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The Baltic Crusades and ecological transformation: the zooarchaeology of conquest and cultural change in the Eastern Baltic in the second millennium AD

Article

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1. Introduction

From a long-term perspective, the Baltic Crusades left a far more profound legacy in north-eastern Europe, particularly in terms of cultural and ethnic transformations, than the more famous but ultimately less 'successful' crusades in the Levant (Tyerman 2007; Phillips 2009). The environment represents a fundamental and previously underappreciated lens on their long-term cultural impact, particularly the roles of regime change, urbanisation, rural colonisation and native resilience in ecological transformation. The Ecology of Crusading project (2010-2014, from here on TEC; Pluskowski 2018a, b) investigated this process using a multi-proxy, multi-scalar, inter-regional approach. One of the most abundant ecological datasets consisted of animal remains recovered from multi-period archaeological contexts (Reitz and Wing 2008), and TEC facilitated the analysis of substantial numbers of mammal, bird and fish bone fragments recovered from archaeological sites in Estonia, Latvia, north-east Poland and western Lithuania, encompassing the historical territories of Livonia and Prussia – the polities created by the Crusades. Animals were fundamental to all aspects of daily life, providing a range of primary and secondary products from food through to clothing and traction. Their selective exploitation also reflected the management of the landscape and essential provisioning networks, whilst the remains of wild species contribute to an understanding of changing levels of biodiversity. This study will therefore compare zooarchaeological trends before and after the Crusades in Livonia and Prussia to answer three key questions:

1. Were there changes in livestock husbandry following the Crusades?
2. What was the impact on biodiversity, as expressed in the exploitation of wild species?

3. How does the impact of the Baltic Crusades on fauna compare to other examples of conquest, regime change and colonisation?

Data includes material recovered from excavations directly linked to TEC, held in archives, in unpublished grey literature and published secondary literature. The results are being published as separate regional syntheses (Makowiecki *et al.* 2018; Maltby *et al.* 2018) and select case studies (Rannamäe and Lõugas 2018). Additional data has also been collected since the completion of TEC which are incorporated into this study, alongside datasets from Poland and western Russia. Previous synthetic studies of variable resolution have considered the zooarchaeological data for pre-crusade Estonia (Maldre 2012), medieval Livonia (Mugurēvičs 2002) and individual regions of northern Poland associated with the emergence and development of the Piast state (Makowiecki 2006, 2007). Paaver's (1965) much earlier seminal work spanned the entire Holocene and focused on wild mammals in the eastern Baltic. However, in terms of coverage this is, to date, the largest zooarchaeological study relating to the historical period in the eastern Baltic region and the first comparative study. It offers a model against which future data can be tested.

2. Regional setting

From the end of the 12th century the native societies of the eastern Baltic were targeted by a series of military campaigns from neighbouring Catholic states framed as crusades (penitential wars sanctioned by the papacy), with the aim of confronting the perceived threat of paganism and protecting Christian converts. Crusading would begin in earnest from the 1190s and by 1230 much of the territory corresponding to modern Latvia and Estonia had been conquered and a new polity created – Livonia. At this time crusades also began

targeting the southern Balts – the Prussians (Christiansen 1997; Urban 1994, 2003). Prussia, corresponding to modern north-east Poland, the Russian Kaliningrad Oblast and south-western Lithuania, was officially militarily subdued by 1283, although native resistance in southern Livonia would last until 1290 (figs. 1a-d).

The conquered territories were reorganised into polities ruled by militarised Christian theocracies consisting of the Teutonic Order, bishops and their cathedral chapters (Biskup et al. 2009; Czaja and Radzimiński 2013). In the process the eastern Baltic was incorporated into the political and religious spheres of Latin Europe. In the 14th century, the theocratic polities expanded. In 1309, the Order's Prussian branch annexed the neighbouring Catholic region of Pomerelia along with its regional centre Gdańsk following a destructive siege of the city in the previous winter. Northern Estonia remained under Danish royal control until it was sold to the Order in 1346, following an unsuccessful native rebellion in 1343. Throughout the 14th century, the Order, which promoted itself as the principal defender of Latin Christendom in north-eastern Europe (Selart 2015), waged a protracted war against the Grand Duchy of Lithuania and Samogitia, which had remained fiercely independent and pagan until the Grand Duke accepted Catholicism following a political union with Poland in 1385. This did not stop the conflict which continued into the first half of the 15th century. Secularisation of the Order's Prussian branch in 1525 and its Livonian branch in 1561 finally brought an end to almost three centuries of theocratic rule. From the perspective of European history, the so-called 'crusader states' of the eastern Baltic are virtually unique; composite societies where Central European colonists and native Baltic communities co-existed under theocratic regimes, although these became increasingly secular in character and outlook.

