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A thousand bites – Insect introductions and late Holocene environments

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Abstract

The impact of insect species directly associated with man-made habitats and human dispersal has been, and remains globally significant. Their early expansion from their original niches into Europe is intrinsically related to discussions of climate change, origins of domesticated plants and animals, the spread of agriculture and infectious diseases. The Holocene fossil records of the dispersal of three storage pest species, *Sitophilus granarius*, *Oryzaephilus surinamensis*, and *Tribolium castaneum*, the housefly, *Musca domestica*, and the human flea, *Pulex irritans* from 221 sites have been mapped ranging from the Near East to Europe and from the Neolithic to the post medieval period. The importance of human induced change as a driver for the spread of synanthropic faunas and the potential for the spread of disease during this process are discussed. The results show links between mobility of farming groups and distribution of synanthropic insect species and produce a roadmap for the different cultural periods of the Late Holocene based on dispersal of these synanthropic insects. During the Neolithic, the first wave of insect introductions shows the northern European frontiers of storage of cereals, introduction of domestic animals and pastoralism and exchange. Pest introductions, linked with the itinerary of the Roman army, reached the most northerly parts of the Empire. During the medieval period, the insect records indicate further expansion and changes which parallel the spread of epidemic diseases like Plague. Understanding the timing and the rates of change of synanthropic insects provides key information about the development of the homogenised and highly anthropogenic environments in which we live today.

Keywords: Holocene, fossil insects, human impact, Europe, biogeography, pests, disease

1. Introduction

Domestication of animals and plants inevitably also involved a suite of insects able to exploit man-made habitats which closely mimicked those occupied in the wild, in some cases to the extent that their ‘natural’ habitats are largely unknown. Several of these almost casual invasions involved the assisted crossing of Wallacean boundaries, but many others involved a more subtle shift from beneath bark, for example, into food stores, or from animal dung in relatively warm countries to warm manure heaps in colder places Ultimately, many have had global impacts on biogeography and initiated a new range of relationships, from parasitic to symbiotic and commensal, as part of the relatively newly created synanthropic environments (cf. Simberloff et al., 2013). Whilst the primary domesticates have been the subject of frequent review and discussion in the archaeological literature (most recently, see Colledge et al., 2013) and the history of vertebrate pests has been extensively studied (cf. Aplin et al., 2012; Jones et al., 2012), other invaders have tended to be only viewed in the recent timeframe, with only rare recourse to the fossil record. The spread of a range of species with man over this longer timeframe is in many cases linked with episodes of landscape clearance and the creation of culturesteppe, an aspect well documented in the distribution of open ground beetles (cf. Andersen, 2000), and occasionally discussed with regard to the fossil record (e.g. Dinnin and Sadler, 1999; Eriksson, 2013).

Whilst Frans Vera (2002) has sought to impose a more dynamic model on the European Holocene landscape, the primary threshold in terms of inexorable and irreversible biogeographic change is provided by the moving boundary of the Neolithic (Colledge et al., 2013), replacing hunting, fishing and gathering, often rapidly and almost exclusively, with crop production and storage. Climate change has been hypothesized as one of the main drivers behind this transition (e.g. Sherratt, 1997), while other factors, for example, population rise and its consequences (Rowley-Conwy and Layton, 2011; Lemmen, 2014), and cultural diversity may also have led to innovation and change (Kandler and Laland, 2009). From the viewpoint of the insect and other fellow travellers, the lack of detailed datasets for the Neolithic, coupled with the limitations of dating, precludes definitive answers and inevitably any earliest occurrence is likely to be eventually overturned, although DNA research offers the possibility of tracing pathways and origins (cf. Jones et al., 2012). A considerable part of the debate, with DNA recently producing useful data about mobility of human populations (Bramanti et al., 2009, Pinhasi et al., 2013), has focussed on the patterns of spread of domestication and agriculture. The current consensus points to dispersal of both plants and terrestrial mammals from a number of different foci (Larson et al., 2007, Brown et al., 2008). Other organisms, including insects, have also had a part in this process. In addition to intentional introductions as part of domestication, the Neolithic is the primary threshold for a number of unintentional introductions, including field, storage and household pests and ectoparasites on humans and their animals (e.g. Panagiotakopulu 2000, Panagiotakopulu 2001; Buckland 1981, 1991; Buckland and Sadler, 1989). In turn, these contributed either directly or indirectly to the spread of new pathogens, harboured in the reservoirs created by sedentary lifestyle and associated activities (Martin, 2003; Panagiotakopulu, 2004a). This "package" was established with the spread of farming around the Mediterranean, to central and northern Europe, before being introduced worldwide (Simberloff et al., 2013; Jones et al., 2011; McMichael, 2004).

The timeframe of these introductions is significant, as it not only provides an independent way to track human movement and the spread of farming, but also gives information about the transition process from hunter gathering to farming and from small settlements to urbanisation. Storage pests are linked with crop losses which periodically may pose significant problems (Halstead and O' Shea, 2004; Oerke, 2006). In the archaeological record such losses are often underestimated or overlooked. Thus, the timeline for the arrival and establishment of pests in different areas provides a *terminus post quem* (earliest possible date) for considering crop introductions, storage and storage losses (for example, in Roman Britain (Buckland, 1978; Smith and Kenward, 2012) as part of the overall discussion). Of similar importance are insect species which may be linked with disease. When it comes to understanding origins and dynamics of vector borne infectious diseases (Parham et al., 2015), these might be some of the few available lines of information (cf. Panagiotakopulu, 2004a on the origins of Plague), but are rarely studied.

Within this context, by mapping the dispersal of selected introduced insect species, this paper aims to systematically examine the role of these species as proxies for understanding the development of synanthropic environments, conditions for potential spread of disease and to look into their spread in relation to human mobility and exchange.

2. Methodology

The insect species considered have been selected on the basis of their importance, abundance of fossil records and continuity over different periods of the Late Holocene. They cover a range of synanthropic habitats and they have different areas of origin. Three species of Coleoptera, the primary storage pest *Sitophilus granarius* (L.), and the secondary pests *Oryzaephilus surinamensis* (L.) and *Tribolium castaneum* (Hbst.), which are some of the most significant pest species worldwide, have been selected for this study In addition, a cosmopolitan fly species, *Musca domestica* L. and one of the most widely spread ectoparasites, *Pulex irritans* L. are discussed in order to place their late Holocene introductions in the general context of synanthropic environments and to link their presence to the potential spread of disease. Their distribution was mapped during different archaeological periods, from the Neolithic to the post medieval period (see Supplementary Data A, Tables A1 -A8), as the bulk of fossil records come from archaeological sites. The data were collated from 142 different geographic locations and 221 sites (see Supplementary Data B, Tables B1-B5). Only site presence was taken into account for the purposes of this paper, to avoid biases with individual species frequencies from samples from a variety of contexts, diverse in terms of preservation and taphonomy. The contexts include excavated houses, farms, middens, wells, contexts around settled areas, tomb offerings, material from shipwrecks, etc. Mode of preservation ranged from desiccation, freezing and waterlogging to calcification, charring and imprints on pottery. Published information was compiled using primarily BugsCEP (Buckland and Buckland, 2006) and unpublished records were also incorporated. Gaps in distribution are in part a result of poor preservation, in particular on semiarid sites around the Mediterranean, and also the lack of relevant research.

3. The Fossil evidence

Information from insect faunas associated with hunter gathering sites pre-dating agriculture is rather thin and largely associated with the restricted faunas of the Arctic, with carrion species and ectoparasites dominating the few relevant assemblages (see Böcher and Fredskild, 1993; Skidmore, 1996). Human lice, man’s most intimate companions, have been recorded from northeast Brazil around 10,000 years ago (Araújo et al., 2000) whilst from the northern hemisphere the earliest record is from the Heman Cave, in the Dead Sea region of Israel, 9000 years ago (Mumkuoglu and Zias, 1991), although DNA evidence points to the possibility of a parasitic relationship with hominins for at least the last 70-40 thousand years, (Kittler et al., 2003; Boutellis et al., 2014).

Human fleas *Pulex irritans*, on the other hand, appear to have a much shorter history with man. Buckland and Sadler (1989) have argued that the primary host lay in the New World, with the Guinea pig, *Cavia porcellus* L., domesticated in the Andes perhaps by 5000 BP (Brothwell, 1983; Larson and Fuller, 2014). This, so-called human flea had reached western Europe by the fourth millennium BC (Remicourt et al., 2014) (see Fig.1) and the need of the species for relatively permanent 'nests' to maintain breeding populations links it with sedentary as opposed to transient groups.

