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1 Early invaders - Farmers, the granary weevil and other uninvited guests in the Neolithic

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3 Eva Panagiotakopulu^{1*} Paul C. Buckland²

4 1 School of GeoSciences, University of Edinburgh, EH8 9XP, Edinburgh, UK

5 *e-mail: eva.p@ed.ac.uk

6 Tel. no. 00441316502531

7 2 Independent researcher, 20 Den Bank Close, S10 5PE, Sheffield, UK

9 Abstract

10 The Neolithic and the spread of agriculture saw several introductions of insect species
11 associated with the environments and activities of the first farmers. Fossil insect research
12 from the Neolithic lake settlement of Dispilio in Macedonia, northern Greece, provides
13 evidence for the early European introduction of a flightless weevil, the granary weevil,
14 *Sitophilus granarius*, which has since become cosmopolitan and one of the most important
15 pests of stored cereals. The records of the granary weevil from the Middle Neolithic in
16 northern Greece illuminate the significance of surplus storage for the spread of agriculture.
17 The granary weevil and the house fly, *Musca domestica* were also introduced in the Neolithic
18 of central Europe, with the expansion of Linear Band Keramik (LBK) culture groups. This
19 paper reviews Neolithic insect introductions in Europe, including storage pests, discusses
20 their distribution during different periods and the reasons behind the trends observed. Storage
21 farming may be differentiated from pastoral farming on the basis of insect introductions
22 arriving with incoming agricultural groups.

24 Keywords

25 Neolithic, fossil insects, *Sitophilus granarius*, storage, Greece, Germany, LBK

27 **Introduction**

28 The beginnings of the Neolithic cultural evolution in Europe are associated with the
 29 introduction of crop plants and domestic animals from the Near East, movement of human
 30 populations (Fernandez et al. 2014; Burger and Thomas 2011) and forest clearance (Fyfe et
 31 al. 2015). Climate change has been advanced by some researchers as one of the drivers
 32 behind the timing and the scale of change and the reason behind mobility of farming groups
 33 (Bar Yosef 2011; Richerson et al. 2001). However separating cultural choice from climate
 34 induced change during the Holocene is near impossible, if nothing else because preservation,
 35 taphonomy and the nature of the archaeological record rarely allow for exact correlation of
 36 events. Discussions have centred on typology of artefacts (Yerkes et al. 2012), the spread of
 37 cereal crops (Colledge et al. 2013; Fuller 2007), found mostly as charred seeds from
 38 Neolithic archaeological sites in Eurasia, morphological change in animal bones, and recently
 39 phylogenetic and isotopic data linked with early domestication (Brown et al. 2008; Bramanti
 40 et al. 2009; Larson and Fuller 2014). Currently research is primarily focussed on analytical
 41 methods and the modelling of existing data, although the eventual closure of gaps in datasets,
 42 in terms of data from under-researched regions and chronological and taphonomic biases,
 43 may undermine any overviews. Studies on fossil insects, particularly invasive pest species,
 44 which take a significant toll on production, and their biogeography in relation to the
 45 expansion of agriculture, are few compared to research upon plants, whether pollen or
 46 macrofossils, and domestic animals. This paper presents new insect evidence from the
 47 Neolithic settlement at Dispilio in northern Greece, reviews the Neolithic record of insect
 48 introductions which coincide with the introduction of farming, and discusses the spread of
 49 early agriculture providing a perspective based primarily on fossil insect data.

50 **Dispilio**

51 The archaeological site at Dispilio (Lat. 40°29'7"N; Long. 21°17'22"E), lies on the southern
 52 shore of lake Orestias, 7 km south of Kastoria in northern Greece (Fig. 1). The lake is at 627
 53 m a.s.l., and is drained by the Aliakmon river to the south. The mean temperature during
 54 July is 21.4 °C and during January 1 °C, and annual precipitation is between 563 and 876 mm
 55 with maxima in December and May. On the lake shore wetland environments are dominated
 56 by reeds *Phragmites australis* (Cav.) and bullrush, *Typha* sp., as well as other aquatic plants

(e.g. *Nyphaea alba* H., *Trapa natans* L., *Myriophyllum* sp.). Oaks, *Quercus*, Elm, *Ulmus*, willows, *Salix*, poplar, *Populus*, beech, *Fagus*, and plane, *Platanus*, form the tree cover of the area around the lake.

The site was discovered by Keramopoulos (1932), and fifty years later, excavations were initiated by G. Hourmouziadis, who continued work until his death in late 2013. Dispilio was inhabited from the early Middle Neolithic (ca. 5800 - 5300 BC) through to the Early Bronze Age (3200 - 2100 BC) (Hourmouziadis 1996, 2002; Sofronidou 2008). The dwellings around the lake were built on wooden piles which are still preserved in parts of the excavation (Fig. 2). Wooden trackways were also in use, probably to facilitate movement around the lake shores. Alongside Neolithic pottery, a variety of organic remains including charcoal, seeds, bones and leather were recovered from the different phases of occupation on site (Hourmouziadis 2002, 2006). Perhaps one of the most significant finds, still to be published in detail, is a wooden tablet with linear script, dated to ca. 5300 BC (Hourmouziadis 1996; Facorellis et al. 2014), which provides some of the earliest evidence for writing in Europe.

Palynology has shown that *Abies*, fir, *Pinus*, pine, *Fagus*, beech, *Carpinus*, hornbeam, *Tilia*, lime, and *Juglans*, walnut, were present in the region from 7500 years ago. Disturbance of the woodland, although small scale initially, coincided with the beginning of the settlement (Koulis and Dermizakis 2008). Other palaeoenvironmental research at Dispilio includes bones of terrestrial animals (Phoca Cosmetatou 2008), fish bones (Theodoropolou 2008), molluscs (Veropoulidou 2009) and plant remains, including charred seeds (Mangafa 2002), wood (Ntinou 2010), and phytoliths (Tsartsidou 2010). Geoarchaeological research has provided information on the nature of the sediments and the site's environmental setting (Karkanas et al. 2011). The sudden death of Hourmouziadis in 2013 resulted in the interruption of the site excavation. Although a final report has yet to be written, the indications from the environmental research are of a settlement at a location strategic for the exploitation of a range of diverse resources.

Methodology

In October 2010, sampling was undertaken to evaluate the potential of Dispilio for the study of insect remains. A section was cleared in the western corner of the Eastern Sector (Fig. 3) to enable the recovery of bulk (5 litre) samples for analysis of insects. A total of twelve blocks (S1-S12) were cut in a vertical succession of 50 mm slices (Fig. 4). As it was evident

that the upper exposed sediments had dried out and there was minimal chance for preservation of insects, sampling began at 140 cm from the modern surface. The basal sample of the section encompassed the top of the underlying sediment, before the initial occupation next to the lake. The stratigraphy of the profile was correlated with the dated profile recorded by Karkanas et al. (2011) from a different part of the East Sector. The samples were sealed in polythene bags in the field and returned to the laboratory for processing and sorting. Processing followed the technique originally devised by Coope and Osborne (1968). The samples were disaggregated in warm water and poured onto a 300 µm sieve. The coarser fraction, which was retained on the sieve, was drained and returned to a bucket where paraffin (kerosene) was added and worked into the sample. The light oil adsorbs onto the cuticle of arthropod remains, and as a result when cold water is added the insect remains float. Flotation was repeated three times for each sample, and the material floated was washed with detergent and hot water to remove the paraffin, and then with alcohol (IMS). Sorting was carried out under a binocular microscope, and the individual insect sclerites recovered were stored in 70% ethanol. Preservation was poor and the limited material recovered from the four basal samples was very fragmented. In addition to the bulk sample dates obtained by Karkanas et al. (2011), an AMS radiocarbon date was obtained from the basal sample of the section.