Despite the human cost of the Baltic Crusades, the population of Livonia and Prussia grew over the course of the 14th and 15th centuries, although its ethnic character transformed. In Livonia, where much of the native population remained intact, it is possible to speak of a composite society largely divided between German-speaking migrants and their descendants living in towns and making up the elite social class, and native people in the countryside (Šnē 2008, 2009a, b). In fact, both towns and castles represented meeting points between the contrasting cultures, accommodating German, native communities and other migrant groups, such as Russian merchants. In Prussia, the indigenous population had been affected more severely by the crusades and a sustained process of rural colonisation from neighbouring German and Polish regions resulted in the gradual Germanisation and Polonisation of the conquered territory. Population growth in both regions, alongside the reorganisation of territory as the new regime sought to mobilise local resources to sustain its political and military assets, would be expected to coincide with significant ecological transformations.

2.1. Conquest, regime change and colonisation

There have been several studies of the impact of conquest and regime change on animal exploitation, which provide useful analogues for contextualising the Baltic Crusades. The most pertinent are zooarchaeological trends associated with the expansion and contraction of the Roman Empire from the 2nd–5th century AD, the Norman Conquest of England in 1066 and the growth of Turku, an ecclesiastical and political centre founded in the wake of the so-called 'Second Swedish Crusade' in Finland in the 13th century. These analogues highlight the variable role of elites, migrants and natives in understanding trends in animal exploitation following military conquests.

The role of migrants is particularly visible with the expansion of the Roman Empire, whose emergence is associated with innovations in breeding livestock (MacKinnon 2017), with a subsequent correlation between the presence of colonists and an increase in the size of livestock in regions conquered by the Romans. In the case of Britain, the disappearance of larger animals and butchery practices by the 5th century reflects the shrinking of Roman political control, the collapse of the villa system and the transition from towns and market centres to small-scale settlements with a reduction in specialised husbandry (Rizzetto et al. 2017). At the same time there is evidence for continuity following regional conquests, as in the case of the dominance of cattle in the Netherlands, Belgium, Germany and Switzerland and no evident changes in husbandry regimes in Portugal, reflecting the Roman tendency to adopt and augment pre-existing production systems. In Britain, although cattle generally increased in importance, being particularly abundant on urban and military sites where the focus on provisioning these centres was paramount (Maltby 2016; 2017b), caprines continued to be well represented on many rural sites (King 1999; Allen 2017). There is also evidence for the cultural transmission of food and the dominance of socio-political factors in shaping trends over ecological variables (Valenzuela-Lamas and Albarella 2017: 405-406).

The role of new elites is particularly visible following the Norman Conquest of England, which was not accompanied by a substantial influx of migrants. Changes in the use of animals were closely tied to the expression of identity and articulation of power by the new regime, including the creation of a regulated hunting culture which preferred red deer over roe and prompted the gradual dissemination of exotics, particularly fallow deer and rabbits. This resulted in a 'sumptuary cuisine' that emphasised a north French diet, with a preference for pork that may have seen the introduction of a new fast maturing breed and the conspicuous consumption of diverse meats, including heron and peafowl. Continental

provisioning systems were introduced, facilitated by standardised, pre-butchered beef and mutton supplied from specialist urban butchers to the new elites, rather than sourced directly from the rural population. At the same time, the introduction of a coin-based taxation system appears to have prompted the rural peasantry to market their prime-aged animals and poultry to town markets, whilst focusing on the production of grain and wool. This probably accelerated a process that was already underway in the previous century where cattle and sheep were being kept to older ages to maximise traction, dung and wool yields, with little impact on the character of local stock. The fishing industry was well established by the Norman Conquest, with the only discernible impact on aquatic species reflected in the increased number of cetacean remains which formed part of the newly defined elite diet (Sykes 2007a, b).

The role of urbanisation, within a parallel process of conquest in the eastern Baltic zone, is visible in Turku. The incremental Swedish conquest of Finland saw the establishment of a new elite based in castles and towns in the 13th century, with an influx of migrants in the 14th century. In medieval and post-medieval Turku, cattle provided the main meat staple, with sheep supplying low grade wool for local markets, followed by pig and goat. This may have represented a shift from the earlier prevalence on caprines, although in the absence of data from rural sites this is difficult to verify. There is evidence for regional variability most likely reflecting a combination of husbandry traditions and ecological factors, nonetheless, the dominance of cattle has been linked to their importance for ploughing and dairy produce in southern Finland and the latter in northern Finland. Whilst cattle do not change in size from the medieval to post-medieval period, a decrease in sheep size has been interpreted as reflecting prioritising scarcer fodder for cattle, resulting in lower levels of nourishment for other stock. The horse stock appears comparable to the east Baltic zone, with height ranges of

120-130 cms into the 18th century. Horse consumption, although present in pre-crusade Finland, is completely absent from Turku. Domestic fowl dominates bird bone assemblages, with scant examples of ducks and geese. There is evidence for fishing and engagement with the stock fish trade, as well as exploitation of seals and seabirds from the nearby littoral. There is a general lack of evidence for fur working within Turku, and hunting appears to have been more important in the north, with roe deer imported to ecclesiastical sites established after the conquest as luxury food (Tourunen 2008).

3. Material and Methods

A total of 442,605 bone fragments from 232 assemblages, derived from 137 sites in the eastern Baltic, have been included in this study (fig. 1), although they are not evenly represented across both regions and include multiple assemblages from the same site or settlement complex (table 1).

