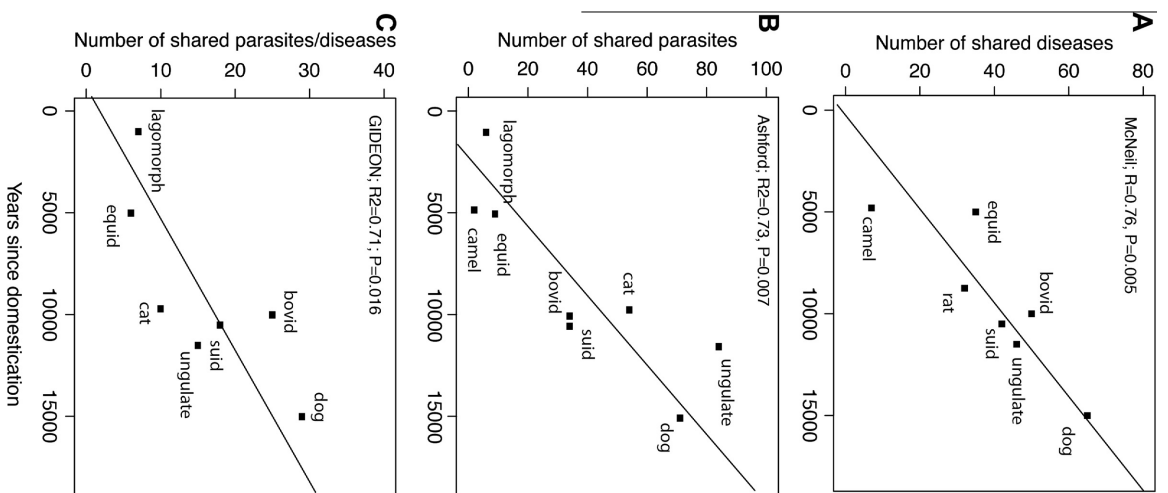
Fig. 1. Relationships between the number of parasites/infectious diseases shared between domestic animals and humans in relation to domestication time using the data from (A) McNeill (1976), (B) Ashford and Crewe (1998), (C) GIDEON database.

We found similar relationships when controlling for potential phylogenetic influences (using the independent contrasts method) taking into account overall pathogen diversity and research effort using another source of data on the parasites and pathogens of animals (McIntyre et al., 2014) (Table 2). This suggests that phylogenetic distances amongst domestic animals and humans

Table 2
Multiple regressions on the effect of domestication time on the richness of domesticated animals (EID2) or on the richness of parasites/microbes/diseases shared between domestic animals and humans. The number of publications reporting each parasite/pathogen/disease for each domestic animal was used as a proxy for the amount of research investigation undertaken on each. The analyses used independent contrasts.

Dependent variable (IC)	Independent variables (IC)	Slope (P)	F-test (P)	R^2, F-total (P)
EID	Domestication time	0.00 (0.65)	5.21 (**0.05**)	
	Research effort (pub number)	0.39 (**0.001**)	17.41 (**0.001**)	$R^2 = 0.67$
				$F_{2,11} = 11.32 (=\mathbf{0.02})$
McNeill	Domestication time	0.002 (**0.04**)	8.49 (**0.04**)	
	Research effort (pub number)	4.11 (0.08)	5.65 (**0.07**)	$R^2 = 0.78$
				$F_{2,4} = 7.07$ (**0.04**)
Ashford & Crewe	Domestication time	0.01 (0.07)	6.65 (**0.007**)	
	Research effort (pub number)	0.16 (0.46)	0.63 (0.10)	$R^2 = 0.55$
				$F_{2,6} = 3.64$ (0.09)
GIDEON	Domestication time	0.01 (**0.003**)	25.95 (**0.004**)	
	Research effort (pub number)	−0.00 (0.35)	1.08 (0.35)	$R^2 = 0.84$
				$F_{2,5} = 63.99$ (**0.009**)