Away from the ectoparasites, relationships tend to be less intimate. For synanthropic Diptera, true flies, their proliferation in settled areas created conditions ripe for the spread of infectious diseases (cf. Greenberg, 1973). Previous papers have considered the sparse fossil record of *Musca domestica* L., the house fly, and its association with health and hygiene in human environments (Panagiotakopulu, 2004b; Skidmore, 1996). It, as other synanthropic flies, is associated with the mechanical transmission of a large number of diseases, which range from trachoma to typhoid, cholera, yaws and tuberculosis (Greenberg, 1973). The earliest records of *M. domestica,* a species perhaps with origins in the Nile Valley (Skidmore, 1996), come from Erkelenz-Kückhoven in the Rhine Valley (Fig.1), around seven thousand years ago (Schmidt, 2013). During the Neolithic, *M. domestica* occurs together with the similarly synanthropic predatory muscid, *Muscina stabulans* L., at Thayngen-Weier in Switzerland (Troels Smith, 1984, Nielsen, 1989). The fly *Thoracochaeta zosterae* (Haliday), at the present day usually associated with accumulations of seaweed, also occurs on this high altitude inland site (Nielsen et al., 2000); in the past it was also regularly associated with latrines and manure (Webb et al., 1998).

Records of synanthropic insect species from the Middle East, North Africa and Europe reflect domestication and farming from the Neolithic onwards. The expansion of these species from their areas of origin to their northern limits (see Fig. 1) and often almost cosmopolitan distribution at the present day, appears to have taken place almost coeval with the spread of agriculture and sedentism. The optimal breeding temperatures of many of the pests of stored products and habitations tend to restrict them to the artificial warmth of the inside of storerooms and other man-made structures in temperate areas.

The grain weevil, *Sitophilus granarius* L. is the prime example of a wholly synanthropic, eusynanthropic species to the extent that natural populations have yet to be located and Plarre (2010) has argued that the species evolved around the same time as the adoption of agriculture. Whilst a case has been made for an origin in acorns (Howe, 1965; Weidner, 1983), fossil specimens have been found associated with both wheat and barley, in a Pre-Pottery Neolithic well at Atlit-Yam, off the Mediterranean coast of Israel by *ca*. 8250 cal BP (ca. 6250 cal BC) (Kislev et al., 2004), and at Dispilio in northern Greece around 7700 cal BP (ca. 5700 cal BC) (Panagiotakopulu, in prep.) (Fig. 1). Buckland (1991) amongst others has suggested that its primary habitat is in the seeds of wild grasses stored by rodents in the region of the natural distribution of the wild ancestors of cereals across the Fertile Crescent. The species is incapable of flight, but likely lived in close proximity to rodent nests and human homes. This would have inevitably led to its introduction into the larger, man-made caches of grain. Cold hardy but needing temperatures above 15° C to maintain breeding populations, its northern limit would be set either by suitable summer temperatures or by grain storage on a sufficient scale to provide heating and insulation. Buckland (1978), drawing on work by Dendy and Elkington (1920), noted that one of the hazards of this insect living in pit-stored grain would be the build up of potentially lethal concentrations of carbon dioxide from the respiring grain.. This hazard might occasionally have prevented expansion to new regions. Unlike the flightless *S. granarius*, relying on human agency for dispersal, other members of the genus may be field pests as well as storage pests, although all require higher base temperatures for flight. *S. zeamais* Mots. is nowadays a cosmopolitan pest of maize, grain and rice (Hill, 1975) and is one of the species in the genus with the ability to fly (Likhayo et al., 2000). Despite its vernacular name of ‘maize weevil’, its earliest record is from Japan, from impressions in Jomon pottery, dated to *ca.* 10500 BP, from Sanbonmatsu, Kagoshima (Obata et al., 2011); later Japanese contexts, from Kakiuchi, Kagoshima, from around 4000 BP, are associated with the inception of rice cultivation in the area. The first record of the rice weevil, *S. oryzae* (L.), which attacks all types of grain and rice (Harde, 1984), is from Han Dynasty tomb offerings in China dated to 185 BC (Chu and Wang, 1975), perhaps an indication for the origins of the species as a pest in China; more research is required, particularly from earlier contexts. Although rice is recorded from early Roman forts on the Rhine Frontier (Knörzer, 1966; Bakels and Jacomet, 2003), its eponymous weevil is first recorded in Europe in early fifteenth century Southampton (Grove, 1995).

Similar trends are observed in the distribution of the saw toothed grain beetle, *Oryzaephilus surinamensis* (L.), although its records are fewer compared to the granary weevil, and largely Roman. Its first occurrence is from charred grain from a late Neolithic site at Mandalon (4450-4340 *cal* BC) in northern Greece (Valamoti & Buckland, 1995). As much of the synanthropic fauna, its original habitat was probably under bark, a habitat from whence there are some modern records (e.g. Crowson, 1958; Zacher, 1927), and it may once have been more widespread in the primeval forests of central Europe (Fig. 1). As a secondary pest of damaged grain, it probably moved into the synanthropic environments after the spread of *S. granarius* and the initial establishment of storage of cereals in central and northern Europe, being picked up on the way, although there is a record, referred to by Zacher (1934) from a Minoan vessel from Egypt and a further early Iron Age record from Israel (Kislev and Melamed, 2000). Its present status as the most frequent pest of stored grain in Britain (Bell, 1991) partly reflects modern harvesting and storage methods. Roman occurrences, from Masada in Israel (Kislev and Simchoni, 2007) to the Antonine Wall in Scotland (Locke, 2016; Smith, 2004), suggest that the support mechanisms of Rome's armies had already given it a wide synanthropic European and Near Eastern distribution by the mid-second century AD. The third member of the primary triumvirate of grain pests, the flat grain beetle, *Cryptolestes ferrugineus* (Steph.) has no pre-Roman fossil records, although again it occurs from Masada (Kislev and Simchoni, 2007) to the Antonine Wall (Locke, 2016; Smith, 2004). It remains widespread under bark, where it may feed on fungi (Halstead, 1993).

The red flour beetle, *Tribolium castaneum* has been noted by Whitehead (1999) in association with *C. ferrugineus* under the flaking bark of an apple tree and this may be a primary habitat, although Solomon and Adamson (1955) note that it is not cold hardy. Its earliest fossil records are from Bronze Age Akrotiri, on the island of Santorini in the Aegean ca. 1744 to 1538 cal BC (Panagiotakopulu et al., 2013) (Fig. 1) and from Pharaonic Amarna ca. 1355 to 1325 cal BC (Panagiotakopulu et al., 2010). Other records begin in the Roman period, extending from Mons Claudianus in the Eastern Desert of Egypt (Panagiotakopulu and van der Veen, 1997) to Carlisle (Smith and Tetlow, 2009). In storage situations it is essentially a secondary pest associated with processed commodities (Horion, 1965) and in northwest Europe its establishment would be associated with centralised activities and larger scale food processing.

4. Discussion

4.1. Synanthropic insects and the Neolithic

Storage was one of the key pathways for the transition between gathering and farming and its origins lie particularly in regions of seasonal climate extremes, either by drought or cold, pre-dating cultivation and domestication (cf. Kujit and Finlayson, 2009). This requirement to concentrate resources over lean times inevitably created abundant food reserves for species previously restricted to the small stores and nests of rodents, under bark, or to the transient habitats of carrion and dung. The security offered by storage was an incentive which perhaps led to permanent settlements, and also provided habitats for a range of insects associated with foodstuffs, faeces and other ejecta, intimately linked with man and domestic animals. Humans, in addition to providing new opportunities for potential pests, also provided more effective dispersal mechanisms for insects which had relied previously primarily on being transported by other organisms, such as hitchhiking on fur, feathers or limbs (e.g. Woodroffe, 1967).

One result of the "Neolithic Revolution" is the spread of a strongly synanthropic insect package out from early farming areas to new frontiers. This early expansion is witnessed by the record of *Sitophilus* sp. during the 7th millennium BC, from Haçilar in Turkey from Anatolia (Helbaek, 1970), onwards to the Aegean a few hundred years later. This is followed by introductions in the Rhine valley, by ca. 5057 cal BC, perhaps following routes across the Aegean and by the rivers of the Danube and Rhine systems. The expansion of the Neolithic Linearbandkeramik (LBK) culture and associated cultivation of barley may have provided a framework for introduction of the grain weevil. Whilst the emphasis on barley has not been substantiated by plant macrofossil work (cf. Bickle and Whittle, 2013), to a certain extent the LBK finds of *S. granarius* by Büchner and Wolf (1997) and Schmidt (1998, 2010) appear to support this. Plant macrofossil evidence has been used to support a model of small garden subsistence (e.g. Bogaard, 2005), although the planned settlements with substantial long houses might equally have included centralised redistributive storage of crops. The presence of *S. granarius* from several sites from early Neolithic Europe (Figs. 1, 2) would imply the movement of cereals on a sufficient scale to maintain breeding populations. Its subsequent absence north of the Alps until the expansion of Rome could be partly an artefact of available samples and their taphonomy, but the early Neolithic occurrences must indicate the significance of storage for the establishment and enforcement of the LBK colonisers across northern and central Europe (Figs. 1, 2).