Each assemblage is associated with a discrete phase of occupation within a delineated archaeological context, although very small assemblages from the same location have been merged. Sites are sub-divided into four categories linked to three consecutive time periods: pre-crusade (from the 10th-13th century, although some sites such as Beltes (Padure) include earlier occupation phases going back into the mid-Iron Age), medieval (14th-15th century) and post-medieval (16th-17th century, which in the case of Tallinn (Härjapea-Kivisilla) extends to the 18th century). Whilst acknowledging the complexity of individual site locations and histories, as well as the nuances and variable resolution of internal chronologies, for the purposes of contextualising the impact of the crusades and developing a model these categories are sufficient. Pre-crusade sites consist of strongholds and smaller settlements;

medieval and post-medieval sites consist of castles (largely the fortified convents and residences of the Teutonic Order) towns and rural settlements. Some sites assigned to the medieval temporal category had early phases that could be dated to the period of active crusading. These included the settlement at Biała Góra, Elbląg castle, the stronghold at Riekstu Hill in Cēsis, Vecdole castle and Mārtiņsala castle, which all had contexts dating to the 13th century. The earliest phases of the courtyard deposits in Karksi castle were dated to the second half of the 13th century, but active crusading had ceased in southern Estonia by this point and this marked a period of consolidation and the development of the conquering regime's infrastructure. Klaipėda town and castle have been included within Prussia since assemblages derive from the period of rule by the Order's Prussian branch, whilst Birutė Hill (Palanga) 20kms to the north, within Curonia, is included in pre-crusade Livonia. Modern names are used for all sites following standard archaeological conventions, except for references to places in written sources where their historical names are used followed by the modern equivalent.

The results for Livonia are based on 29 pre-Crusade assemblages, 26 medieval assemblages (including 5 from Viljandi representing 59% of the total mammalian data) and 8 post-medieval assemblages, the lowest in the entire study area with material from Tallinn representing 63% of the data. For Prussia, the results are based on 94 pre-crusade assemblages (including 18 from Gdańsk representing 35% of the total data), 46 medieval assemblages (including 18 from Gdańsk, representing 50% of the total data) and 30 post-medieval assemblages (including 12 from Gdańsk, representing 81% of the total data) (fig. 1). To ensure a more balanced comparison, data from Gdańsk and in some cases Viljandi and Tallinn has been treated separately where appropriate. The zooarchaeological data are complemented by written sources relating primarily to the Teutonic Order's castles and their

associated districts (*Ämter*). These have been unevenly preserved and largely derived from the later 14th–16th century in Prussia, whilst in Livonia they are extremely limited and fragmentary, largely from the 15th and 16th centuries.

3.1. Recording and Quantification

Only identifiable bone fragments from datable contexts have been included in this comparative study, although all unidentifiable fragments were recorded and grouped into size categories which reinforce the principal trends. Those materials not associated with a discrete chronological range (e.g. Turaida (Renga 1999), and earlier excavations at the castles in Cēsis (Mugurēvičs unpublished) and Ropaži (Maltby et al. 2018)) were also not included within this study. All remains from TEC-related excavations were recovered through hand collection, sieving and flotation, whilst recovery techniques for materials obtained from other sites were variable and most often involved only hand collection. For the purposes of this study, NISP (Number of Identified Specimens) has been used as the principal means of inter-site comparison, calculated as the sum of fragments for each species and then diachronically compared between sites (Reitz and Wing 2000, 191; O'Connor 2000, 54–68). NISP has been chosen over MNI as it represents the best means for large scale multi-site comparison (Sykes 2007a), although both methods have their drawbacks (Watson 1979; O'Connor 2000, 56; Lyman 2008;).

In merging the data from different contexts dated to the same chronological range, results are associated with the three cultural periods that serve to contextualise the impact of the crusades. What is then emphasised is the representation of different species in relation to each other, reflecting tendencies rather than comparable absolute values. Single assemblages,

particularly ones with small numbers of fragments, may not be representative of animal exploitation. However, it is possible to mitigate this problem to some extent with a comparison of material from a larger number of sites. The use of NISP also enabled bone fragments recorded by different groups of analysts, using slightly different systems, to be compared. Biometric data was derived from measurements of fused animal bone fragments mainly following von den Driesch (1976) for mammals and birds, and Morales and Rosenlund (1979) for fish. General data for fish was taken from Fishbase (Froese and Pauly 2006). Animal bones were identified using the reference collections of institutions involved in TEC. Statistical tools were also used to understand the significance of trends in the recorded faunal assemblages (O'Connor 2003, 79; Cannon 2001; Simpson 1949).