Results and Discussion

***Sitophilus granarius*, *Dispilio* and other Neolithic insect records**

From the samples processed, few insect remains were recovered and these were retrieved primarily from the basal samples. Although waterlogging of the site should have led to optimal preservation, the drainage of the area prior to excavation and its rewetting during winters had led to the destruction of much of the organic material (see Fig. 2). Nevertheless, small fragments of uncharred wood, molluscan fragments, fish bones, large pieces of charcoal and a few insect fragments survived. The insect remains from the basal sample, S12, were very fragmented and the bulk of the assemblage comprised of elytra of reed beetles, *Plateumaris* spp. The genus is typical of semi-aquatic environments, and can be found on reeds, rushes and other aquatic plants, although one species, *Plateumaris discolor* (Panzer) is more characteristic of acid mires (Cox 2007). As well as the wetland fauna, three elytra of the

cereal pest *Sitophilus granarius* (L.) were recovered from this sample. A similar pattern emerged from samples 11, 10 and 9 with single sclerites of *S. granarius* present from samples 10 and 9; there was no preservation in samples from the upper part of the section.

S. granarius although flightless is now cosmopolitan, having been transported by humans with cereals to even the most isolated parts of the world (Hill 1975). The beetle has its origins in the Fertile Crescent probably in nests of rodents (Buckland 1981) and it is a storage, as opposed to a field pest. It requires temperatures from 20-32 °C for oviposition and moisture below 12% (Birch 1944). Although cold hardy (Solomon and Adamson 1955), in regions with colder climate it survives only indoors in heated buildings. In cases where there are no significant resident populations of the weevil, frequent reintroductions of infested cereals are needed to maintain populations, which may provide evidence for centralised storage, trade networks and frequent supplies of infested grain.

An AMS radiocarbon date of 7730 to 7670 cal BP (5780 to 5720 cal BC) from a piece of black pine, *Pinus nigra* Arn., was obtained from the basal sample of the section, S12. This coincides with the beginning of the settlement, according to Hourmouziadis (2006), at the beginning of the middle Neolithic around 5800 BC. The granary weevil specimens from the basal sample are the earliest fossil records of the species from Europe and indicate its early introduction to northern inland Greece.

Further east, Helbaek (1970) notes *Sitophilus* sp. from Haçılar in Asiatic Turkey around 7500 (uncalibrated) BP (= ca. 6400 cal BC). *S. granarius* has been recorded from the Pre Pottery Neolithic C (PPNC) period site at Atlit Yam, near Haifa on the coast of Israel in a well of ca. 6200 cal BC (Kislev et al. 2004) (Fig. 5, Table 1). In addition to the *Dispilio* record, other Neolithic early records from Europe include evidence from the sites of Eythra, ca. 5250 BC (Schmidt 2004), Erkelenz-Kückhoven ca. 5057 BC (Schmidt 1998) and Plaussig ca. 5250 BC (Schmidt 2013) associated with the Linear Band Keramik (LBK), a culture which took its name from the linear decorated pottery associated with it. A further LBK site with *S. granarius* from Göttingen (Büchner and Wolf 1997) in the same region of Germany dates to ca 4935–4800 BC. In northern Greece, during the late Neolithic at Servia (ca. 4500 - 4200 BC) the species is preserved in the form of imprints in pottery (Hubbard 1979: 227) (see Fig. 5, Table 1), and there is an Early Cycladic (3200-2200 BC) record of *S. granarius* from Akrotiri (Panagiotakopulu, in press). There are other early Mediterranean records from

Egypt. Solomon (1965) notes it from barley deposited in a pharaonic tomb beneath the Step Pyramid of Saqqarah about 2300 BC and Helbaek (in *op. cit.*) notes further specimens of *Sitophilus* sp. 600 years older from another tomb at Saqqarah. Chaddick and Leek (1972) provide a record from the 6th Dynasty (*ca.* 2323–2150 BC) tomb of Queen Ichetis at the same site, and there is a 10th Century BC record from Tel Arad in Israel (Hopf and Zachariae 1971).

Two congeners, *Sitophilus oryzae* (L.) and *S. zeamais* Mots., probably have their origins further east in Asia. In contrast to *S. granarius*, they are both capable fliers (Fogliazza and Pagani 1993), and as a result, they can be pests in the field as well as the storeroom (Plarre 2010). The earliest record of the genus, *S. zeamais*, comes from Japan as imprints on pottery from deposits of *ca.* 10500 BP at Sanbonmatsu, Kagoshima, (Obata et al. 2011), whilst for *S. oryzae* the earliest record is later, from a Han Dynasty tomb in China of 185 BC (Chu and Wang 1975). In Europe, its earliest occurrence is in a late medieval deposit in Southampton (Grove 1995).

In Central Europe, LBK deposits include two more pest species, which are now cosmopolitan, the spider beetles *Niptus hololeucus* (Fald.) and *Gibbium psylloides* (Czen.) from the site at Eythra, near Leipzig (Schmidt 2013) (see Fig. 5, Table 1). *N. hololeucus* is a flightless temperate species which breeds on a range of different materials including faeces (Koch 1971). Its proposed origin by Zacher (1927), who believed that the golden spider beetle was introduced to Europe from the Crimea in the 1830s and spread through trade to northern Europe and North America, was discussed by Buckland (1976) in connection with finds from a Roman sewer in York (probably 4th century AD). There are further Roman and medieval finds, from Bearsden (140 AD - 168 AD) on the Antonine Wall in Scotland (Locke 2016) and medieval sites at Leicester (1250 AD-1540 AD) in the English Midlands (Girling 1981) and Neuss (30 AD - 60 AD) in the Rhineland (Cymorek and Koch 1969). Its natural habitat includes nests of birds and those of social Hymenoptera, where it is probably a scavenger (Howe and Burges 1952). Sporadic accidental introductions by trade and gift exchange to sites in western Europe, perhaps from West Asia, and local extinctions have been a feature of this and other relatively thermophilous species throughout the late Holocene. *G. psylloides* shows a similar pattern of fossil records from the Neolithic and later periods in Europe, occurring in 1st-2nd century Roman deposits at Lattes in Hérault (Ponel et al. 2005) and early post-medieval Marseilles (Ponel and Yvinec 1997); other fossil records are largely

Egyptian (Panagiotakopulu 2001). Primarily distributed around the Mediterranean at the present day, it is found on a range of stored products, although modern records may also include *G. aequinoctiale* (Bellés and Halstead 1985), perhaps a more recent introduction of a vicariant from the New World.

The cadelle beetle, *Tenebroides mauritanicus* (L.) has been found in LBK deposits at Erkelenz-Kückhoven (Schmidt 1998) and Plaussig (Schmidt in King et al. 2014) and the middle Neolithic Grossgartach culture site at Singen Offwiese in deposits of ca. 4500-4000 BC (Schmidt 2007, 2013). Another early record comes from a cave at Wadi Gawasis on the Red Sea Coast of Egypt, ca. 1850 BC (Borojevic et al. 2010) and it again appears in a Roman well at Hanau in Hesse, Germany (Kenward and Large 1999) and a range of British Roman sites northwards to lowland Scotland (Smith 2004). Whilst *T. mauritanicus* is believed to have its origins in Africa (Denux and Zagatti 2010), there are records from under bark in southern Europe (Crowson 1958) and it may be part of the Palaearctic *Urwald* (= primary forest) insect fauna (sensu Buckland 1979). Another grain pest, *Oryzaephilus surinamensis* (L.), has similar origins and is also first recorded from a late Neolithic site at Mandalo in Macedonia in deposits of ca. 4500- 4340 cal BC (Valamoti and Buckland 1995). This, the saw-toothed grain beetle, is now a cosmopolitan pest on cereals, cereal products and various other commodities (Fogliazza and Pagani 1993; Halstead 1993) It is cold hardy and in the wild has also been found under bark (Zacher 1927).

