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Citation for published version:
Panagiotakopulu, E & Buckland, PC 2018, 'Early invaders - Farmers, the granary weevil and other uninvited guests in the Neolithic' Biological Invasions, vol 20, no. 1, pp. 219-233. DOI: 10.1007/s10530-017-1528-8

Digital Object Identifier (DOI):
10.1007/s10530-017-1528-8

Published In:
Biological Invasions

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

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Abstract

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

Keywords

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

Introduction

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

Dispilio

The archaeological site at Dispilio (Lat. 40°29′7″N; Long. 21°17′22″E), lies on the southern shore of lake Orestias, 7 km south of Kastoria in northern Greece (Fig. 1). The lake is at 627 m a.s.l., and is drained by the Aliakmon river to the south. The mean temperature during July is 21.4 °C and during January 1 °C, and annual precipitation is between 563 and 876 mm with maxima in December and May. On the lake shore wetland environments are dominated 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 Dermitzakis 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 Haçilar 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, Guttmann-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 subsequently cultivated plants was fundamental for the transition to settled farming communities.

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

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

Acknowledgements

The British School at Athens is thanked for support through a Fitch Senior Visiting Fellowship to EP to undertake pilot research from Dispilio. The Leverhulme Trust is acknowledged for funding over the years to PCB and EP which helped in formulating some of the ideas in this paper. Cathy Morgan and Vaggelio Kyriatzi are thanked for their support to EP during her fellowship in the Fitch Laboratory. Thanks are also due to Anastasios Panayotakopoulos for his help with the illustrations. Marina Sofronidou and colleagues from the Dispilio excavation are warmly acknowledged for their help. The late Georgios Hourmouziadis is acknowledged for embracing this research, for his vision and generosity. Last but not least the editor Francis Howarth, the editor-in-chief Daniel Simberloff and anonymous reviewers are acknowledged for their insightful and constructive comments which improved the paper.

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Fig. 2 Photograph of the Dispilio excavation showing the East sector during a. late summer (photograph copyright Dispilio excavations courtesy of M. Sofronidou) and b. late autumn

Fig. 3 Excavation matrix of Dispilio with the East sector area sampled noted

Fig. 4 Stratigraphic description of the section sampled the from East Sector, Dispilio, northern Greece

Fig. 5 Neolithic records of introduced insects from : a. 7000-6000 BC b. 6000-4500 BC c. 4500-3500 BC d. 3500-2500 BC. For further detail see Table 1

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

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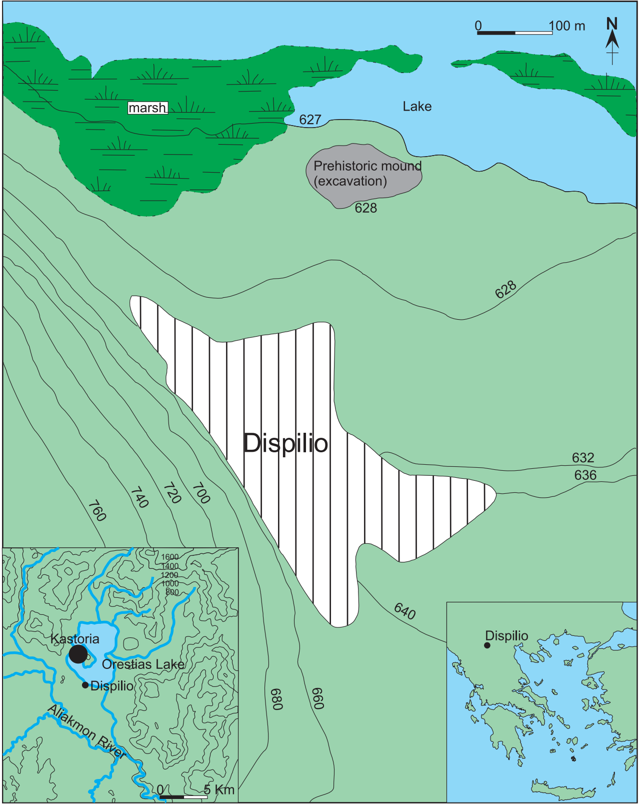