4. Results

The results are sub-divided into domestic mammals, wild mammals, birds and fish (table 1). The focus of this article is on mammals which represent the most important and abundant category, consisting of 392,968 bone fragments. The significantly smaller quantities of birds and fish, which are affected much more by preservation conditions and recovery techniques, are included to provide a holistic model of faunal exploitation, whilst acknowledging the impact of the Baltic Crusades on fishing has been the focus of parallel isotopic studies (Orton et al. 2011, 2018). Statistical analyses (including percentage ratios) have excluded all those assemblages with less than 1000 fragments (12 from pre-crusade Livonia, 36 from pre-crusade Prussia (including 12 from Gdańsk), 12 from medieval Livonia (including 5 from Viljandi), 9 from medieval Prussia (including 4 from Gdańsk), 4 from post-medieval Livonia and 10 from post-medieval Prussia, (including 6 from Gdańsk) in order to prevent the overemphasis of rare species in small assemblages, and for the purposes of comparative

quantification sheep and goat values have been grouped together and collectively referred to as caprines. Given the size of the dataset, MDA (Multiple Discriminant Analysis) and a Kolmogorov-Smirnov test were used to test the robustness of the period and region assemblage groupings. The results indicated the data distribution was non-normal, predictably reflecting the variation evident in the periods, sites and regions (see supplementary data). However, Pre-crusade sites are statistically distinctive, although that distinction becomes significantly less visible in the medieval and post-medieval period assemblages. This reflects the relative diversity of site types across and variability within the post-crusade assemblages.

4.1. Domestic Mammals

A total of 106,988 remains of domestic mammals were recorded from sites within the historical bounds of Livonia, with 30,186 fragments from pre-crusade sites of which 88% derived from the three main livestock groups – cattle, pigs and caprines. This reinforces the trends highlighted by Paaver (1965) in his summary of faunal exploitation for nine Latvian sites from the 9th-13th centuries, where domestic species representation ranged from 72% (Tērvete and Asote) through to 95% (Aiskraykle), with an overall median of 91%. A total of 64,249 remains were recorded from medieval sites in Livonia, with the main species representing 96% of the total, whilst 12,553 remains from post-medieval sites represent the smallest period-based dataset in the study, with the principal domesticates accounting for 97% of the total (fig. 2). In the pre-crusade period cattle dominate overall (40%), followed closely by caprines (37%) and pigs (23%), with regional variations (cf. Maldre 2012). In the medieval period, the importance of native husbandry is emphasised by the continued representation of caprines on Livonian sites (28%), but the dominance of cattle (47%) can be

readily associated with the beef supply to castles and towns. When excluding the data from Viljandi, the trend is comparable (cattle 45%, pigs 28%, caprines 27%) and continues to be visible in the smaller dataset from the post-medieval period (cattle 59%, pigs 22%, caprines 18%).

A total of 281,641 remains of domestic mammals were recorded from sites within the historical bounds of Prussia. Of the 152,712 recorded from pre-crusade sites the majority (89%) derived from cattle, pig and caprines; 58,031 remains were recorded from medieval sites, with 96% dominated by the three main livestock species; 70,887 remains were recorded from post-medieval sites with a comparable emphasis of 97%. Their relative importance changes both spatially and temporally (fig. 2). In the pre-crusade period, cattle (45%) dominate over pig (38%) and caprines (17%), whilst in the medieval period, the dominance of cattle becomes more pronounced (53%), with pigs remaining a more important component (32%) than caprines (15%). The general trend continues into the post-medieval period (cattle 59%, pig 22%, caprines 18%). In all three periods Gdańsk follows these trends albeit with a slightly higher average value for caprines than pigs in the post-medieval period. When the Gdańsk assemblages are excluded, the general trends remain the same, but the proportions of pig rise (highest in the medieval period at 44%) reflecting the skewing influence of the city's beef provisioning. There is some regional variability in livestock preferences in both regions, particularly in the medieval period, whilst the general trends are most pronounced in urban contexts.

In Livonia, there is an emphasis on supplying largely cattle aged between 3-5 years to the new markets in the post-crusade period, with most pigs and caprines slaughtered within the first two years of their life. In terms of livestock size, there is little evidence for changes, with

withers heights for cattle remaining at 100-120 cms into the post-medieval period and pig sizes remaining within the pre-crusade domestic range. Whilst there is no evidence of general diachronic changes in the size of caprines, the larger size of sheep and goats in Riga compared to other contemporary Livonian sites may also reflect regional differences including feeding regimes (Maldre 2003: 166; Maltby et al. 2018; Rannamäe and Lõugas 2018). In Prussia on the other hand, there are more discernible changes in livestock. The pre-crusade mortality profiles for cattle, pigs and caprines indicate they were primarily reared for meat and fat, with dairy products as a likely by-product. In the post-crusade period, there is a clear emphasis on supplying older cattle for consumption with most animals aged two years or older and over 50% of caprines aged at least 18 months old when slaughtered. Whilst cattle are on average slightly smaller in the medieval (102-103 cms) than pre-crusade periods (104-105 cms), the range between the smallest and largest individuals increases, alongside bone shaft thickness values. A multi-modal distribution of characteristics suggests the presence of two sub-populations in the medieval period, interpreted as the continuity of native stock and the introduction of new animals and/or the improvement of existing stock. In the post-medieval period with data derived largely from Gdańsk, the average height of cattle increases by c. 6 cm. Average sheep size increases from the pre-crusade to medieval periods, but then decreases in the post-medieval period. The average size of pigs gradually increases between the three periods, with an absence of large individuals from the medieval period corresponding to earlier wild boar (Makowiecki et al. 2018) (fig. 3).