As well as the suite of storage pests from the LBK in the Rhineland, *Musca domestica*, the house fly, was recovered from Erkelenz-Kückhoven (Schmidt 2010). Its requirement for elevated temperatures for breeding suggested to Skidmore (1996) that the species has origins in warmer climes, perhaps the Nile valley. It exploits a variety of environments, but is primarily associated with the dung of domestic animals (Skidmore 1985). Other early West European records include Schipluiden in the Netherlands at ca. 3500 BC (Hakbijl 2006) and Thyangen Weier in Switzerland, from ca. 3500-3000 BC (Nielsen et al. 2000). The species' temperature requirements imply that the recovery of house flies puparia from the fields at the latter site, which lies at nearly 500m above sea level, provides evidence of manuring (Nielsen et al. 2000), for which there is evidence from other Neolithic sites in artefact distribution (cf. Radley and Cooper 1968, Guttman-Bond et al. 2016) and isotopic research on fossil plant remains (Bogaard et al. 2013). Neolithic house fly records also include Federsee in southern Germany, ca. 3000 BC (Schmidt 2004) and the pile dwelling at Alvastra in southern Sweden ca. 3000 BC, (Skidmore in Lemdahl 1995).

From 3600 to 2500 cal BC there are records of an additional introduced species, the human flea, *Pulex irritans* L. Two of the four sites with human fleas, are located in France, Saint-Maximin-la-Sainte-Baume ca. 3600 cal BC (Remicourt et al. 2014) and Chalain ca. 3200 - 2980 cal BC (Yvinec et al. 2000). In addition to these, there were human flea records from Shipluiden ca. 3500 cal BC (Hakbijl 2006) and Skara Brae at Orkney ca. 3100 -2500 cal BC (Buckland and Sadler 1997) (see Fig. 5, Table 1).

Insects, Agropastoralists and the European Neolithic

The beginnings of plant domestication during the Neolithic in south west Asia have been linked with the importance of storage as a mechanism which facilitated the transition (Kujit 2008). Despite the clear demographic advantages of sedentary communities, able to produce and support offspring in every year, rather than every 3- 4 years (Sussman 1972), in the temperate zone, the break point in expansion remains production of an agricultural surplus, capable of being stored and utilised as both the seed grains and food of the next wave of colonisers. It is probable that only with centralised control over surplus was this barrier effectively broken.

Archaeological information for the initiation of surplus tends to be thin and it is only rarely, when preservation allows it, that evidence for the use of structures and materials (e.g. mud bins, sacks, etc.) is recovered. Such evidence for dedicated facilities comes as early as 11000 years ago from Dhra' in Jordan during the PPNA (Pre Pottery Neolithic A) and involves large quantities of wild cereals, probably cultivated rather than collected (Kuijt and Finlayson 2009). The less well preserved storage areas enclosed by mud walls from Netiv Hadgud (Bar Yosef and Gopher 1997) provide an additional example.

Whether the outcome of intensification or a necessity resulting from sedentism and increasing population numbers, bulk storage marks the origins of a Near Eastern Neolithic which is based on seven cereal and pulse species: einkorn (*Triticum monococcum* L.), emmer (*T. turgidum* L.), barley (*Hordeum vulgare* L.), lentil (*Lens culinaris* Medikus), pea (*Pisum sativum* L.), chickpea (*Cicer arietinum* L.), and bitter vetch (*Vicia ervilia* L.). By the late sixth millennium BC, in the southern Levant there is evidence for extensive storage facilities; Tel Tsaf exemplifies surplus accumulation and points to social complexity and stratification (Garfinkel et al. 2015). In this context the evidence for *S. granarius* from the Levantine PPNC (Kislev et al. 2004), is relevant as it indicates that storage of wild plants and

248 subsequently cultivated plants was fundamental for the transition to settled farming
249 communities.

250 Research on charred plant remains from aceramic Neolithic sites from southwest Asia and
251 southeast Europe, in particular the Levantine core area, the Aegean and Cyprus, has shown
252 on the basis of weed assemblages that farming was probably associated with a wave of
253 colonisation from the Levant to the Aegean (Colledge et al. 2004). Indeed, the early Neolithic
254 in the Aegean follows closely the spread of farming along the Levantine coast and the early
255 Neolithic also includes a similar package of crops (Valamoti and Kotsakis 2007).

256 Climate, in particular the 8200 BP cold climatic event in the northern hemisphere, has been
257 considered as the reason for the initial spread of farming into Europe and there is some
258 discussion about mobility of farmers to the eastern Mediterranean as a result of climate
259 change (see Weninger et al. 2006). However, in addition to problems inherent with close
260 dating of the archaeology, there is evidence for Neolithic sites already established by that
261 point both in the Levant and the Aegean. This indicates that the spread of agriculture might
262 have been a more complex affair (Kotsakis 2001). In northern Greece wetlands played a
263 significant role for settlement (Gkoumas and Karkanas 2016), with several early and middle
264 Neolithic sites located in proximity to a variety of resources. The early middle Neolithic
265 record of *S. granarius* from Dispilio provides evidence for both diffusion and storage, which
266 in relation to the writing tablet from the site might be pointing to a socially stratified agrarian
267 society. Although fossil insect assemblages have been little studied on Mediterranean sites,
268 the additional Neolithic records of *S. granarius* and *O. surinamensis* from Macedonia, may
269 relate to a similar pattern of storage and exchange (see Fig. 5, Table 1). The impact of grain
270 pests, however, goes beyond the occasional nutty bits in a granary loaf to wholesale
271 destruction of stored foodstuffs and seed grain. Hoffman (1954) estimated that 5% of French
272 cereal production before the Second World War was lost to *S. granarius* alone. Losses are not
273 evenly distributed and dearth in one region may be accompanied by surplus in another. The
274 apparent invasion of France by *Sitotroga cerealella* (Ol.), the Angoumois grain moth, the
275 subject of an early entomological monograph (du Monceau and Tillet 1762), provides an
276 example of a serious pest, which lead to famine. Soft-bodied pests, however, are unlikely to
277 leave a fossil record, although at Masada in Israel, destroyed in AD 73, the Almond Moth,
278 *Ephestia cautella* (Walker) is preserved by desiccation (Kislev and Simchoni 2007). Attempts

at estimating storage loss and its impact on human communities in the remote past are therefore highly speculative (cf. Buckland 1978).

In the long debate about acculturation and colonisation, dietary characteristics of different groups may be significant. Vencl (1986) has argued that the North European model of acculturation of Mesolithic groups (from around 10000 to 5000 BC) to a settled farming economy is inappropriate for Central Europe, and the evidence of bone isotope chemistry is increasingly showing that the dietary division between hunter gatherers and farmers is radical no matter where it comes from (e.g. Bonsall et al. 2000; Richards et al. 2003). Several models, perhaps borne of the end of Mesolithic/transition to Neolithic Ertebølle sites in the southern Baltic region, saw amicable co-existence between groups adopting disparate approaches to the forest and its resources, although ethnographic parallels (e.g. Wolf 1982) and mass grave evidence revealing traumatic injuries indicate otherwise (Golitzko and Keeley 2007). Confronted by an alien herbivore that neither runs away nor expresses surprise at a hunter, the natural reaction of the latter is to spear and taste it. Such activity would not endear him to the farming community, and he and his kin, like any predator on domestic animals or raiders of the crops, become another item in the farmer's hit list. The terminal confrontation between Yaghan and sheep farmers in Tierra del Fuego after the mid 19th century (Yesner et al. 2003), or perhaps the Beothuk of Newfoundland, cut off from coastal resources by European fishermen almost a century earlier (Rowe 1977) provide some of the latest of many examples. The moving agricultural frontier across Europe must have been very similar, with many small scale killings, supplemented by the denial of essential resources and by the hand of new diseases acquired from close association with domestic stock (Wolfe et al. 2007).