In terms of pathways of introductions, in addition to the movement from the Fertile Crescent to Europe, there is an indication for movement in the opposite direction, with a late Aegean Neolithic record of *O. surinamensis,* following infestations of *S. granarius,* and spreading from Europe southwards (see Figs. 1, 3). If anything, the records of storage pests show early active networks, exchange and movement from one part of Europe to the other. In addition to the establishment of *S. granarius* in the Rhine Valley, the wave of Neolithic introductions include *M. domestica,* the house fly. The species is also present at Schipluiden in the Netherlands (Hakbijl, 2006) and at Thayngen Weier around six thousand years ago, from Neolithic Federsee (ca. 3000 cal BC) in Baden-Württemburg (Schmidt, 2004) and further on from Alvastra on Lake Vättern in southern Sweden ca. 3000 cal BC (Skidmore in Lemdahl, 1995) (Figs. 1, 4). This provides an additional aspect of the early expansion of agriculture into northern Europe; its association with manure indicates its spread together with pastoral groups and their domestic animals, pushing northwards to southern Scandinavia. These early introductions include the human flea with earliest records from Saint Maximin in south-east France around 3600 cal BC (Remicourt et al., 2014) and Schipluiden in the Netherlands around 3500 cal BC (Hakbijl, 2006). A large number of fossils of the species have been recovered from Chalain ca. 3200 BC (Yvinec et al., 2000). The furthest north Neolithic flea record is from Skara Brae on Orkney ca. 3100-2500 cal BC (Figs. 1, 4). Its spread has been linked with the gift exchange of furs (Buckland and Sadler, 1989). These fleas were an additional unwanted gift and part of the Neolithic invasion package.

The timing and nature of the arrival of these species in Europe, and their spread bear some resemblance to the Neolithic expansion itself; in some cases it was unforced and fortuitous but often it had to overcome cultural and ecological barriers (e.g. Golitko and Keeley 2007), and was only forced through after several attempts.

4.2 Synanthropic environments and potential for the spread of disease

Prior to the introduction of farming, tropical diseases, including mosquito borne diseases, as well as infections associated with predation, handling of wild animals and consumption of raw meat, were the primary health hazards for hunter gatherers. Neolithic farming and communal living, often shared with domestic animals, and lack of any concept of hygiene as perceived in modern times, created ideal conditions for the spread of many diseases (Wolfe et al., 2007). Several of these diseases are insect borne or insect associated (see Fig. 5). Sedentary farming groups were periodically troubled with failure of crops and losses in storage. Bad years would lead to lack of resources, or, in extreme situations, to famine, poor health and death. The establishment of urban centres led to increase in demographic growth, the proximity of living clusters (with all subsequent consequences, e.g. waste and sewage, lack of sanitary conditions, etc.) and increase in potential disease hosts, created novel opportunities for the spread of infectious disease. The mobility of farmers and their menagerie brought pathogens with their hosts to new regions (cf. Semenza and Menne, 2009; McMichael, 2004; Baum and Bar Kal, 2003; Wilcox and Gubler, 2005) adding infectious diseases to the Neolithic package. Later, the broad range of introductions which accompanied the Roman armies, as well as trade, were key changes, in terms of crossing natural biogeographic barriers. Norse colonisation of the North Atlantic islands in the medieval period extended this process further.

Although rarely studied, flies provide vital information on hygiene within settlements. The introduction to Europe of house flies, known to mechanically spread a number of pathogens from protozoa to viruses, during the Neolithic (Fig. 5), is important as an earliest date for the spread of associated diseases to humans and a flag for potential pathogen reservoirs. Other flies were also part of this process; the biting stable fly *Stomoxys calcitrans* L. is a carrier of ricketsias *Ricketsia* spp., among other bacteria and parasites. This fly may also be an intermediary host for helminths (Gage et al., 2008). Its remains have been found at the Neolithic site of Thayngen Weier in Switzerland (Guyan, 1981).

As discussed above, human fleas, another disease vector for ricketsias, and a secondary vector for bubonic plague (*Yersinia pestis*), are found relatively frequently in man-made environments. Given the probability of a South American origin of the species (e.g. Dittmar, 2000), the Neolithic European records of *Pulex irritans* L. are interesting points in the timeline of introductions, illustrating the rapidity with which gift exchange/trade facilitated movement of potential disease vectors. After these occurrences, there are several records from Amarna (1353 - 1325 BC) dating to the New Kingdom period in Egypt (Fig. 4, Table B5), Iron Age in the Netherlands (Hakbijl, 1989) and the British Isles, as well as Roman faunas from the British Isles (Kenward et al., 2000; see Fig. 4). There is significant difference in terms of numbers of sites with flea specimens during the medieval period (Table B5), although this may be partly related to taphonomic and sampling problems (e.g. more house floors being sampled, etc). It is clear that everyone, from kings and archbishops to peasants, had lice and fleas at some time in the lives if not throughout. Effective flea and lice control only came with the invention of the vacuum cleaner and systemic insecticides (cf. Busvine, 1976; Sveinbjarnardóttir and Buckland, 1983), so it could be that the fossil record reflects rising urban populations driving the spread of the species. The fossil evidence indicates that fleas were abundant in towns and this, in well documented disease cases as for example that of Eyam in Derbyshire (Massad et al., 2004), could be the reason behind the transmission of Plague to rural populations after initial urban epidemics. Even taking into account the information about areas where, according to Benedictow (2010), Plague did not spread (i.e. Iceland, Greenland, etc.), the numbers of medieval sites with human fleas is higher than from any previous period. In northern Europe at least, the increased number of people in urban centres was probably one of the reasons for the frequency of fleas (e.g. 254 individuals of *P. irritans* from the Magistrate Court site in Hull (Hall et al., 2000)) and one of the main reasons for the dimensions of the pandemic.

4.3 Pest distribution and climate change

Most species associated with stored products are able to utilise the artificial warmth and insulation provided by bulk storage, and their exposure to external temperatures is therefore limited. Species associated with accumulations of waste, from manure to cess, are similarly isolated, although dispersal may involve a temperature threshold, which may ultimately define their range boundaries. The failure of the housefly to establish itself in Greenland provides a good example. The question remains as to whether and to what extent climate change was one of the drivers behind insect pest introductions or whether these were primarily a result of expanding agricultural horizons. The nature of the data, which are largely associated with human settlement, makes it difficult to provide a definitive answer.

Climate change, specifically, the end of the humid period in Africa (de Menocal, 2015) has been invoked as the main reason behind the concentration of settlement and urbanisation in the Nile Valley from 6000-4000 BC (Kuper and Kröpelin, 2006), however, a similar model cannot be applied to the European Neolithic and cannot explain other biological invasions. When it comes to insects, macroclimate is of more immediate importance for field pests, as it directly affects their frequency and expansion, and related crop yields (see Bebber et al., 2013, 2014). Bad years with consequent high losses would also be indicative of climatic variability affecting agricultural productivity (Tubiello et al., 2007; Rosenzweig et al., 2001), although archaeological sampling is rarely sufficiently precise (cf. Panagiotakopulu et al., 2014). Indirectly, the distribution of storage pests may be affected by climate change. Delayed onset of winter may provide a larger window for pest activity and the converse would also be true. Higher temperatures during harvest, for example, may lead to "warmer grain" and higher rates of infestation, and changes in precipitation and humidity as well as weather extremes may also play a role (Cook et al., 2004).

An overview of the fossil record (Fig. 6) indicates waves of dispersal with the first introductions starting in the Neolithic, during which fossil faunas included eight sites with *S. granarius,* seven of these in Europe, and the first record of *O. surinamensis* (Figs. 1, 2, 3). Climate could have played a secondary role for these initial introductions. The furthest north of the three Neolithic records of *M. domestica* from Sweden, was perhaps close to the limit where climate posed a barrier to the initial diffusion of agriculture in western Europe.