Horses are well represented in the pre-crusade assemblages in both Livonia (8.5% of all mammals) and Prussia (3.2%; excluding Gdańsk 3.7%), after which the numbers drop to just over 1% in the medieval period and then just below in the post-medieval. This reflects changes in the role – and therefore depositional contexts – of the horse, rather than relative

abundance of the equine population. Horse meat was widely consumed in the pre-crusade period, particularly in Livonia, whilst whole individuals and disarticulated parts were also deposited within cemeteries in parts of Prussia, Lithuania and southern Livonia (Bliujienė 2009; Shiroukhov 2012; Bliujienė et al. 2017; Lang 2017). This study has only compared horses in assemblages from settlement sites. After the Crusades, the cultic role of the horse was suppressed by the theocracy, which instead promoted the intensive breeding of horses for diverse roles, including as military and pack animals. This appears to have drawn predominantly on native stock with a small number of larger, imported individuals (noted for example in Greater Poland and Lower Silesia), reflected within the Livonian height range for adults of 107-149 cms, and the Prussian range of 101-150 cms, with the largest horses in the latter population (above 147 cms) appearing in very small quantities only from the medieval period (fig. 4).

A comparable native range is also evident in neighbouring Lithuania, which would have contributed to the Order's stock procured during raids (Maltby et al. 2018). Here, the native equine population is best represented at the cemeteries of Marvelė and Veršvai with a height range of 120-136 cm, although some larger individuals (with estimated heights of 136-144 and 153 cm) may not have belonged to local breeds (Bertašius, Daugnora 2001). Whilst Ekhdal (1998) has estimated from written sources that the Order's Prussian estates contained around 16,000 horses at the start of the 15th century, the horse remains from archaeological contexts generally represent the disarticulated and discarded carcasses of retired animals. There are also rare examples of horses buried *in situ* in battlefield contexts (e.g. Grunwald; Wolski, 2008: 75, 79-81) and within destroyed buildings (e.g. at Cēsis castle; Maltby et al. 2018; Pluskowski et al. 2018). In total these represent a fraction of the documented equine population, but they do provide vital data on the relative stature of animals across the study

area. There is some evidence for the continued consumption of horse meat by indigenous communities and in extreme conditions of starvation. It is probable that larger quantities of horses are to be found on post-crusade rural settlements, which are underrepresented across the eastern Baltic.

Stable isotope studies were also conducted on the remains of the four principal domesticates from Prussia, with the aim of investigating whether there were shifts in feeding regimes following the reorganisation of land use after the conquests. Osteometric analysis of faunal remains from sites in the Kulmerland suggested the maintenance of existing husbandry regimes and potentially the introduction of new stock by incoming colonists. A diachronic shift in $\delta^{15}N$ values between early and later medieval samples was also particularly noticeable in caprines and pigs, suggesting the management of animals on more intensively cultivated land, with possibly higher stocking rates, and in the case of pigs, evidence of increased rearing on animal products, probably in urban environments. At the same time there is evidence for continuity, in isotopic terms, between the early and the later medieval period corresponding to osteological observations. The management of most horses continued unchanged, although some individuals appear to have been given special treatment in this region (Scull et al. 2018) as well as central Livonia (Pluskowski et al. 2018). This corresponds to written data for the treatment of breeding animals and warhorses (Ekhdal 1998).

4.2. Wild Mammals

Wild mammals represent a small proportion of faunal remains from all categories of sites in both Prussia and Livonia across all the time periods. However, there is a shift in terms of

their relative representation from the pre-crusade to medieval period in both regions. In Livonia, 10,974 wild mammal bones were recorded, representing 10% of remains from the pre-crusade period (with a site average of 10.8%), dropping to 1.2% in the medieval period (with a site average of 1.4%) and 1.5% in the post-medieval period (with a site average of 2.3%, skewed by Viljandi). The latter clearly does not quantitively reflect either the availability of wild mammals in the landscapes of Livonia, nor hunting practices, which are otherwise attested in written sources. Significant biogeographical changes occur in Livonia in the 17th-19th centuries, particularly regarding large carnivores and wild ungulates, but also including the proliferation of the European hare in Estonia (Mugurēvičs 2002). In Prussia, 13,163 wild mammal bones were included in the study, representing 7.5% of the total assemblage from the pre-crusade (with a site average of 7%); 2% from the medieval (with a site average of 2.5%) and less than 1% from the post-medieval (with a site average of 1.3%).

When key terrestrial species were sub-divided into those primarily exploited for meat and those for fur (excluding beavers which were commonly exploited for both), the former category clearly dominates and is overwhelmingly represented by wild ungulates, with 93% of remains from pre-crusade sites (particularly red deer, roe deer, wild boar and elk), 91% from medieval sites (particularly roe deer, red deer and wild boar) and 97% from post-medieval sites (particularly roe deer, red deer and wild boar) (fig. 5).