From Central Europe evidence comes from the LBK sites (c. 5400 - 4900 BC), which are clearly very different from those of contemporary cultures in northwest Europe, with large houses apparently organised into villages. Childe's (1958) view of an egalitarian Neolithic may still prevail (e.g. Gomart et al. 2015), although his ideas of temporary occupation and swidden agriculture has been superseded by one in which settlement continuity is emphasised (Lüning 1982; Bickle and Whittle 2013). In a study based largely upon the pottery, van de Velde (1979) tentatively suggested that there was some trace of hierarchy within settlements. Data on production of lithic artefacts (Zimmermann 1995) and redistribution of raw materials also show an hierarchical system (Classen and Zimmermann 2004; Hofmann and Bickle

2009). Most work with plant macrofossils from this period has centred on charred seed material, which provides only a partial view of plant utilisation. At Meindling, near Straubing on the Danube, Bakels (1992, 2009) records six cultivated species: emmer (*Triticum dicoccum* Schrank), einkorn, pea, lentil, linseed (*Linum usitatissimum* L.) and poppy (*Papaver somniferum* L.); einkorn dominates over emmer at this locality. This is the pattern seen elsewhere in Central Europe during this period (see Jacomet 2007).

In the Rhineland, Luning (1982) has argued that the typical threefold division of the characteristic longhouses of sites, such as Langweiler, divided living from storage area by means of a central working area, much after the fashion of later longhouses. These ideas were abandoned in favour of a model of intensive mixed farming with high labour input in small plots (Bogaard 2005), which would need large storage areas or hierarchical societies (but see Müller 2013). However the records of the grain weevil, *S. granarius* and other storage pests are pertinent to this, in that in Europe this assemblage is only able to maintain populations where long term storage on a centralised scale is practised. This association with bulk storage is what limits the distribution of the weevil and it is only much later, with the provisioning of Roman garrisons, that it moves further north (e.g. Buckland 1991; Smith and Kenward 2011). Additional introductions during the LBK, the spider beetles *G. psylloides* and *N. hololeucus*, probably arrived with crop and other materials transported by farming groups to the Rhine valley. The cadelle *T. mauritanicus* is also present, exploiting stored products. In the case of the house fly, *M. domestica*, it was probably dispersed with domestic animals and their dung, following them over northwest Europe. Winter stalling, utilising leaf fodder, necessary to maintain stock through winters in forested environments, is evidenced from the late Neolithic at Thayngen-Weier in Switzerland (Troels-Smith 1984; Nielsen et al. 2000), although there is as yet no firm evidence for its association with LBK.

During the period after the LBK from the fourth millennium to the mid third millennium BC, the Aegean records of *S. granarius* from Servia and *O. surinamensis* from Mandalo, are the only potential insect evidence for bulk storage (see Table 1). Although after its initial introduction to the Rhine valley, *S. granarius* would be expected to spread with storage farming, this does not appear to be the case. *T. mauritanicus* is the only species associated with storage from northwest Europe from this period. Whilst research is limited, there is a notable absence of grain storage pests from 3500 BC to the end of the Neolithic. During this period, the records of invasive species are restricted to *M. domestica* and *P. irritans*

(Panagiotakopulu and Buckland 2017; Remicourt et al. 2014). The most northerly known occurrence of the house fly, from the Funnel Beaker and Pitted ware site of Alvastra in southern Sweden, appear to be associated with an essentially pastoral group. In the absence of the evidence for storage pests, partly a result of the gaps in research, it is difficult to provide useful discussion on trade and long distance movement of foodstuffs, and interpretation of archaeological evidence is often purely theoretical. Subsistence towards the final Neolithic may have become more locally based with less reliance upon trading and gift exchange networks, but this begs the question why the initial wave of Neolithic introductions did not continue to expand during the rest of the period. The excavated evidence shows that that the late LBK sees massacres (Wahl and Trautmann 2012; Meyer et al. 2013; Teschler-Nicola 2012) and whole villages ending as a result of violence (Wild et al 2004). Conflict however was not restricted to the intercultural and some injuries on LBK skeletons had clearly been inflicted by LBK weapons (Scarre 2005); one can envisage raids over winter food resources and seed grains on an unstable moving frontier.

In a landscape still with extensive forests (but see Vera 2000 and subsequent discussion, e.g. Fyfe 2007), it was still easier to risk taking from a neighbour's stores than further clearance and if seed grains had been lost to pests, the only other option might have involved starvation, or a drift towards a more pastoral existence. Data indicating a more transient nature of the warfare during the end of the Neolithic (Christensen 2004) provide critical information both for the nature of settlement and farming, although accurate dates from relevant contexts and DNA and isotopic data from plants and animals, including humans, remain sparse. In terms of insect assemblages, a pattern of dominance of pastoral activities continues in northwest Europe during the Bronze and into the Iron Age, and it is only with the Roman army that storage associated pests again dominate synanthropic faunas (Panagiotakopulu and Buckland 2017).

Conclusions

The past distribution of introduced insects which specialise on stored products provides valuable information for understanding the spread of early farming. In Europe, the Neolithic lake settlement at Dispilio has evidence for the early introduction of a storage pest, the grain weevil, *Sitophilus granarius*. Its fossil records link the spread of agriculture in northern Greece and the Linear Band Keramik in the Rhine valley and stress the importance of

accumulated crop surplus and losses to pests in storage in the expansion of farmers from the Fertile Crescent to northern Europe, from steppe to forest. Insect invaders, ranging from storage pests to synanthropic flies and ectoparasites, which accompanied Neolithic expansion, suggest the range of movement and exchange networks. Current data indicate that the initial introductions of storage pests in northwest Europe were not perpetuated beyond the Middle Neolithic, implying the lack of bulk crop storage in the area and perhaps the collapse of exchange networks and movement of cereals. The house fly, *Musca domestica*, and the human flea, *Pulex irritans* however, persisted after their first European introductions, perhaps in relation to pastoral farming. Further fossil insect research will provide much needed data to understand better the mechanisms for species introductions, their spread and establishment and an independent line of evidence for deciphering the ecological changes which have led ultimately to the modern homogenisation of farming.

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Table 1 Fossil records of Neolithic introduced pest species from Near East and Europe

References

- Bakels CC (1992) Fruits and seeds from the Linearbandkeramik settlement at Meindling, Germany, with special reference to *Papaver somniferum*. *Analecta Praehistorica Leidensia* 25:55-68
- Bakels CC (2009) The Western European Loess Belt. *Agrarian History, 5300 BC - AD 1000*. Springer, Berlin
- Bar-Yosef, O (2011) Climatic fluctuations and early farming in west and east Asia. *Curr Anthropol* 52:175 -193
- Bar-Yosef O, Gopher, A (1997) An Early Neolithic Village in the Jordan Valley, Part I: The Archaeology of Netiv Hagdud. Peabody Museum of Archaeology and Ethnology, Harvard University, Cambridge, MA
- Bellés X, Halstead, D (1985) Identification and geographical distribution of *Gibbium aequinoctiale* Boieldieu and *G. psyllodes* (Czenpinski) (Coleoptera : Ptinidae). *J Stored Prod Res* 2:151-155
- Birch LC (1944) Two strains of *Calandra oryzae* L. (Coleoptera). *Aust J Exp Biol Med* 22: 271-275
- Bickle P, Whittle A (2013) The first farmers of central Europe: diversity in LBK lifeways. Oxbow, Oxford
- Bogaard A (2005) 'Garden agriculture' and the nature of early farming in Europe and the Near East. *World Archaeol* 37:177-196
- Bogaard A, Fraser RA, Heaton THE, Wallace M, Vaiglova P, Charles M, Jones G, Evershed RP, Styring AK, Andersen NH, Aerbogast R-M, Bartosiewicz L, Gardeisen A, Kanstrup M, Maier U, Marinova E, Ninov L, Schäfer M, Stephan E (2013) Crop manuring and intensive

land management by Europe's first farmers. PNAS 110:31 12589-12594. doi:
10.1073/pnas.1305918110

Bonsall C, Cook GT, Lennon R, Harkness D, Scott M, Bartosiewicz L, McSweeney K
(2000) Stable Isotopes, radiocarbon and the Mesolithic-Neolithic transition in the Iron Gates.
Documenta Praehistorica 27:119-132

Borojevic K, Steiner WE JR, Gerisch R, Zazzaro C, Ward, C (2010) Pests in an ancient
Egyptian harbour. J Archaeol Sci 37:2449-2458. doi.org/10.1016/j.jas.2010.04.013