Trade in cereals and processed commodities probably sustained insect populations but the evidence for insect pest introductions implies that there was limited activity in central and northern Europe. During the Bronze Age there are five sites, out of ten overall, with *S. granarius* in Europe, all of them in the Mediterranean. In the Iron Age, only two of the six records were European, also in the Mediterranean (see Figs. 2, 6). In terms of introductions, the Iron Age faunas included the house fly and human fleas in the Netherlands and the British Isles. Although limitations (e.g. lack of research, lack of preservation) need to be taken into account, the implication of the Bronze and Iron Age records is either of increased pastoralism or storage which was inimical to pest survival or preservation. A sharp change took place with the start of the Roman period which was characterised by a high number of sites with pests. This period saw fifty five sites with *S. granarius* and forty one with *O. surinamensis* - most of which are British (see Fig. 6, Tables B1, B2), a reflection on the state of research. These records are probably associated with transport of food for the Roman army. The peak in site numbers with relevant records could also be linked to warmer temperatures which could have aided the proliferation of pests and led to significant infestations. There was a similar trend during the medieval period (sixty one sites with *S. granarius* records and forty three sites with *O. surinamensis*, see Fig. 6). These were accompanied by an expansion of sites with human fleas, *P. irritans*; from eleven sites in the Roman period, all from the British Isles, the record in the medieval period expands to thirty two sites. In part, as already noted, variation in site records during different periods reflects availability of samples and preservation. However, if flea infestations were linked with wetter (Xu et al., 2014) or warmer conditions for hosts (cf. Benedictow, 2010) or a combination of both (Stenseth et al., 2006), the Medieval Climatic Optimum (Mann et al. 2009; McMichael, 2011) perhaps provided context suitable environments for the increase of sites with human fleas (Fig. 6). The trend during the post-medieval period was for lower numbers of sites with storage pests (twenty four sites with *S. granarius* and fourteen with *O. surinamensis*), while the sites with fleas decline (from thirty two to eight). These changes may reflect the cooling associated with the Little Ice Age.

4.4 Biological imperialism, armies and maritime trade

As many other pests and weeds and some crop plants (cf. van der Veen et al., 2008), the expansion of the Roman Empire provided new pathways, particularly for stored product pests. The pattern of introductions can be clearly seen in the British Isles, where first and second century introductions of *S. granarius* from well - dated sites follow the footsteps of the Roman army from Invasion northwards to the Antonine Wall in lowland Scotland by the mid-second century AD (Dickson et al., 1979; Locke, 2016; Smith, 2004) (Fig. 7). A review of the British data by Smith and Kenward (2011) reinforces Buckland's conclusions concerning the importance of scale in that *S. granarius* appears to be largely absent from the rural landscape, while it occurred in forts and towns (see Table B1) and occasionally in larger farms. One of these sites was an essentially suburban villa, at Bays Meadow, Droitwich, Worcestershire (Osborne, 1977), and a second occurs in the villa at Grateley in Hampshire (Campbell in Kenward, 2009), but rarely on lesser sites (but cf. Hughes, 1995). *O. surinamensis* is found in the majority of sites with *S. granarius*. This period also shows a number of sites containing *T. castaneum*, perhaps indicative of processed cereals, i.e. flour, for consumption. The "red flour beetle" numbers diminish after the Roman period. King and others (2014) have argued that the grain fauna in Britain all but disappeared in the post-Roman period, when large scale commodity shipment largely ceased, and that this fauna returned after the Norman Conquest. We would argue that this was probably not the case and it overlooks the grain fauna, including *S. granarius*, from the late seventh century watermill at Northfleet in Kent (Smith, 2011). In the absence of large scale movement and storage of foodstuffs, it is probable that permanent insect pest populations were restricted to a few places where grain was milled regularly on a scale beyond that required for local domestic consumption, but the problem of presence or absence of a species in a given fossil assemblage is just as likely to be caused by the paucity of suitable samples. Unfortunately, there is little comparative research from continental Europe, where the scale of post-Roman collapse was less severe.

A similar pattern is evident in the early medieval period with Norse expansion, both west to the North Atlantic islands and east into Russia. With the exception of Greenland, there are several introductions of *S. granarius* and *O. surinamensis* to the Faroe Islands, Iceland, northern Norway and the Novgorod region. Human fleas are taken to Greenland, thereby completing its circumpolar distribution. Despite the presence of suitably warmed habitats in middens and turf-built houses, the house fly did not reach the North Atlantic islands, where its place is largely taken by the heleomyzid *Heleomyza borealis* Bohe. (Skidmore, 1996). In both Greenland and Iceland, the preservation of insect assemblages and the number of sites studied makes it possible to link the Norse settlements with assemblages specific to a hay based pastoral economy. These include various other insects found outside their natural distribution range which became established, sometimes ephemerally (cf. Buckland et al., 2009), on the North Atlantic islands in strictly synanthropic environments as part of the Norse colonisation (Panagiotakopulu, 2014).

The development of ships which were unloaded at quaysides rather than on the beach during the medieval period led to increasing numbers of on-board faunas which were only occasionally offloaded when boats were cleared of dunnage and ballast (cf. Buckland, 1991) The larger ships of the Hanseatic League, and the creation of their common market during the late medieval period, facilitated further introductions. Although there is limited research, changes in the maritime trade in the post medieval period made it possible for a range of species to travel from one part of the world to the other. The first record of the house fly from a ship comes from Henry VIII’s flagship the *Mary Rose*, sunk off Plymouth in 1545 (Robinson, 2005). The presence of the oriental cockroach, *Blatta orientalis* L. in the shipwreck of the Spanish galleon *San Esteban* which sunk in Padre islands, Texas, in 1554 (Durden, 1978) give good examples of how far species can travel accidentally. The limited evidence from the 18th century Dutch East Indiaman shipwreck, the *Amsterdam*, wrecked near Folkstone in 1749, give an indication of the range of these incognito travellers. From the shipwreck comes *Cathartus quadricollis* (Guérin-Méneville), the South American square neck beetle, and the rice weevil, *S. oryzae* (Hakbijl, 1986), whilst the bean weevil

Acanthoscelides obtectus (Say), also of New World origin, appears on Svalbard, at the Dutch whaling station of Smeerenberg in the seventeenth century (Wijngaarden-Bakker and Pals, 1981). The huts of Barents' overwintering station of 1596-7 on Novaya Zemlya in the Russian Arctic included the blister beetle, *Lytta versicatoria*, although this was ground up in a medicine rather than in cargo, dunnage or ballast (Hakbijl and de Groot, 1997).

5. Conclusions

Assessing the spread of introduced insect pest species over the longer timeframe provides a different view on global ecological change as a result of human impact which recent research tends to ignore (e.g. Thomas, 2013, but see Simberloff et al., 2013). The consideration of past biogeography of beetle storage pests, the house fly and the human flea, provides refined information which informs the discussion on the origins of the relevant species and their movement into man-made environments, and reconstructs their early spread, an itinerary which follows the footsteps of humans. In summary:

- The distribution of the flightless weevil *Sitophilus granarius* during the Neolithic provides evidence for the spread of early farming and indicates the northern limits for the introduction of bulk storage of cereals.
- The Neolithic dispersal of *Musca domestica* across Europe as far as southern Sweden is probably associated with the mobility of agropastoral groups.
- According to the fossil records of *Oryzaephilus surinamensis,* in addition to introductions in northern Europe, the species was also spread southwards.
- The long term records of synanthropic insects in northern Europe show waves of introductions since the Neolithic, with peaks during the Roman and the medieval period.
- The introduction of storage pests in the British Isles during the Roman period follows the itinerary of the Roman army and must be primarily associated with centralised storage, redistribution and processing of cereals.
- During the medieval period, the high number of sites with human fleas could provide an explanation for the dispersal of the Black Death in Europe.

More fossil insect research is needed in order to understand further Holocene insect introductions accompanying humans, in particular from areas in Europe where the records are incomplete. Filling the gaps, applying new analytical techniques on fossil assemblages, such as DNA, with an emphasis on species of economic importance and disease vectors, and linking the data with discussions on human mobility and insect borne diseases can provide an innovative outlook on past environments.

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List of Figures

Figure 1. Map of origins, earliest records in years BP, and suggested early distribution of *Sitophilus granarius* L., *Musca domestica* L., *Oryzaephilus surinamensis* (L.), *Tribolium castaneum* (Hbst.), and *Pulex irritans* L. For further details, see Supplementary Tables A1, A2 and Tables B1-B5.

Figure 2. Fossil records of *Sitophilus granarius* (L.) from Palaearctic sites from the Neolithic to the post medieval period. For further information on particular records and sites see Table B1.

Figure 3. Fossil records and distribution of *Oryzaephilus surinamensis* (L.) and *Tribolium castaneum* (Hbst.) from Palaearctic sites from the Neolithic to the post medieval period. For further information on particular records and sites see Supplementary Tables B2, B3.