The relatively low quantity of fur-bearing mammals in both regions is not surprising and does not reflect their role in the fur trade that had developed already in the pre-crusade period, as their pelts would have been processed on rural sites and outposts that are poorly represented archaeologically (Maltby 2017a, 2018). Fur preparation in urban centres tended to involve working pelts more likely to result in leather offcuts and fibres, rarely encountered due to

preservation and recovery techniques (e.g. Rębkowski 2006). Hunting played a consistent role at high-status sites (strongholds, castles) in all three periods, but game only contributed a small proportion of the total nutrition derived from meat, as elsewhere in Europe (e.g. Ervynck 1992, 2004; Sykes 2007a; Pluskowski 2010), with leather, antler and horn (the latter from bison and auroch) opportunistically utilised. Nonetheless, the long-term effects of hunting pressure are most likely indicated in the decrease in wild boar size in Prussia from the pre-crusade to post-medieval periods (fig. 3c).

There is limited evidence for the exploitation of marine mammals. In Livonia, ringed seal and grey seal were consumed by communities with direct access to littoral waters in all three periods and transported in small quantities inland to sites such as Lõhavere (Lõugas 1997; Russow et al. 2013). There is also some evidence for porpoise consumption, which along with the seal functioned as an appropriate high-status (and fasting) food (Mänd 2016: 14). In the Order's Prussian territories, the evidence is more limited. In Gdańsk, a very small assemblage of bones from seal and harbour porpoise from all three periods (only porpoise in the post-medieval) points to similar high-status roles assigned to these species within the urban context, and it is likely they were exploited by communities with access to the southern Baltic littoral. In Klaipėda castle, there is also fragmentary evidence for the exploitation of porpoise in the 16th century.

Principal Component Analysis (PCA) was conducted on fragment counts of assemblages with NISP>1000 to highlight correlates of domestic and wild mammal representation in relation to categories of site, sub-divided by region / period and illustrating the structure of species variability (figs. 6a-c). Wild mammals, which consistently represent small proportions of assemblages, have been grouped together. The results clearly illustrate the

relationship between the distinctive components and periods, which are comparable in both regions. Outliers can be related to the composition of specific assemblages. In the pre-crusade period (fig. 6a), there is a pronounced emphasis on horses and wild mammals, with the stronghold at Kałdus as the major outlier. This can be related to a particularly rich assemblage linked to the high-status community in this regional power centre in the Prussian-Polish borderland. Outliers weighted towards cats are from the settlement at Kałdus and the stronghold in Gdańsk, reflecting the high representation of the species in these regional centres with the deposition of their remains partly connected with skinning activities also seen on other early medieval north European proto-urban sites. In the medieval and post-medieval periods, there is a notable shift towards livestock and cats are especially emphasised. This can be interpreted as signalling the importance of urban assemblages, particularly in the outliers. The shift away from wild mammals corresponds to a decline in the diversity of assemblages, signalling the end of the intensive hunting practices of the pre-crusade period (see below). Throughout there is a stronger emphasis on pigs in Prussia than Livonia, reflecting the continued importance of pig rearing in the former Polish-Prussian borderlands which were incorporated into the Teutonic Order's territories.

4.3. Birds

A total of 5538 bird bone fragments were recorded from Livonian sites, the majority of which (76%) derived from medieval contexts. From Prussian sites, 3302 bird bone fragments were recorded, with the majority (74%) derived from pre-crusade assemblages. In assemblages from both regions at least 50-80% of bird remains derived from domestic fowl, followed by geese (both domestic and wild) and wild ducks with only a dozen other species represented. This trend has also been observed in previous studies of Gdańsk and other Baltic coastal

centres (Makowiecki and Gotfredsen 2002); in pre-crusade Gdańsk domestic fowl make up 78% of all bird remains, and continue to dominate in the medieval period. The representation of wild species tends to reflect access to specific habitats, such as the lakes favoured by geese and ducks, and woodlands preferred by capercaillie and black grouse. Other wild species, largely passerines alongside occasional raptors and seabirds, are comparatively rare making up less than 1% of individual bird assemblages in all periods. Falconry is evident in Poland from at least the 10th century (Sielicki 2009: 46-50; Makowiecki et al. 2014) and may have been introduced into the eastern Baltic through Scandinavian contacts; goshawk remains have been found at the hillfort in Asote (Latvia) in 10th-13th century layers (Mugurēvičs 1997: 153; Girininkas, Daugnora in press). There is also archaeological evidence for one imported species, peafowl which is present in the centres of the Piast state from the 11th century and is then subsequently found on the Order's Prussian sites (Makowiecki et al. 2018).

4.4. Fish

In Livonia, the quantities of identifiable fish bone fragments are quite limited due to a lack of routine sieving on sites, and consisted of 3592 fragments from pre-crusade sites, 2754 from medieval sites and 737 from post-medieval sites. In Prussia, 23,493 fish bones were recorded from pre-crusade sites, with 10,178 from post-crusade sites. These include a sample of the largest assemblage recovered to date from east Prussia, from the site of Święta Góra (Staświny Site 1), as well as the complex of sites from Gdańsk, reflecting the recovery techniques used during the excavations which included sieving and flotation. Regional trends in fish consumption in the eastern Baltic on either side of the crusading period can be related to local availability and the development of markets and provisioning / trade networks. In the pre-crusade period, migratory sturgeon is the most important species at sites with direct