Bramanti B, Thomas MG, Haak W, Unterlaender M, Jores P, Tambets K, Antanaitis-Jacobs I,
Haidle MN, Jankauskas R, Kind C-J, Lueth F, Terberger T, Hiller J, Matsumura S, Forster P,
Burger J (2009) Genetic Discontinuity Between Local Hunter-Gatherers and Central Europe's
First Farmers. Science 362:137-140. doi:10.1126/science.1176869

Brown TA, Jones, MK, Powell, W, Allaby, RG (2008) The complex origins of domesticated
crops in the Fertile Crescent. Trends Ecol Evol 24:103-109. doi.org/10.1016/
j.tree.2008.09.008

Büchner S, Wolf G (1997) Der Kornkäfer - *Sitophilus granarius* (Linné) - aus einer
bandkeramischen Grube bei Göttingen. Archäologisches Korrespondenzblatt 27:211-220

Buckland PC (1976) *Niptus hololeucus* Fald. (Col., Ptinidae) from Roman deposits in York.
Entomol. monthly Magazine 111:233-234

Buckland PC (1978) Cereal production, storage and population: a caveat. In: Limbrey S,
Evans JG (eds) The effect of man on the landscape: the Lowland Zone. Council for British
Archaeology Research Report 21, London pp 43-45

Buckland PC (1979) Thorne Moors: a palaeoecological study of a Bronze Age site. Dept. of
Geography, University of Birmingham, Birmingham

Buckland PC (1981) The early dispersal of insect pests of stored products as indicated by
archaeological records. J Stored Prod Res 17:1-12

Buckland PC (1991) Granaries, stores and insects. The archaeology of insect synanthropy. In:
Fournier D, Sigaut F (eds) La preparation alimentaire des cereales. PACT 26, Rixensart,
Belgium, pp 69-81

Buckland PC, Sadler, JP (1997) Insects. In: Edwards KJ Ralston IBM (eds) Scotland.
Environment and Archaeology 8,000 BC to AD 1000. Wiley & Sons, Chichester, pp 105-108

Burger J, Thomas MG (2011) The palaeopopulation genetics of humans, cattle and dairying
in Neolithic Europe. In: Pinhasi R, Stock JT (eds) Human bioarchaeology and the transition
to agriculture. Wiley and Sons, New York, pp 371-384

472 Chaddick PR, Leek FF (1972) Further Specimens of Stored Products Insects Found in
 473 Ancient Egyptian Tombs. *J Stored Prod Res* 8:83-86
 474 Childe, VG (1958) *The prehistory of European Society*. Penguin Books, Middlessex,
 475 Harmondsworth
 476 Christensen J (2004) Warfare in the European Neolithic. *Acta Archaeologica* 75:129–156
 477 Chu HF, Wang L-Y (1975) Insect carcasses unearthed from Chinese antique tombs. *Acta*
 478 *Entomol. Sin.* 18:333-337
 479 Classen E, Zimmermann A (2004) Tessellation and triangulations: Understanding Early Neolithic
 480 social networks. In: Ausserer, KF (ed.) *Enter the past: proceedings of the 30th CAA conference held*
 481 *in Vienna, Austria, April 2003*. Oxford pp 467–471
 482 Colledge S, Conolly J, Dobney KM, Manning K, Shennan S (2013) *Origins and Spread of*
 483 *Domestic Animals in Southwest Asia and Europe*. Institute of Archaeology Publications,
 484 University College London
 485 Colledge S, Conolly J, Shennan S (2004) Archaeobotanical evidence for the spread of
 486 farming in the eastern Mediterranean. *Curr Anthropol* 45:35-58
 487 Coope GR, Osborne, PJ (1968) Report on the Coleopterous Fauna of the Roman Well at
 488 Barnsley Park, Gloucestershire. *Trans Bristol Glos Archaeol Soc* 86:84-87
 489 Cox ML (2007) *Atlas of the seed and leaf beetles of Britain and Ireland*. Pisces Publ.,
 490 Newbury
 491 Crowson RA (1958) Some observations on a coleopterological visit to Central Italy.
 492 *Entomologist's monthly Magazine* 94:248-251
 493 Cymorek S, Koch K (1969) Über Funde von Körperteilen des Messingkäfers *Niptus*
 494 *hololeucus* (Fald.) in Auslagerungen aus dem 15-16. Jahrhundert (Neuss, Neiderrhein) und
 495 Folgerungen daraus für die Ausbreitungsgeschichte der Art in Europa. *Anzeiger für*
 496 *Schädlingskunde und Pflanzenschutz* 42:185-186
 497 Denux, O, Zagatti P (2010) Coleoptera families other than Cerambycidae, Curculionidae
 498 sensu lato, Chrysomelidae sensu lato and Coccinellidae. Chapter 8.5. In: Roques A, Kenis M,
 499 Lees D, Lopez-Vaamonde DL, Rabitch W, Rasplus J-Y, Roy, DB (eds) *Alien terrestrial*
 500 *arthropods of Europe*. *Biorisk* 4:315-406
 501 du Monceau D, Tillet M (1762) *Histoire d'un insecte qui dévore les grains dans l' Angoumois*.
 502 Guerin and Delatour, Paris
 503 Facorellis Y, Sofronidou M, Hourmouziadis G (2014) Radiocarbon dating of the Neolithic
 504 lakeside settlement of Dispilio, Kastoria, Northern Greece. *Radiocarbon* 56:511–528

505 Fernández E, Pérez-Pérez A, Gamba C, Prats E, Cuesta P, Anfruns J, Molist M, Arroyo-
 506 Pardo E, Turbón D (2014) Ancient DNA Analysis of 8000 B.C. Near Eastern Farmers
 507 Supports an Early Neolithic Pioneer Maritime Colonization of Mainland Europe through
 508 Cyprus and the Aegean Islands. PLoS Genetics doi:10.1371/journal.pgen.1004401
 509 Fogliazza DD, Pagani M (1993) Insect pests in stored foodstuffs in Italy. Part 1: Coleoptera.
 510 *Tecnica Molitoria* 44:937-951
 511 Fuller D (2007) Contrasting patterns in crop domestication and domestication rates: recent
 512 archaeobotanical insights from the Old World. *Ann Bot-London* 100:903-924
 513 Fyfe R (2007) The importance of local-scale openness within regions dominated by closed
 514 woodland. *J Quaternary Sci* 22:571-578. doi: 10.1002/jqs.1078
 515 Fyfe RM, Woodbridge J, Roberts N (2015) From forest to farmland: pollen-inferred land
 516 cover change across Europe using the pseudobiomization approach. *Glob Change Biol*
 517 20:1197-1212. doi: 10.1111/gcb.12776
 518 Garfinkel Y, Ben-Shlomo D, Kuperman T (2015) Large-scale storage of grain surplus in the
 519 sixth millennium BC: the silos of Tel Tsaf. *Antiquity* 83:309-325
 520 Girling MA (1981) The environmental evidence. In: Mellor JE, Pearce T (eds) *The Austin*
 521 *Friars*, Leicester. Council for British Archaeology, Research Report 35. London, pp 169-173
 522 Gkouma M, Karkanas P (2016) The physical environment in Northern Greece at the advent
 523 of the Neolithic. *Quatern Int*. doi.org/10.1016/j.quaint.2016.08.034
 524 Golitko M, Keeley LH (2007) Beating ploughshares back into swords: warfare in the
 525 Linearbandkeramik. *Antiquity* 81:332-342
 526 Gomart L, Hachem L, Hamon C, Giligny F, Ilett M (2015) Household integration in
 527 Neolithic villages: A new model for the Linear Pottery Culture in west central. *J Anthropol*
 528 *Archaeol* 40:230-249. doi:10.1016/j.jaa.2015.08.003
 529 Grove K (1995) A Study on Insect Remains in Archaeological Deposits. In: *The*
 530 *Archaeology of Chichester and District 1995*. Southern Archaeology and Chichester District
 531 Council, pp 39-40
 532 Guttman-Bond EB, Dungait JAJ, Brown A, Bull ID, Evershed RP (2016) Early Neolithic
 533 agriculture in County Mayo, Republic of Ireland: geoarchaeology of the Céide Fields,
 534 Belderrig, and Rathlackan. *JONAS* 30:1-32
 535 Hakbijl T (2006) Insects. In: Louwe Kooijmans LP, Jongste PFB (eds), *Schipfluiden a*
 536 *Neolithic settlement on the Dutch North Sea coast c. 3500 cal. BC*. *Analecta Praehistorica*
 537 *Leidensia* 37-38:471-482