Figure 4. Fossil records of *Musca domestica* L. and *Pulex irritans* L. from palaearctic sites from the Neolithic to the post medieval period. For further information on particular records and sites see Supplementary Tables B4, B5.

Figure 5. Infectious diseases, including insect borne diseases, and pathways of transmission from the early Holocene to the modern day, developed from an initial idea by Baum and Bar Kal (2003). Synanthropic insects and ectoparasites are an important part for both creating environments for the establishment and spread of disease. The chronology used is broad and for the purposes of the diagram. For information on particular chronological periods and records, please see Supplementary Data.

Fig. 6. Total numbers of sites with fossil records of *Tribolium castaneum* (Hbst.), *Sitophilus granarius* (L.), *Musca domestica* L., *Oryzaephilus surinamensis* (L.) and *Pulex irritans* L. discussed in this paper, in the context of the Late Holocene climate (from McMichael 2011). For information on specific records and chronology from particular periods, see Supplementary Data.

Fig. 7. Closely dated Roman sites with *Sitophilus granarius* L. in Britain indicating the spread of the species with the movement of the Roman army north to the Antonine wall. The records from London, Colchester, Pomeroy Wood, Dragonby and York date to the 1st century AD, whilst the records from Exeter, Nantwich, Papcastle, South Shields, Bearsden and Inveresk fall within the 2nd century AD. For more information please see Table B1.

Supplementary Data

A. Chronology

Table A1.Neolithic chronology of geographic regions mentioned in the paper.

Table A2. Bronze Age chronology of geographic regions mentioned in the paper.

Table A3. Iron Age timeframe of geographic regions mentioned in the paper.

Table A3. Roman Age of geographic regions mentioned in the paper.

Table A4. Post Roman Age of geographic regions mentioned in the paper.

Table A5. Medieval period timeline of geographic regions mentioned in the paper.

Table A6. Post medieval period of geographic regions mentioned in the paper.

B. Fossil records

Table B1. Palaearctic archaeological sites with fossil records of *Sitophilus granarius* (L.). A full list of the relevant references is provided in *The bibliography of Quaternary Entomology* collated by Buckland, Coope and Sadler (Qbib, <http://bugscep.qbib.com>).

Table B2. Palaearctic archaeological sites with fossil records of *Oryzaephilus surinamensis* (L.). A full list of the relevant references is provided in *The bibliography of Quaternary Entomology* collated by Buckland, Coope and Sadler (Qbib, <http://bugscep.qbib.com>).

Table B3. Palaearctic archaeological sites with fossil records of *Tribolium castaneum* (Hbst.). A full list of the relevant references is provided in *The bibliography of Quaternary Entomology* collated by Buckland, Coope and Sadler (Qbib, <http://bugscep.qbib.com>)

Table B4. Palaearctic archaeological sites with fossil records of *Musca domestica* L. A full list of the relevant references is provided in *The bibliography of Quaternary Entomology* collated by Buckland, Coope and Sadler (Qbib, <http://bugscep.qbib.com>).

Table B5. Palaearctic archaeological sites with fossil records of *Pulex irritans* L. A full list of the relevant references is provided in *The bibliography of Quaternary Entomology* collated by Buckland, Coope and Sadler (Qbib, <http://bugscep.qbib.com>).

Figure 1

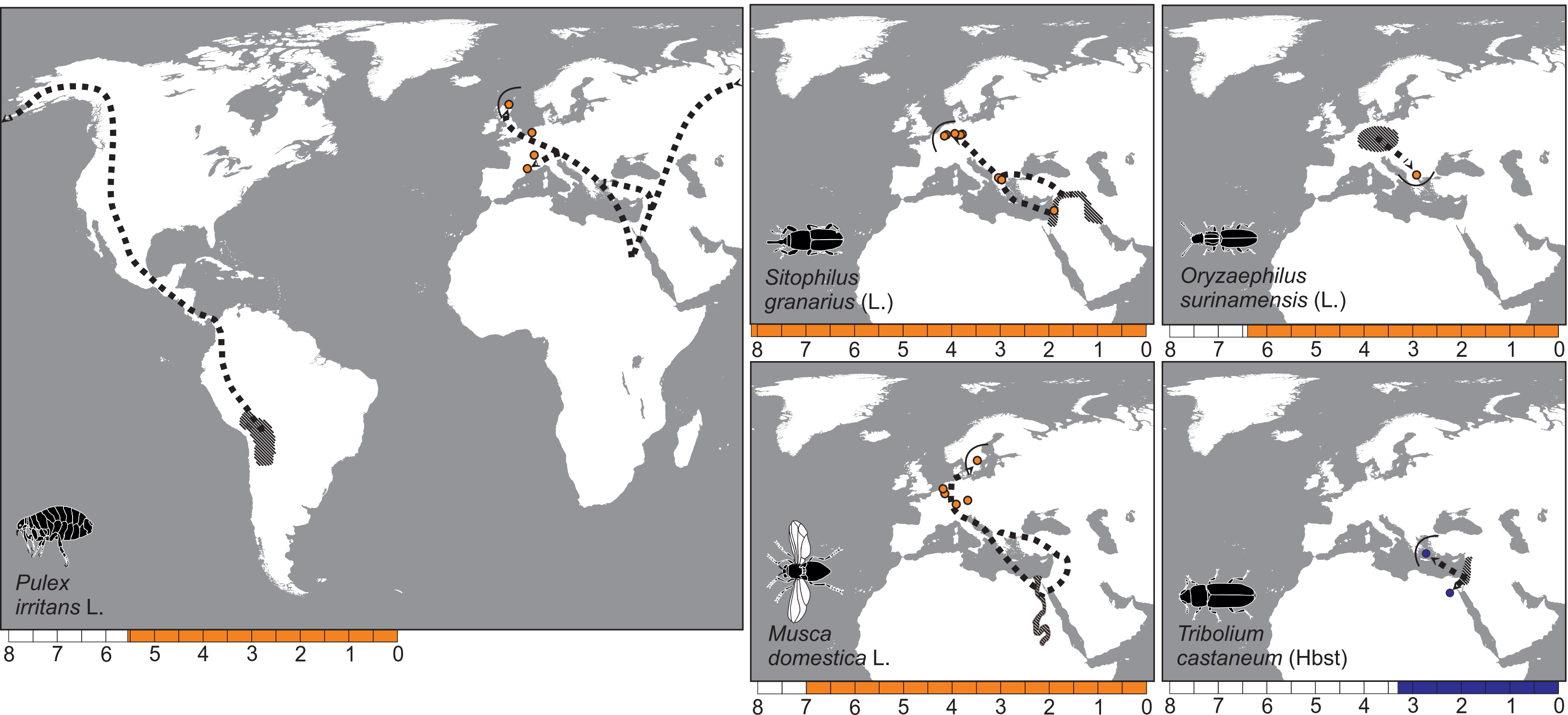

Pulex irritans L.
8 7 6 5 4 3 2 1 0
Sitophilus granarius (L.)
8 7 6 5 4 3 2 1 0
Oryzaephilus surinamensis (L.)
8 7 6 5 4 3 2 1 0
Musca domestica L.
8 7 6 5 4 3 2 1 0
Tribolium castaneum (Hbst)
8 7 6 5 4 3 2 1 0