access to the Gulf of Gdańsk, with marine species dominated by cod and freshwater by cyprinids. On the western side of the Lower Vistula, the most important species was cod, while on the eastern side cyprinids and catfish dominate. Sites in the Kulmerland are dominated by cyprinids and pike, alongside large numbers of cod, sturgeon and catfish. In western (coastal) Prussia sturgeon dominates, whilst the interior of eastern Prussia is exclusively represented by cyprinids. The distribution of cod and herring away from coastal areas, as imported stockfish, as well as migrating sturgeon, can be linked to access to the Vistula which connected the centres of the Piast state (Makowiecki et al. 2018). In Livonia, whilst the sample size is significantly smaller, the regional pattern is comparable with a reliance on freshwater species, particularly pike, perch and cyprinids and an absence of marine species from interior pre-crusade sites. Urban and castle sites in the medieval and post-medieval periods have marine species and the presence of small numbers of cod and herring in urban contexts in Tartu and Valmiera indicate the trade in marine fish extended inland during this period (Lõugas 2001, 2016), with a larger representation in towns with access to littoral waters such as Riga, Ventspils, Pärnu and Tallinn (Russow et al. 2013: 162).

These trends were accentuated in the post-crusade period. Given the theocracy's emphasis on fasting culture, fish represented an important food item for high-status communities, as well as the growing urban centres. Once again, the distribution of species reflects local availability and access to networks, the main difference being a thickening of trading networks associated with the formation of the Christian polities in the eastern Baltic and the Hanse. Written sources also indicate the Teutonic Order sought to regulate and control access to fish as a valuable resource (Maltby et al. 2018; Makowiecki et al. 2018). As a result, locally caught cyprinids dominate virtually all assemblages, with sturgeon continuing to be represented on sites with access to the Baltic littoral, the Lower Vistula and Daugava. Imported marine

species, dominated by small numbers of cod and herring, are found on coastal sites and those connected with the post-crusade trade network. Whilst they are absent from the east Prussian interior, they occur as occasional imports on some high-status and urban inland sites in Livonia, such as in the later phases of Karksi castle, the town of Viljandi and Āraiši castle. An extensive isotopic study of cod bone samples from across the case study regions indicated a diachronic shift in source, from Arctic Scandinavian waters in the pre-crusade period to local Baltic waters from the 14th century (Barrett et al. 2008; 2011; Orton et al. 2011; 2018). However, this locally caught cod was initially confined to high-status sites (Ventspils is exceptional but had direct access to the littoral), and from the 15th century it begins to be found in urban contexts. The proliferation of cod, as stockfish and local catches, may reflect the dissemination of a new cuisine by German migrants, whilst carp only appears in Prussia after the crusading period and its dissemination can be linked to the Teutonic Order and monastic institutions which were its initial consumers (Makowiecki 2001).

5. Discussion

A comparison of the zooarchaeological data from Livonia and Prussia indicates comparable exploitation strategies following the conquests, with variability expressing localised social and ecological differences, within and across both regions. Key themes that emerge are husbandry continuities and improvements, changes in biodiversity and the emergence of a fishing industry.

5.1. Were there changes in livestock husbandry following the Crusades?

Previous studies have consistently highlighted the importance of stock raising in the eastern Baltic from later prehistory. O'Connor's (2010) inter-regional synthesis of northern Europe drew attention to a general Baltic preference for pig-rearing in the early medieval (i.e. pre-crusade) period, whilst more detailed studies in Estonia (Maldre 2012) and Poland (Makowiecki 2006, 2007) have highlighted degrees of local variability. O'Connor linked this prevalence of pigs to comparatively less grazing and arable land, with wood pannage as an alternative strategy. As the results above indicate, the picture is more complex and whilst pigs dominate slightly over cattle in Prussia, except for centres such as Gdańsk already reliant on beef for their principal source of meat, cattle, sheep and goats are more prevalent in Livonia with pigs playing a tertiary role. At the same time, there is regional variability. In pre-crusade Prussia, 56% of sites follow the dominant trend, skewed by the large number of sites in the Kulmerland, whilst within Gdańsk 42% of sites are dominated by pig, reflecting access to enduring stretches of woodland with the centre's hinterland even as the landscape was becoming more open. In Livonia, all sites conform to the general trend except for Lõhavere hillfort where pigs dominate, and at Āraiši lake settlement where they play a secondary role after cattle.

In the eastern Baltic, the zooarchaeological trends following the crusades are directly related to three factors: continuity in the involvement of the existing population in stock rearing, the presence of migrants in rural areas and towns as new consumers. It is important to note that agricultural intensification is not solely associated with the latter, as evidence from Livonia indicates this already took place before the crusades in some regions and in the case of southern Livonia during the late medieval period corresponding to population growth rather than external colonisation (Brown 2018a). At the same time, in east Prussia, agricultural intensification coincides with increased colonisation (Brown 2018b). However, in the

medieval period in both regions, cattle provided the main supply of meat for urban centres and castles. There is more variability between regions than categories of site, reflecting differences in land use and continuities in husbandry regimes, such as the emphasis on pigs in the Kulmerland on either side of the crusading period and the secondary place of caprines in Livonia. In general terms this coincides with an increase in cultivation and deforestation, although this varied across the eastern Baltic.