538 Halstead DGH (1993) Keys for the identification of beetles associated with stored products -
 539 II. Laemophloeidae, Passandridae and Silvanidae. *J Stored Prod Res* 29:99-197
 540 Helbaek H (1970) The plant husbandry of Hacilar. In: Mellaart J (ed) *Excavations at Hacilar*.
 541 Edinburgh University Press, Edinburgh pp 189-244
 542 Hill DS (1975) *Agricultural insect pests of the tropics and their control*. Cambridge U.P.
 543 Hoffmann A (1954) *Coleoptères Curculionides 2. Faune de France 59*. Lechevalier, Paris pp
 544 487-1208
 545 Hofmann D, Bickle P (2009) *Creating communities: new advances in central European*
 546 *Neolithic research*. Oxbow, Oxford
 547 Hopf M, Zachariae G (1971) Determination of botanical and zoological remains from Ramat
 548 Matred and Arad. *Israel Exploration Journal* 21:63-64
 549 Hourmouziadis GH (1996) *Το Δισπηλιό Καστοριάς. Ένας λιμναίος προϊστορικός οικισμός*.
 550 Codex, Thessaloniki
 551 Hourmouziadis GH (2002) *Dispilio, 7500 Years After*. Codex, Thessaloniki
 552 Hourmouziadis GH (2006) *Ανασκαφής Εγκόλπιον*. Capon, Athens
 553 Howe RW, Burges HD (1952) Studies on beetles of the family Ptinidae. VII. The biology of
 554 five Ptinid species found in stored products. *Bulletin of Entomological Research*, 43, 153-186
 555 Hubbard RNL (1979) Appendix 2: Ancient Agriculture and Ecology at Servia. In, *Rescue*
 556 *Excavations at Servia 1971-1973: A Preliminary Report*. *Annual of the British School of*
 557 *Archaeology at Athens* 74:226-228
 558 Jacomet S (2007) Neolithic plant economies in the alpine foreland 5500 to 3500 BC. In:
 559 Colledge S, Connolly J (eds) *The origins and spread of plants in Southeast Asia and Europe*,
 560 pp 221-258
 561 Karkanis P, Pavlopoulos K, Kouli K, Ntinou M, Tsartsidou G, Facorellis Y, Tsourou Th
 562 (2011) Palaeoenvironment and site formation processes of the Neolithic lakeside settlement
 563 of Dispilio, Kastoria, Northern Greece. *Geoarchaeology* 26:83-117
 564 Kenward HK, Large F (1999) Insect remains from a Roman well at ‘Salisweg’, Hanau,
 565 Hessen, Germany. *Reports from the Environmental Archaeology Unit, York*, 99/5. York
 566 Keramopoulos A (1932) Excavations and researches in the Upper Macedonia. *Archaeological*
 567 *Ephimeris* 48:48–133 (In Greek)
 568 King G, Kenward H, Schmidt E, Smith D (2014) Six-legged hitchhikers: an
 569 archaeobiogeographical account of the early dispersal of grain beetles. *JONA* 23:1-18

570 Kislev M, Hartmann A, Galili E (2004) Archaeobotanical and archaeoentomological
 571 evidence from a well at Atlit-Yam indicates colder, more humid climate on the Israeli coast
 572 during the PPNC period. *J Archaeol Sci* 31:1301-1310
 573 Kislev M, Simchoni O (2007) Hygiene and insect damage of crops and food at Masada. In:
 574 Aviram J, Foerster G, Netzer E, Stiebel GD (eds) *Masada VIII. The Yigael Yadin*
 575 *Excavations 1963-1965. Final Reports*, Israel Exploration Society and Hebrew University of
 576 Jerusalem, Jerusalem pp 133-170
 577 Koch, K (1971) Zur Untersuchung subfossiler Käferreste aus römerzeitlichen und
 578 mittelalterlichen Ausgrabungen im Rheinland. *Rheinische Ausgrabungen* 10:378-448.
 579 Kotsakis K (2001) Mesolithic to Neolithic in Greece. Continuity, discontinuity or change of
 580 course? *Documenta Praehistorica* XXVIII:63-73
 581 Koulis K, Dermitzakis MD (2008) Natural and cultural landscape of the Neolithic settlement
 582 of Dispilio: palynological results. *Hellenic J Geosciences* 43:29-39
 583 Kuijt I (2008) Demography and Storage Systems During the Southern Levantine Neolithic
 584 Demographic Transition. In: Bocquet-Appel, J-P, Bar-Yosef, O (eds) *The Neolithic*
 585 *Demographic Transition and its Consequences*. Springer, New York, pp 287 -313
 586 Kuijt I, Finlayson B (2009) Evidence for food storage and predomestication granaries 11,000
 587 years ago in the Jordan Valley. *PNAS* 106: 10966-10970
 588 Larson G, Fuller DQ (2014) The Evolution of Animal Domestication. *Annu. Rev. Ecol. Evol.*
 589 *Syst.* 45:115-136
 590 Lemdahl G (1995) Insect remains from the Alvastra pile dwelling. In: Göransson, H. (ed)
 591 *Alvastra pile dwelling. Palaeoethnobotanical studies. Theses and papers in archaeology, N.S.*
 592 *A6*. Lund University Press, Lund, pp 97-99
 593 Locke J (2016) Insect remains. In: Breeze DJ (ed) *Bearsden. A Roman fort on the Antonine*
 594 *Wall*. Society of Antiquaries of Scotland, Edinburgh, pp 289-299
 595 Lüning J (1982) Research into the Bandkeramik settlement of the Aldenhovener Platte in the
 596 Rhineland. *Analecta Praehistorica Leidensia* 15:1-30
 597 Mangafa M (2002) The archaeobotanic study of the settlement. In: Hourmouziadis G (ed)
 598 *Dispilio, 7500 years after*. University Studio Press, Thessaloniki, pp 115–34 (In Greek)
 599 Meyer C, Lohr C, Strien H-C, Gronenborn D, Alt K (2013) Interpretationsansätze zu
 600 "irregulären" Bestattungen während der linearbandkeramischen Kultur: Gräber en masse und
 601 Massengräber. In: Müller-Scheessel N (ed) *"Irreguläre" Bestattungen in der Urgeschichte:*
 602 *Norm, Ritual, Strafe...? Akten der Internationalen Tagung in Frankfurt a. M. vom 3 bis 5*