Figure 2

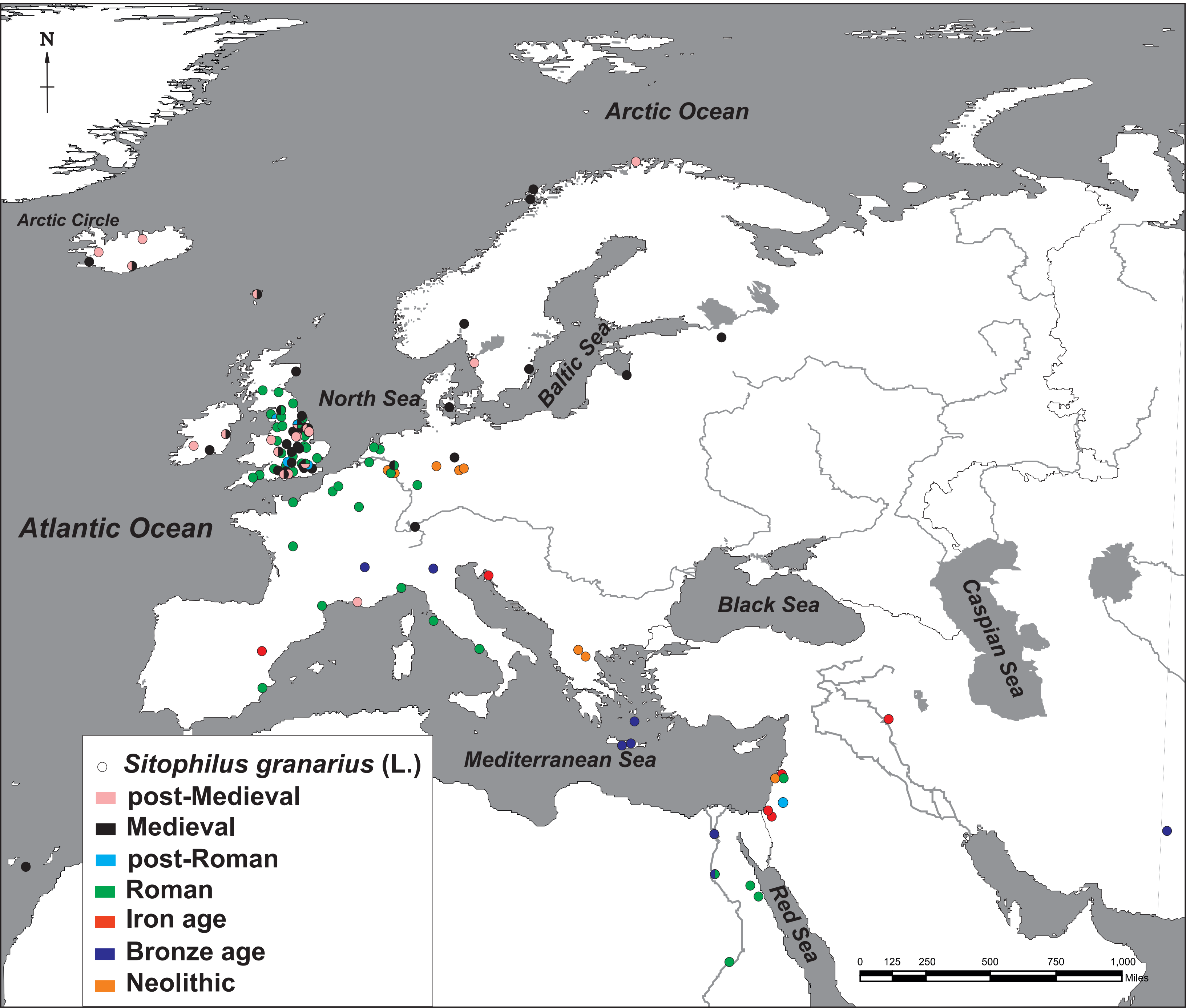
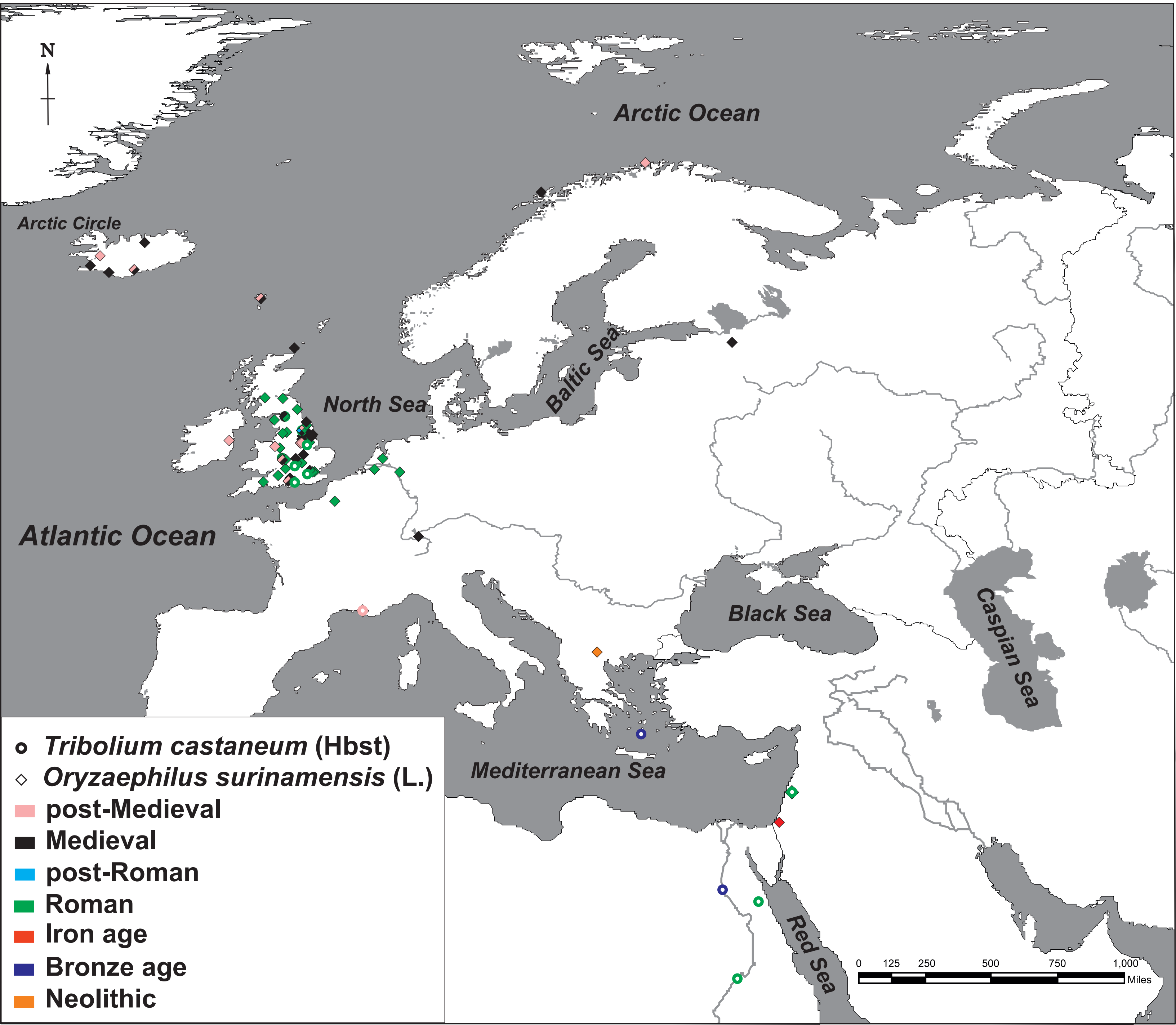

N
Arctic Ocean
Arctic Circle
North Sea
Baltic Sea
Atlantic Ocean
Black Sea
Caspian Sea
Mediterranean Sea
Red Sea
○ *Sitophilus granarius* (L.)
post-Medieval
Medieval
post-Roman
Roman
Iron age
Bronze age
Neolithic
0
125
250
500
750
1,000
Miles

Figure 3



N
Arctic Ocean
Arctic Circle
North Sea
Baltic Sea
Atlantic Ocean
Black Sea
Caspian Sea
Mediterranean Sea
Red Sea
0 125 250 500 750 1,000
Miles
○ *Tribolium castaneum* (Hbst)
◇ *Oryzaephilus surinamensis* (L.)
■ post-Medieval
■ Medieval
■ post-Roman
■ Roman
■ Iron age
■ Bronze age
■ Neolithic