P values < 0.5 are indicated in bold.
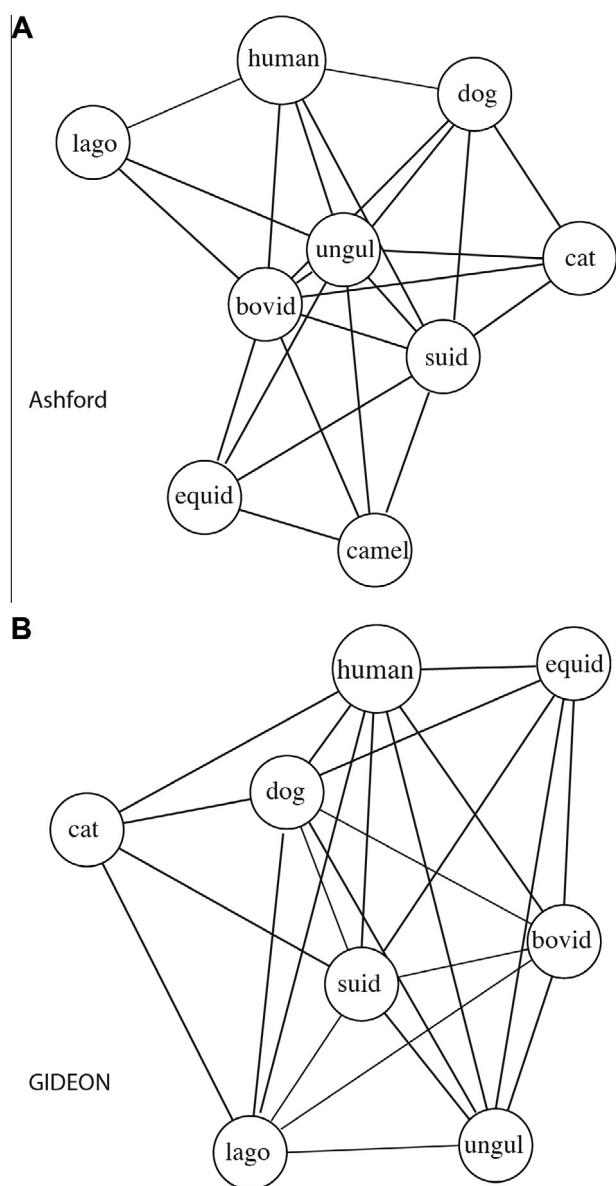
Fig. 2. Unipartite networks depicting the pattern of shared pathogens/parasites by humans and domestic animal species using data from the (A) Ashford and Crewe (1998) and (B) GIDEON database. The links among nodes (each species) depict shared pathogens/parasites.

do not affect the observed relationship between the number of parasites/pathogens shared and time since domestication.

We were unable to find any strong associations between the number of pathogens/parasites shared and the nature of the relationships (working animals, food animals, etc) or their proximity (i.e. indoor/outdoor) with humans (Table 1).

3.2. Host centrality and time since domestication

Unipartite networks of interactions amongst domestic animals and humans based on the occurrence of parasites/pathogens shared using the Ashford and Crewe and GIDEON datasets are presented in Fig. 2.

We found positive relationships between the centrality (EC) of domestic animals and the time since domestication using both Ashford and Crewe ($R^2 = 0.8301$, $P = 0.0016$) and GIDEON ($R^2 = 0.6894$, $P = 0.021$) (Fig. 3). The more central a domestic animal host, i.e. the more this host contributes to the sharing of parasites/
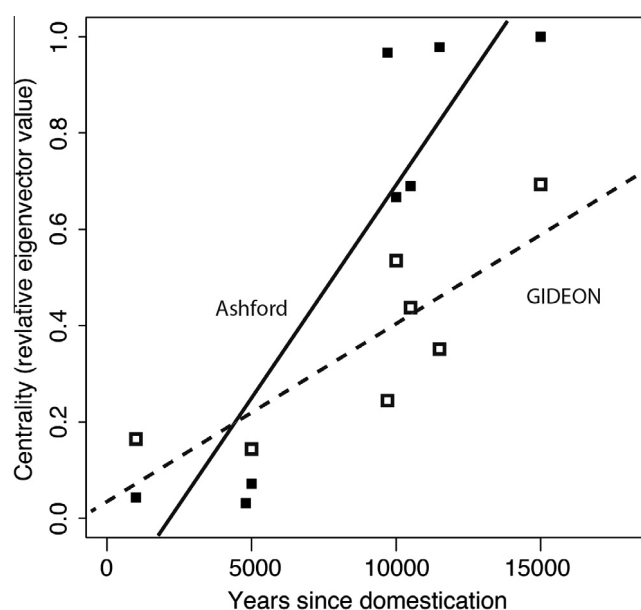
Fig. 3. Relationships between centrality of domestic animals (eigenvalue centrality) from unipartite networks based on pathogens/parasites shared and domestication time using data from the (A) Ashford and Crewe (1998) and (B) GIDEON database.

pathogens with other domestic animals and humans, then the greater is its time since domestication.