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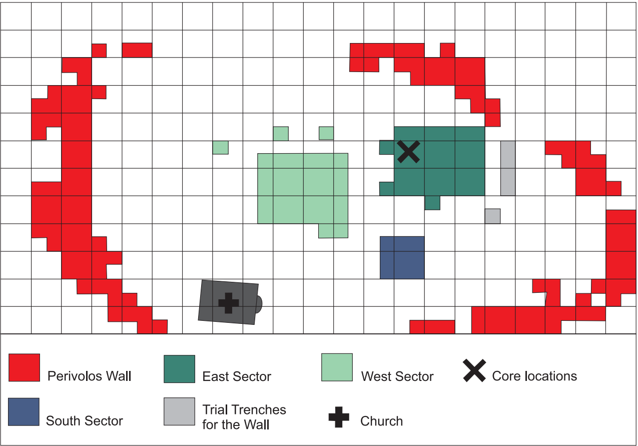
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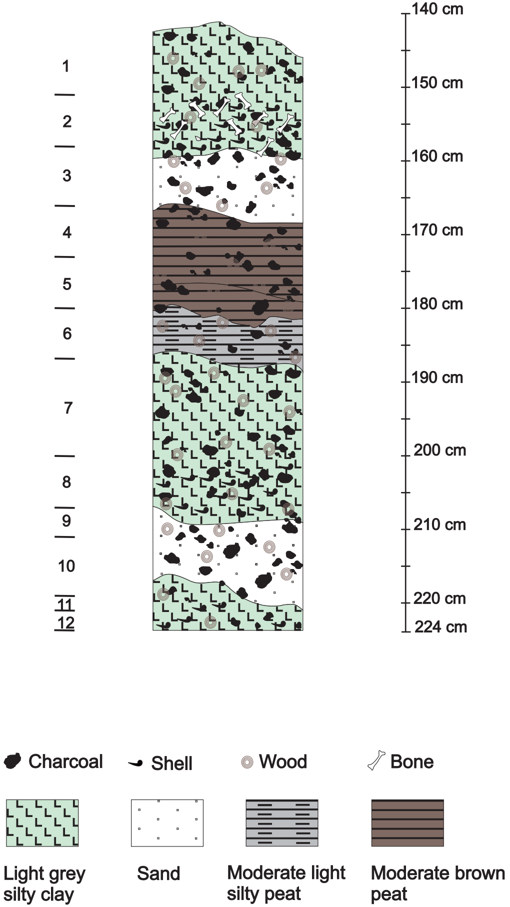
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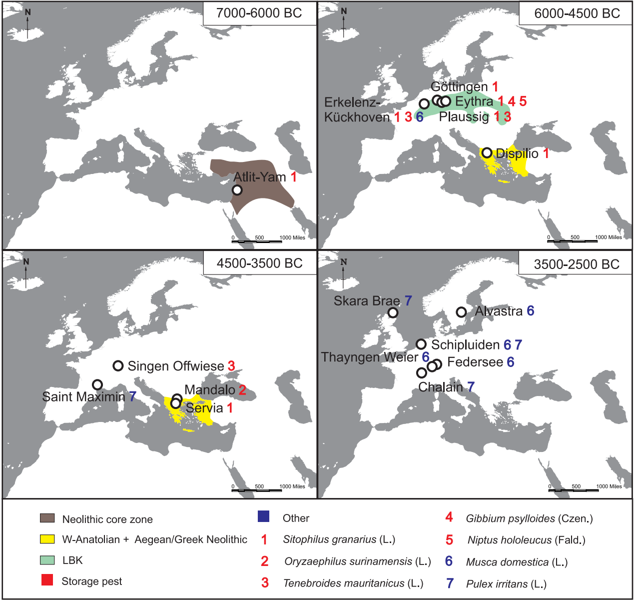
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Neolithic core zone
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LBK
Storage pest
Other
1 Sitophilus granarius (L.)
2 Oryzaephilus surinamensis (L.)
3 Tenebroides mauritanicus (L.)
4 Gibbium psylloides (Czen.)
5 Niptus hololeucus (Fald.)
6 Musca domestica (L.)
7 Pulex irritans (L.)

Site	Geographic Area	Species	Chronology	Period	Reference
Atlit-Yam	Israel	*Sitophilus granarius* (L.)	ca. 8250 cal BP (ca. 6200 cal BC)	Pre Pottery Neolithic C (PPNC)	Kislev et al. 2004
Dispilio	Greece	*Sitophilus granarius* (L.)	ca. 5700 cal BC	Aegean Middle Neolithic	Panagiotakopulu ibid
Plaussig	Germany	*Sitophilus granarius* (L.)	7219 cal BP (ca. 5250 cal BC)	Linear Band Keramik (LBK)	Schmidt 2013
Eythra	Germany	*Sitophilus granarius* (L.)	7034 cal BP, 7269 BP-7180 cal BP (ca. 5250 cal BC)	LBK	Schmidt 2010, 2013
Erkelenz-Kückhoven	Germany	*Sitophilus granarius* (L.)	5057 cal BC	LBK	Schmidt 1998, 2013
Göttingen	Germany	*Sitophilus granarius* (L.)	6030 BP (ca. 4935–4800 cal BC)	LBK	Büchner and Wolf 1997
Erkelenz-Kückhoven	Germany	*Musca domestica* L.	5057 BC	LBK	Schmidt 1998
Eythra, Germany	Germany	*Gibbium psylloides* (Czen.)	ca. 5250 cal BC	LBK	Schmidt 2013
Eythra, Germany	Germany	*Niptus hololeucus (*Fald.)	ca. 5250 cal BC	LBK	Schmidt 2013
Plaussig	Germany	*Tenebroides mauritanicus* (L.)	ca. 5250 cal BC	LBK	Schmidt in King et al 2014
Erkelenz-Kückhoven	Germany	*Tenebroides mauritanicus* (L.)	5057 cal BC	LBK	Schmidt 1998
Singen Offwiese	Germany	*Tenebroides mauritanicus* (L.)	4500-4000 cal BC	Grossgartach culture	Schmidt 2007, 2013
Servia	Greece	*Sitophilus granarius* (L.)	ca. 4500 - 4200 cal BC	Aegean Late Neolithic	Hubbard 1979
Mandalo	Greece	*Oryzaephilus surinamensis* (L.)	4450-4340 cal BC	Aegean Late Neolithic	Valamoti and Buckland 1995
Saint-Maximin-la-Sainte-Baume	France	*Pulex irritan*s L.	ca. 3600 BC	Late Neolithic	Remicourt et al. 2014
Schipluiden	Netherlands	*Pulex irritan*s L.	ca. 3500 cal BC	Late Neolithic	Hakbijl 2006
Chalain, Jura	France	*Pulex irritan*s L.	ca. 3200 - 2980 BC	Late Neolithic	Yvinec et al. 2000
Thayngen-Weier	Switzerland	*Musca domestica* L.	ca. 3500-3000 cal BC	Cortaillod culture	Troels Smith1984; Nielsen et al. 2000
Schipluiden	Netherlands	*Musca domestica* L.	ca. 3500 cal BC	Late Neolithic	Hakbijl 2006
Federsee	Germany	*Musca domestica* L.	ca. 3000 cal BC	Late Neolithic	Schmidt 2004

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