Figure 4

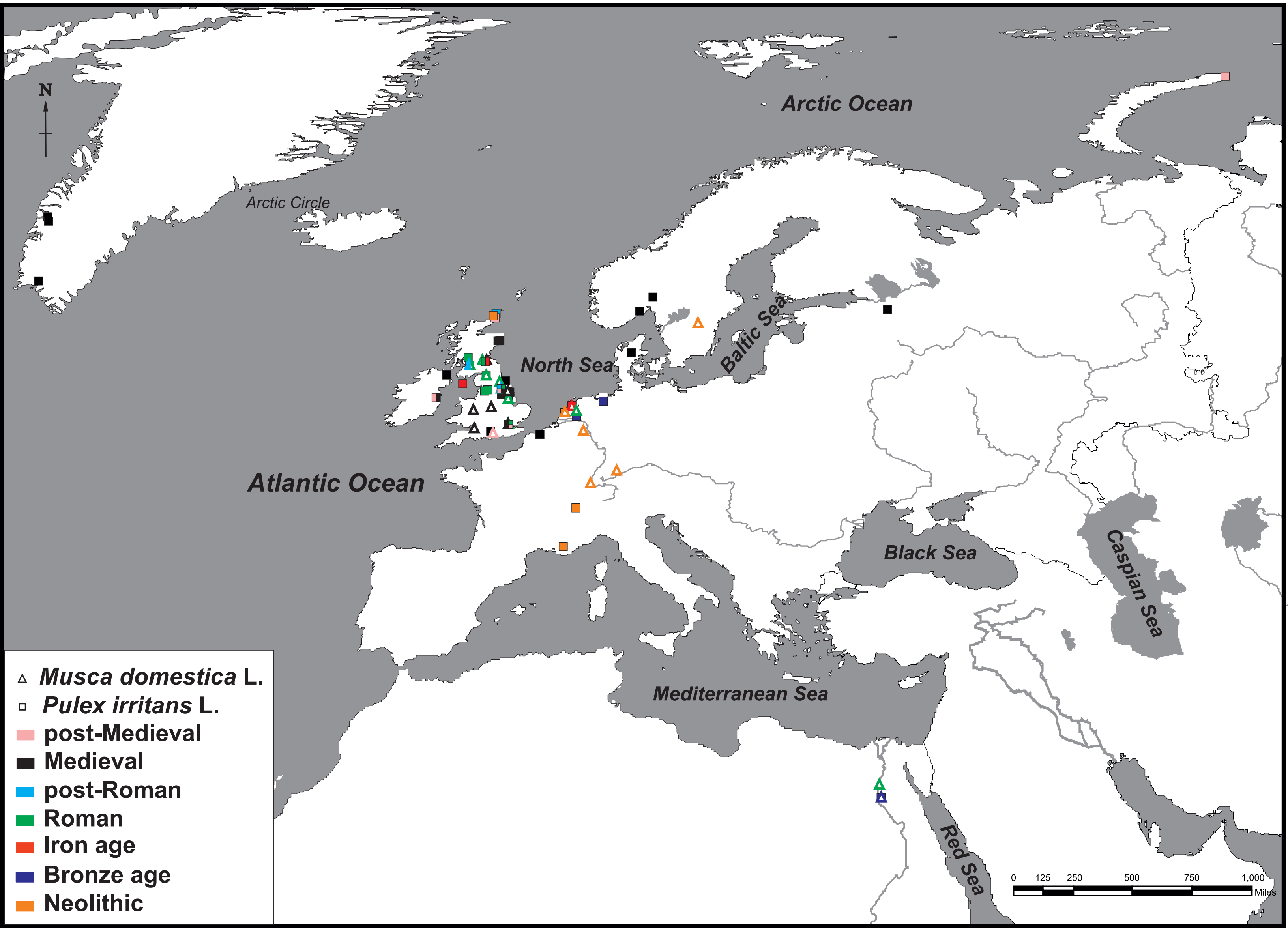

N
Arctic Ocean
Arctic Circle
North Sea
Baltic Sea
Atlantic Ocean
Black Sea
Caspian Sea
Mediterranean Sea
Red Sea
△ *Musca domestica* L.
□ *Pulex irritans* L.
post-Medieval
Medieval
post-Roman
Roman
Iron age
Bronze age
Neolithic
0
125
250
500
750
1,000
Miles

Figure 5

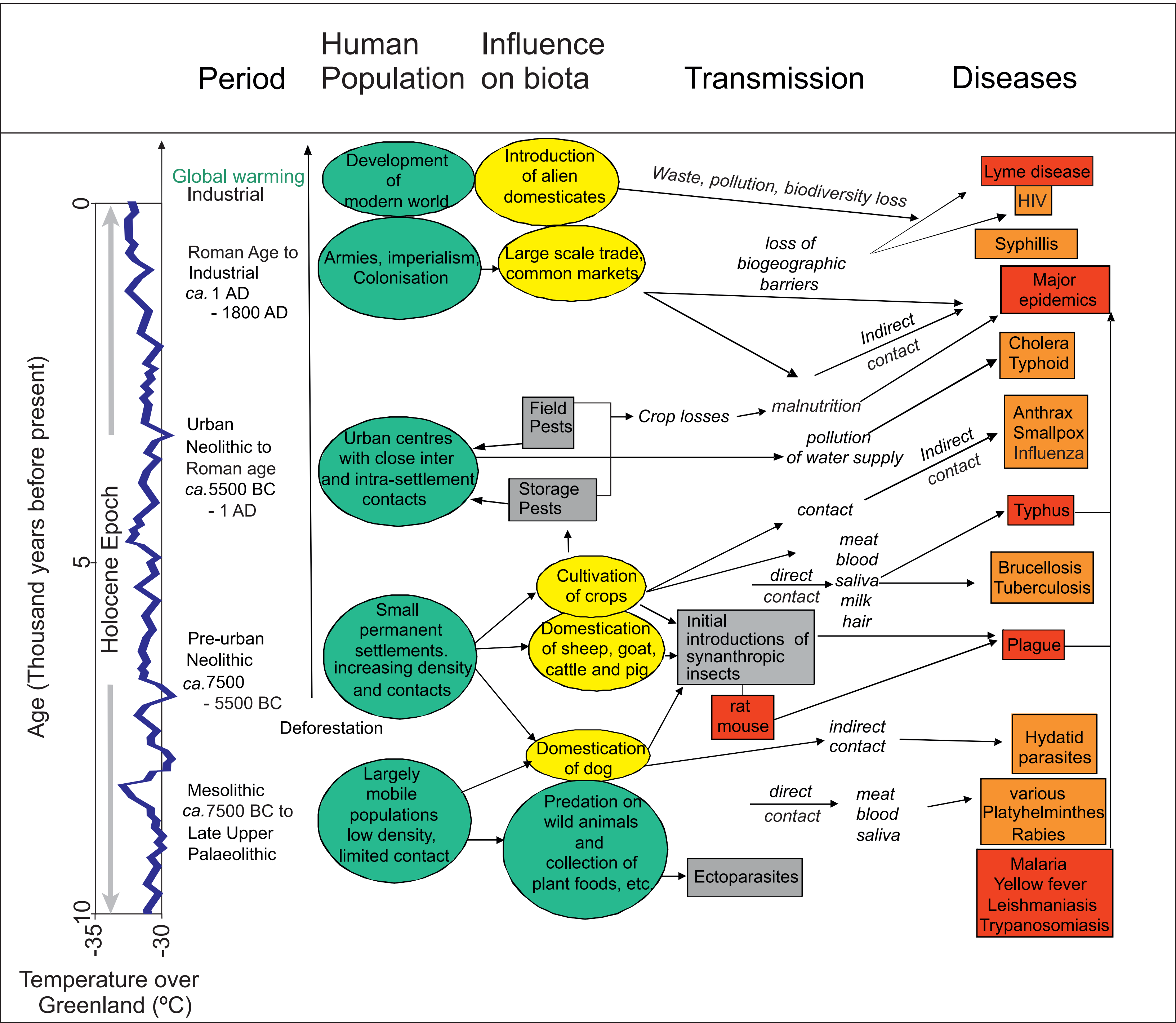

Period
Human Population
Influence on biota
Transmission
Diseases
Age (Thousand years before present)
0
5
10
-35
-30
Temperature over Greenland (°C)
Holocene Epoch
Global warming
Industrial
Roman Age to Industrial ca. 1 AD - 1800 AD
Urban Neolithic to Roman age ca.5500 BC - 1 AD
Pre-urban Neolithic ca.7500 - 5500 BC
Mesolithic ca.7500 BC to Late Upper Palaeolithic
Deforestation
Development of modern world
Introduction of alien domesticates
Armies, imperialism, Colonisation
Large scale trade, common markets
Urban centres with close inter and intra-settlement contacts
Field Pests
Storage Pests
Small permanent settlements. increasing density and contacts
Cultivation of crops
Domestication of sheep, goat, cattle and pig
Domestication of dog
Largely mobile populations low density, limited contact
Predation on wild animals and collection of plant foods, etc.
Ectoparasites
Initial introductions of synanthropic insects
rat mouse
Waste, pollution, biodiversity loss
loss of biogeographic barriers
Indirect contact
Crop losses
malnutrition
pollution of water supply
Indirect contact
contact
direct contact
meat blood saliva milk hair
indirect contact
direct contact
meat blood saliva
Lyme disease
HIV
Syphillis
Major epidemics
Cholera Typhoid
Anthrax Smallpox Influenza
Typhus
Brucellosis Tuberculosis
Plague
Hydatid parasites
various Platyhelminthes Rabies
Malaria Yellow fever Leishmaniasis Trypanosomiasis