603 Februar 2012. Römisch-Germanische Kommission des Deutschen Archäologischen Instituts
 604 and Habelt, Bonn, pp 111–22
 605 Müller J (2013) Demographic traces *of* technological innovation, social change and mobility:
 606 from 1 to 8 million Europeans (6000–2000 BCE). In: Kadrow S, Włodarczak P (eds)
 607 Environment and subsistence—forty years after Janusz Kruk's 'Settlement studies'. Rudolf
 608 Habelt, Bonn, pp 493-506
 609 Nielsen BO, Mahler V, Rasmussen P (2000) An arthropod assemblage and the ecological
 610 conditions in a byre at the Neolithic settlement of Weier, Switzerland. *J Archaeol Sci* 27:
 611 209-218
 612 Ntinou M (2010) Palaeoenvironment and human activities: anthracology at the lakeside
 613 Neolithic settlement of Dispilio, Kastoria. *Anaskamma* 4:45–60 (In Greek)
 614 Obata H, Manabe A, Nakamura N, Onishi T, Senba Y (2011) A new light on the evolution
 615 and propagation of prehistoric grain pests: the World's oldest maize weevils found in Jomon
 616 pottery, Japan. *PloS One*, 6:3, e14785. doi.org/10.1371/journal.pone.0014785
 617 Panagiotakopulu E (2001) New records for ancient pests: archaeoentomology in Egypt. *J*
 618 *Archaeol Sci* 28:1235-1246
 619 Panagiotakopulu E (in press) Flies, beetles, food and burial – Archaeoentomology
 620 of the New Trenches at Akrotiri. In: Doumas C (ed) *The excavations at Akrotiri, 40 years*
 621 *later. Archaïologiki Etaireia*, Athens
 622 Panagiotakopulu E, Buckland PC (2017) A thousand bites – Insect introductions and late
 623 Holocene environments. *Quaternary Sci Rev* 156:23-35
 624 Phoca-Cosmetatou N (2008) The terrestrial economy of a lake settlement: a preliminary
 625 report on the faunal assemblage from the first phase of occupation of Dispilio (Kastoria,
 626 Greece). *Anaskamma* 2:47–68 (In Greek)
 627 Plarre R (2010) An attempt to reconstruct the natural and cultural history of the granary
 628 weevil, *Sitophilus granarius* (Coleoptera: Curculionidae). *Eur J Entomol* 107:1-11
 629 Ponel P, Guiter F, Rocq C, Andrieu-Ponel V (2005) Le paléoenvironnement du site de
 630 Lattes/St Sauveur au 1er siècle de notre ère, reconstruit à partir de l'analyse des assemblages
 631 de Coléoptères subfossiles. In: Piquès G, Buxo R (eds) *Onze puits gallo-romains de Lattara*
 632 *(Ier siècle av. n.è. – IIe s. de n.è.). Lattara 18, Edition de l'Association pour le*
 633 *Développement de l'Archéologie en Languedoc-Rousillon, Lattes*, pp 319-326
 634 Ponel P, Yvinec J-H (1997) L'archéoentomologie en France. *Les nouvelles de l'archéologie*,
 635 68:31-44

636 Radley J, Cooper LB (1968) A Neolithic site at Elton: an experiment in field recording.
 637 Derbyshire Archaeological Journal 88:37-46
 638 Remicourt M, Andrieu-Ponel V, Audibert C, Baradat A, Battentier J, Blaise E, Bonnardin S,
 639 Caverne J-B, Fernandes P, Furestier R, Girard B, Lachenal T, Lepère C, Locatelli C, Martin
 640 L, Parisot N, Ponel P, Pousset D, Rué M, Schmitt A, Sénépart I, Thirault E (2014) Les
 641 occupations pré et protohistoriques du Clos de Roque, a Saint-Maximin-la-Sainte-Baume
 642 (Var). In: Sénépart I, Leandri F, Cauliez J, Perrin T, Thirault E (eds) Chronologie de la
 643 Préhistoire récente dans le Sud de la France. Acquis 1992-2012. Actualité de la recherche
 644 Actes des 10e Rencontres Méridionales de Préhistoire Récente. Porticcio (France) - 18 au 20
 645 octobre 2012. Archives d'Écologie Préhistorique, Toulouse, pp 523-548
 646 Richards MP, Schulting R.J, Hedges, REM (2003) Sharp shift in diet at onset of Neolithic.
 647 Nature 425:366
 648 Richerson PJ, Boyd R, Bettinger RL (2001) Was Agriculture Impossible during the
 649 Pleistocene but Mandatory during the Holocene? A Climate Change Hypothesis. Am
 650 Antiquity 66: 387-411
 651 Rowe FW (1977) Extinction: the Beothucks of Newfoundland. McGraw-Hill Ryerson Ltd,
 652 Toronto
 653 Scarre C (2005) Holocene Europe. In: Scarre C (ed) The Human past: World Prehistory and
 654 the Development of Human Societies. Thames and Hudson, London, pp 392-431
 655 Schmidt E (1998) Der Kornkäfer *Sitophilus granarius* Schön. (Curculionidae) aus der
 656 Schuttschicht des bankeramischen Brunnens von Erlenzen-Kückhoven. Öst Rhein. Amtfür
 657 Bodendenkmalpflege (Hg.) (Brunnen der Jungsteinzeit. Internat. Symposium Erkelenz 27-20
 658 Okt. 1997). Materialenzur Bodendenkmalpflege 11:261-269
 659 Schmidt E (2004) Untersuchungen von Wirbellosenresten aus jung und endneolithischen
 660 Moorsiedlungen des Federsees. In: Schlichtherle H (ed) Ökonomischer und Ökologischer
 661 Wandel am Vorgeschichtlichen Federsee. Hemmenhofener Skripte 5, Janus, Freiburg,
 662 Landesdenkmalamt Baden-Württemberg, Archäologische Denkmalpflege, Referat 27, pp
 663 160–86
 664 Schmidt E (2007) Untersuchung von Wirbellosen-Thanatozönosen. In: Maier U, Vogt R
 665 (eds) Pedologisch-moorkundliche Untersuchungen zur Landschafts und Besiedlungs
 666 geschichte des Federseegebiets, Stuttgarter Geographische Studien 138:157-171

667 Schmidt E (2010) Insektreste aus bandkeramischen Brunnen. Tote Käfer lassen eine
 668 bandkeramische Brunnenumgebung entstehen. Conference Abstract Mitteleuropa im 5.
 669 Jahrtausend vor Christus, 32. Westfälische Wilhelms-Universität, Münster
 670 Schmidt E (2013) Vorratsschädlinge im Mitteleuropa des 5. Jahrtausends. In: Gleser HG,
 671 Becker V (eds) Beiträge zur Internationalen Konferenz in Münster 2010. Mitteleuropa im 5.
 672 Jahrtausend vor Christus Bd. 18. Münster, Berlin, pp 319-329
 673 Skidmore P (1996) A dipterological perspective on the Holocene history of the North
 674 Atlantic Area. Dissertation, University of Sheffield
 675 Skidmore P (1985) The biology of the Muscidae of the World. W Junk, Dordrecht
 676 Smith DN (2004) The insect remains from the well. In: Bishop MC (ed) Inveresk Gate:
 677 excavations in the Roman civil settlement at Inveresk, East Lothian, 1996-2000. STAR
 678 Monograph 7. Midlothian, Loanhead, pp 81-88
 679 Smith D, Kenward H (2011) Roman grain pests in Britain: implications for grain supply and
 680 agricultural production. *Britannia* 42:243-262
 681 Sofronidou M (2008) The prehistoric lakeside settlement of Dispilio, Kastoria: a first
 682 introduction. *Anaskamma* 1:9–26 (In Greek)
 683 Solomon, ME (1965) Archaeological records of storage pests: *Sitophilus granarius* (L.)
 684 (Coleoptera, Curculionidae) from an Egyptian pyramid tomb. *J Stored Prod Res* 1:105-107
 685 Solomon ME, Adamson BE (1955) The powers of survival of storage and domestic pests
 686 under winter conditions in Britain. *B Entomol Res* 46:311-355
 687 Sussman, RW (1972) Child transport, family size, and increase in human population during
 688 the Neolithic. *Curr Anthropol* 13:258-259
 689 Theodoropoulou T (2008) Man and lake: fishers and fishing in prehistoric Dispilio.
 690 *Anaskamma* 2:25–45 (In Greek)
 691 Teschler-Nicola M (2012) The Early Neolithic site Asparn/Schletz (Lower Austria):
 692 Anthropological evidence of interpersonal violence. In: Schulting R, Fibiger L (eds) *Sticks,*
 693 *Stones, and Broken Bones*. Oxford University Press, Oxford, 101–120
 694 Troels-Smith J (1984) Stall-feeding and field-manuring in Switzerland about 6000 years ago.
 695 *Tools and Tillage* 5:13-25
 696 Tsartsidou G (2010) Phytolith analysis from the sediments of Dispilio: an approach of
 697 understanding the subsistence practices of the prehistoric settlement. *Anaskamma* 4:77–88.
 698 (In Greek)