4. Discussion

Taken altogether, our results show that the building of shared parasitic and microbial communities between domesticated animals and humans is related to the time since their domestication. This increase in the number of parasites and pathogens shared with humans is independent of potential phylogenetic effects and of research efforts on parasites/diseases. Moreover, the number of pathogens/parasites shared with humans seems to be independent of the overall richness found in domestic animals. Finally, no particular associations between the number of pathogens/parasites shared and the nature of their proximity with humans can be found. The increase in the number of parasites and pathogens shared between humans and domesticated animals appears to be strongly related to the time since animal domestication.

Our results confirm the hypothesis of McNeill (1976) using several other data sources and more accurate information on the dates and origins of domestication (Driscoll et al., 2009). The number of parasites and infectious diseases shared between domesticated animals and humans increases with time since domestication, even when controlling for the total number of parasites/pathogens hosted by domesticated animals and phylogenetic relationships amongst domesticated animals. These results stress the importance of time in the building of shared parasite/pathogen communities between humans and domesticated animals (Wolfe et al., 2007).

Results of network analyses, and specifically the investigation of network topology by centrality confirmed that central domesticated hosts, which shared high numbers of parasites/pathogens with all other domesticated hosts and humans, are those that were domesticated a long time ago. As central hosts (i.e. central nodes) are the hosts that are highly connected to and reachable from any other hosts, they also present the greatest transmission vehicle in the network for parasites/pathogens (Gómez et al., 2013).

Using eigenvalue centrality (EC) as a measure of centrality, we showed that centrality was positively correlated with time since domestication. Domesticated hosts that were associated longer with humans are also those that favor parasites/pathogen transmission not only to humans but also to all other domesticated animals. However, this network analysis did not take into account the source of the donor and receiver of infections.

The results of several phylogenetic studies show that cattle and swine were not only the sources of parasite and microbe infections for humans, they were also recipients of parasites and microbes, spreading from humans in the opposite direction. The occurrence of Taenia in humans seems to have predated the domestication of cattle and swine by Neolithic farmers, as their ancestors first became infected while consuming raw meat such as partially consumed prey items of carnivores and scavengers (Hoberg et al., 2001). Later, 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).

Phylogenetic studies have hat Mycobacterium bovis originated from an Mycobacterium tuberculosis strain (Smith et al., 2009). Other studies suggested that ancestors of human Ascaris are derived from nematodes hosted by wild boar at the very start of their domestication (but see Criscione et al., 2007).

Most animal domestication originates from the Middle East, Central, Southwest, Southern and East Asia with few animals domesticated in Africa, Western Europe and in the New World (Diamond, 1997; Driscoll et al., 2009; Larson et al., 2005; Naderi

et al., 2008; VonHoldt et al., 2010) (Table 1). The llama, the sole livestock species domesticated in the New World at roughly the same period as other camelids from the Old World, hosts very few pathogens (according to the EID2 database) and does not seem to share many pathogens with humans. All of the investigated mammals show close relationships with humans, either within their work, or as a result of their use as a food and product supply (meat, leather or fur; Table 1). Wolfe et al. (2007) showed that eight of the fifteen temperate diseases they investigated reached humans from domestic animals compared to only three of the ten tropical diseases examined; a pattern that questions the potential dispersion of zoonotic diseases associated with domestication. The dispersion routes and increase in the geographical range of domestic animals from domestication centres should be related to ancient global trade and cultural diffusion, which would also be dependent upon the length of time since domestication.

Studies on the phylogeny and phylogeographics of parasites and microbes of domestic animals, which should be investigated together with closely related species in wild animals, are still scarce. Phylogeographic investigations of microbes may depict the spreading routes of domesticated animals in the Old World as well as in the New World (i.e. the dog would be a good example). As already emphasized by Wolfe et al. (2007), these all too rare studies have been based on specimens collected opportunistically from domestic animals with no systematic surveys over the spectrum of domestic and wild species. We must also add that any future studies should focus on the centres of domestication, most of which occurred in Asia (from the Middle East to East Asia).

We are still far from being fully able to understand the patterns and processes behind emerging infectious disease dynamics. Whereas an emphasis is put on biodiversity changes for obvious reasons (Keesing et al., 2010), by investigating the direct links between humans and wildlife (Wolfe et al., 2005), relatively few studies have in comparison investigated the domestic animal compartment. A major research effort should be initiated on zoonotic parasites and microbes that are shared with domestic animals. Efforts should also be moved towards Asia where most animal domestication processes took place and from where the first global commercial trade emerged, in particular in Southeast Asia, a hotspot of both threats to biodiversity (Schipper et al., 2008) and zoonotic emerging diseases (Jones et al., 2008; Coker et al., 2011). Such studies will enable further understanding of the evolution of emerging infectious diseases.

Acknowledgments

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