Figure 6

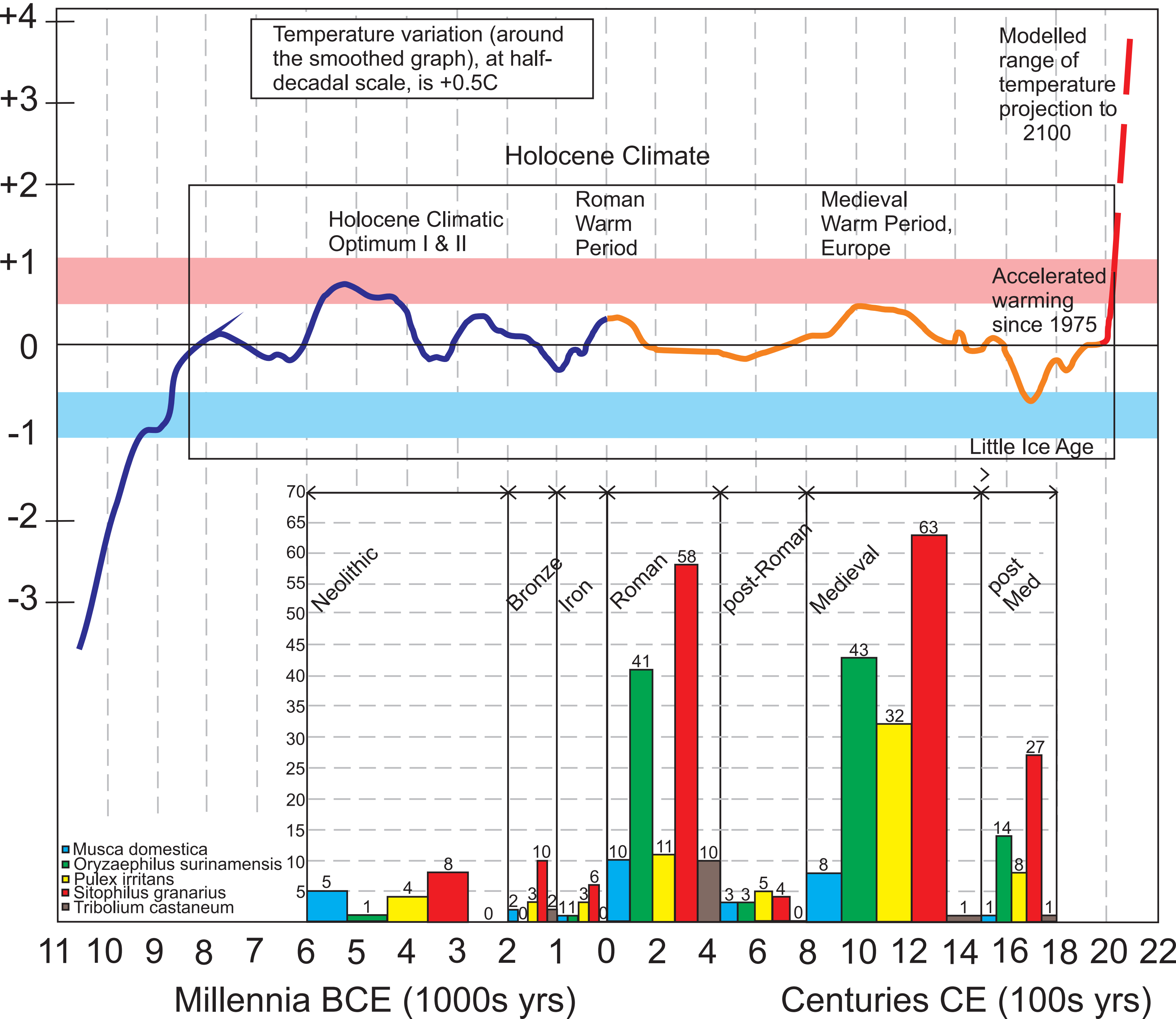
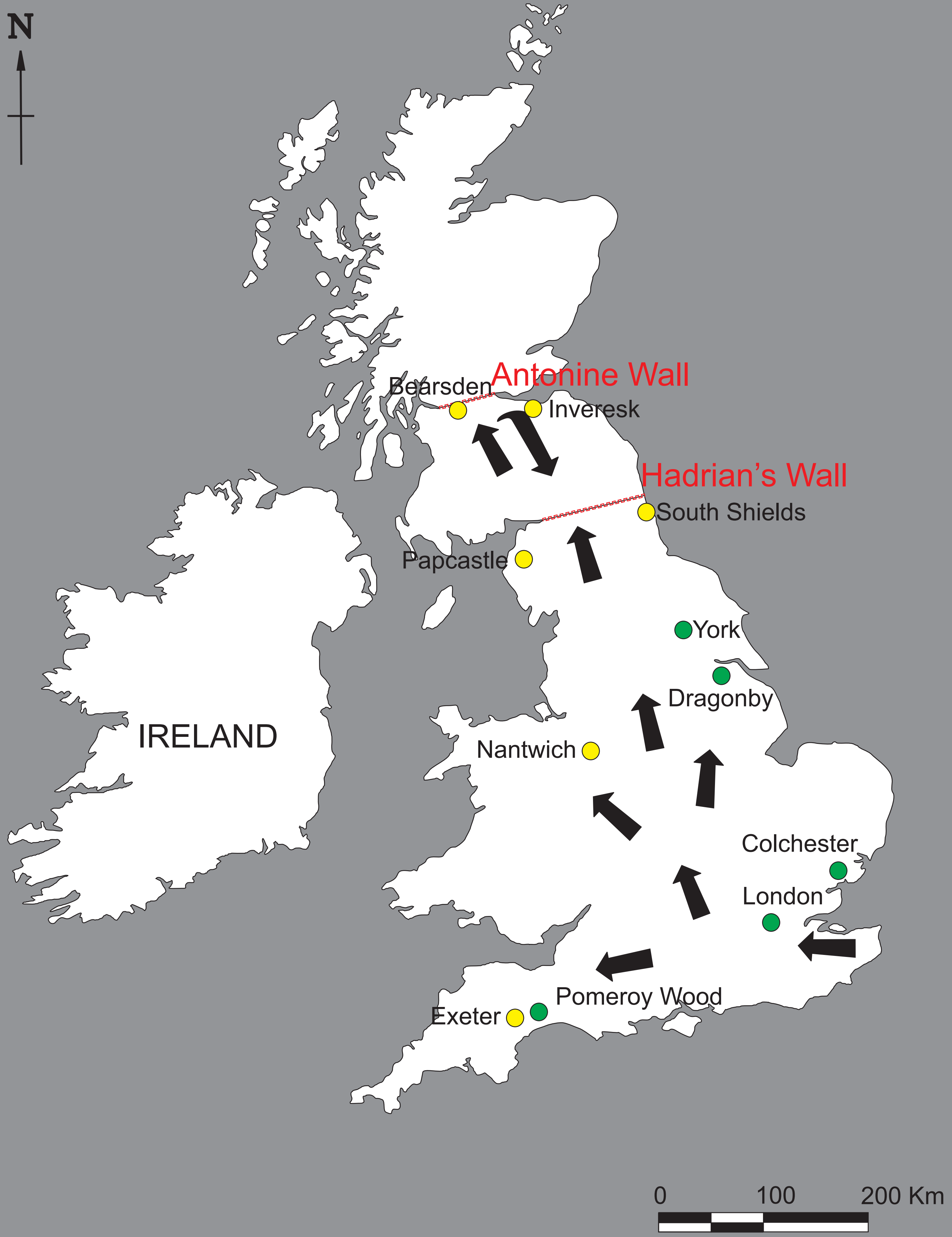

+4
+3
+2
+1
0
-1
-2
-3
Temperature variation (around the smoothed graph), at half-decadal scale, is +0.5C
Modelled range of temperature projection to 2100
Holocene Climate
Holocene Climatic Optimum I & II
Roman Warm Period
Medieval Warm Period, Europe
Accelerated warming since 1975
Little Ice Age
70
65
60
55
50
45
40
35
30
25
20
15
10
5
Neolithic
Bronze
Iron
Roman
post-Roman
Medieval
post Med
5
1
4
8
0
2
0
3
10
2
1
1
3
6
0
10
41
11
58
10
3
3
5
4
0
8
43
32
63
1
1
14
8
27
1
Musca domestica
Oryzaephilus surinamensis
Pulex irritans
Sitophilus granarius
Tribolium castaneum
11
10
9
8
7
6
5
4
3
2
1
0
2
4
6
8
10
12
14
16
18
20
22
Millennia BCE (1000s yrs)
Centuries CE (100s yrs)

Figure 7


N
Antonine Wall
Bearsden
Inveresk
Hadrian's Wall
South Shields
Papcastle
York
Dragonby
IRELAND
Nantwich
Colchester
London
Pomeroy Wood
Exeter
0
100
200 Km