699 van de Velde P (1979) On Bandkeramik social structure. *Analecta Praehistorica Leidensia*
 700 12:1-242
 701 Valamoti SM, Buckland PC (1995) An early find of *Oryzaephilus surinamensis* L.
 702 (Coleoptera: Silvanidae) from Final Neolithic Mandalo, Macedonia, Greece. *J Stored Prod*
 703 *Res* 31:307-309
 704 Valamoti SM, Kotsakis K (2007) Transitions to agriculture in the Aegean: the
 705 archaeobotanical evidence. In: Colledge S, Conolly J, (eds) *The Origins and Spread of*
 706 *Domestic Plants in Southwest Asia and Europe*. Institute of Archaeology, University College
 707 London pp 75-91
 708 Vencl S (1986) The role of hunting-gathering populations in the transition to farming: a
 709 Central European perspective. In: Zvelebil M (ed) *Hunters in transition. Mesolithic farmers*
 710 *of temperate Eurasia and their transition to farming*. Cambridge University Press, Cambridge
 711 pp 43-51
 712 Veropoulidou E (2009) Freshwater molluscs and land snails at the Neolithic Dispilio,
 713 Kastoria. *Anaskamma* 3:13-26 (In Greek)
 714 Wahl J, Trautmann I (2012) The Neolithic massacre at Talheim: A pivotal find in conflict
 715 archaeology. In: Schulting R, Fibiger L (eds) *Sticks, Stones, and Broken Bones*. Oxford
 716 University Press, Oxford, pp 77–100
 717 Weninger B, Alram-Stern E, Bauer E, Clare L, Danzeglocke U, Jöris O, van Andel T (2006)
 718 Climate forcing due to the 8200 cal yr BP event observed at Early Neolithic sites in the
 719 eastern Mediterranean, *Quaternary Res.*, 66, 401–420
 720 Wild EM, Stadler P, Häußler A, Kutschera W, Steier P, Teschler-Nicola M, Wahl J, Windl
 721 HJ (2004) Neolithic massacres: Local skirmishes or general warfare in Europe. *Radiocarbon*
 722 46:377–385
 723 Vera FWM (2000) *Grazing ecology and forest history*. Wallingford, CABI
 724 Wolf E (1982) *Europe and the People without History*. University of California Press,
 725 Berkeley
 726 Wolfe ND, Dunavan CP, Diamond J (2007) Origins of major human infectious diseases.
 727 *Nature* 447:279-283
 728 Yerkes RW, Khalaily H, Barkai R (2012) Form and Function of Early Neolithic Bifacial
 729 Stone Tools Reflects Changes in Land Use Practices during the Neolithization Process in the
 730 Levant. *PLoS ONE* 7(8): e42442. doi:10.1371/journal.pone.0042442

731 Yesner DR, Figuerero Torres MJ, Guichon, RA, Borrero, LA (2003) Stable isotope analysis
 732 of human bone and ethnohistoric subsistence patterns in Tierra del Fuego. J Anthropol
 733 Archaeol 22:279-291
 734 Yvinec J-H, Ponel P, Beaucournu J-C (2000) Premiers apports archeoentomologiques de l'
 735 etude des Puces: aspects historiques et anthro- pologiques (Siphonaptera). Bull. Soc.
 736 Entomol. Fr. 105:419-425.
 737 Zacher F (1927) Die Vorrats-, Speicher- und Materialschadlinge und ihre Bekämpfung.
 738 Verlagsbuchhandlung Paul Parey, Berlin
 739 Zimmermann A (1995) Austauschsysteme von Silexartefakten in der Bandkeramik
 740 Mitteleuropas. Universitätsforschungen zur prähistorischen Archäologie 26. Habelt, Bonn
 741

● Charcoal

○ Shell

⦿ Wood

☞ Bone

Light grey
silty clay

Sand

Moderate light
silty peat

Moderate brown
peat

■ Neolithic core zone

■ W-Anatolian + Aegean/Greek Neolithic

■ LBK

■ Storage pest

■ Other

1 *Sitophilus granarius* (L.)

2 *Oryzaephilus surinamensis* (L.)

3 *Tenebroides mauritanicus* (L.)

4 *Gibbium psyllodes* (Czen.)

5 *Niptus hololeucus* (Fald.)

6 *Musca domestica* (L.)

7 *Pulex irritans* (L.)

Site	Geographic Area	Species	Chronology	Period	Reference
Atlit-Yam	Israel	<i>Sitophilus granarius</i> (L.)	ca. 8250 cal BP (ca. 6200 cal BC)	Pre Pottery Neolithic C (PPNC)	Kislev et al. 2004
Dispilio	Greece	<i>Sitophilus granarius</i> (L.)	ca. 5700 cal BC	Aegean Middle Neolithic	Panagiotakopulu ibid
Plaussig	Germany	<i>Sitophilus granarius</i> (L.)	7219 cal BP (ca. 5250 cal BC)	Linear Band Keramik (LBK)	Schmidt 2013
Eythra	Germany	<i>Sitophilus granarius</i> (L.)	7034 cal BP, 7269 BP-7180 cal BP (ca. 5250 cal BC)	LBK	Schmidt 2010, 2013
Erkelenz-Kückhoven	Germany	<i>Sitophilus granarius</i> (L.)	5057 cal BC	LBK	Schmidt 1998, 2013
Göttingen	Germany	<i>Sitophilus granarius</i> (L.)	6030 BP (ca. 4935–4800 cal BC)	LBK	Büchner and Wolf 1997
Erkelenz-Kückhoven	Germany	<i>Musca domestica</i> L.	5057 BC	LBK	Schmidt 1998
Eythra, Germany	Germany	<i>Gibbium psylloides</i> (Czen.)	ca. 5250 cal BC	LBK	Schmidt 2013
Eythra, Germany	Germany	<i>Niptus hololeucus</i> (Fald.)	ca. 5250 cal BC	LBK	Schmidt 2013
Plaussig	Germany	<i>Tenebroides mauritanicus</i> (L.)	ca. 5250 cal BC	LBK	Schmidt in King et al 2014
Erkelenz-Kückhoven	Germany	<i>Tenebroides mauritanicus</i> (L.)	5057 cal BC	LBK	Schmidt 1998
Singen Offwiese	Germany	<i>Tenebroides mauritanicus</i> (L.)	4500-4000 cal BC	Grossgartach culture	Schmidt 2007, 2013
Servia	Greece	<i>Sitophilus granarius</i> (L.)	ca. 4500 - 4200 cal BC	Aegean Late Neolithic	Hubbard 1979
Mandalo	Greece	<i>Oryzaephilus surinamensis</i> (L.)	4450-4340 cal BC	Aegean Late Neolithic	Valamoti and Buckland 1995
Saint-Maximin-la-Sainte-Baume	France	<i>Pulex irritans</i> L.	ca. 3600 BC	Late Neolithic	Remicourt et al. 2014
Schipluiden	Netherlands	<i>Pulex irritans</i> L.	ca. 3500 cal BC	Late Neolithic	Hakbijl 2006
Chalain, Jura	France	<i>Pulex irritans</i> L.	ca. 3200 - 2980 BC	Late Neolithic	Yvinec et al. 2000
Thayngen-Weier	Switzerland	<i>Musca domestica</i> L.	ca. 3500-3000 cal BC	Cortailod culture	Troels Smith 1984; Nielsen et al. 2000
Schipluiden	Netherlands	<i>Musca domestica</i> L.	ca. 3500 cal BC	Late Neolithic	Hakbijl 2006
Federsee	Germany	<i>Musca domestica</i> L.	ca. 3000 cal BC	Late Neolithic	Schmidt 2004

Alvastra	Sweden	<i>Musca domestica</i> L.	ca. 3000 cal BC	Funnel Beaker and Pitted Ware culture	Lemdahl 1995
Skara Brae, Orkney	Scotland	<i>Pulex irritans</i> L.	ca. 3100 -2500 cal BC	Late Neolithic	Buckland and Sadler 1997