There is no evidence for general changes in the size of livestock in Livonia following the crusades and sporadic, tentative examples of imports. This implies that local stock was maintained and whilst herd size invariably increased, there were no attempts at improving animals for higher meat, wool or dairy yields. aDNA studies of sheep in Estonia have reinforced the notion of stock continuity until the 19th century when there is evidence for genetic divergence. However, the studies also confirmed the expansion of the sheep population in the centuries after the crusades (Rannamäe et al. 2016), and the numerical prevalence of caprines is evident in assemblages (fig. 2). In Prussia, the situation is slightly different and can be related to the influx of migrants into rural areas who either brought larger stock and/or, with improved fodder were able to breed larger individuals (fig. 3). The connection between cattle, ploughing and expanding the area under cultivation may also suggest why the new regime was most successful at maximising yields in regions with Christian Slavic and German subjects, in contrast to Balt and Finno-Ugrian communities. Increases in size are evident in sheep in regions which experienced intensive colonisation such as the Kulmerland, and this correlates with the emergence of a local wool industry providing relatively cheap, low-quality products. The post-medieval decrease in size may reflect a shift in husbandry priorities, whilst the increase in Gdańsk cattle may reflect improved grazing in the Vistula Fens. It is also important to note that new butchery

technology, particularly the use of cleavers and standardised cuts, is a post-crusade introduction that is most visible in sites associated with the new regime and is only adopted by the native population much later, although large, heavy blades are used to a small degree in some of the pre-crusade centres of the Piast state (Seetah et al. 2013). The difference between Livonia and Prussia can therefore be related to diverging histories of migration following the crusades, particularly in rural Prussia and the dominance of indigenous husbandry regimes, particularly in rural Livonia.

The horse is a special case as it was widely bred by the Teutonic Order as both a pack animal and for heavy cavalry. The zooarchaeological data confirms that the equestrian culture in medieval Prussia and Livonia was similar, with the bulk of the population consisting of small, pony-sized animals comparable to pre-crusade individuals, and a comparatively small number consisting of larger stallions used as cavalry (fig. 4). Written evidence indicates that the Order's convents played an important role in the management of horse stock (Ekdahl 1991, 1998).

5.2. What was the impact on biodiversity, as expressed in the exploitation of wild species?

Assessing the impact of the Baltic Crusades on biodiversity is not straightforward, requiring the use of several proxies. The noted decline in the representation of both the quantity and range of wild species from pre-crusade to medieval assemblages, also highlighted by the MDA (figs. 6a-c), can be scrutinised further in two ways; using a species diversity index and linking groups of species with shared habitat preferences. Calculating changes in species diversity over time using Simpson's (1949) index, an overall decrease can be noted from the pre-crusade to medieval period in both Livonia and Prussia, evident in both assemblages with

>1000 NISP (fig. 7a) and the broader dataset of assemblages with >100 NISP (fig. 7b). When applied to zooarchaeological data, the index is not a direct reflection of biodiversity in the surrounding landscape, but rather a measure of human exploitation which can be related to a combination of choice (including socio-economic access) and availability. Moreover, taxonomic abundance is also a function of assemblage size, with rarer species more likely to be represented in larger samples of bone. These values therefore need to be compared with other categories of data, including palynological reconstructions of habitats within the associated landscapes (Brown 2018a, b; Stančikaitė et al. 2009).

The relative shifts in diversity are most clearly visible where assemblages from the same site or cluster of sites can be compared, although in Gniew, Jedwabno and Pień there is a slight increase in diversity in the medieval period, and in Toruń (site 15) in the post-medieval period. The largest assemblage from the cluster of sites in Gdańsk indicated a general decrease in diversity values from the pre-crusade to post medieval periods, but where data was available from multi-period sites there were examples of increasing diversity in Site 2 from the pre-crusade to medieval period and at ul. Młynska 21 and the Granary Island from the medieval to post-medieval period. Palynological data does indicate significant deforestation in the pre-crusade period within the hinterland of Gdańsk, but substantial tracts of woodland and wetlands endured into the post-medieval period, providing suitable habitats for a range of wild ungulates (Latałowa et al. 2009; Brown 2018b). The localised fluctuations in diversity provide insights into the socio-topography of the town with households' varying access to wild species. In the case of the frontier castle of Ełk, with access to wild resources in the 'Great Wilderness' attested by written and palynological data from eastern Prussia showing a limited impact on the environment until after the 16th century, the low diversity index reflects a reliance on livestock rather than game. Inventoried game along with the

procurator's list of pelt values from Lötzen (Pol. Giżycko), 45 kilometres to the north-east, indicates the presence of a diverse range of wild mammal species within the castle's district in the 15th century (Jarzebowski et al. 2018), confirming the high biodiversity within the Masurian Lake District.

Shifts in groups of wild species hunted primarily for their meat (and thus removing the representational problem of fur-bearers) with shared habitat preferences also contributes to an understanding of changing biodiversity. The first group consists of wild ungulates which prefer denser woodlands, namely red deer, wild boar, bison and aurochsen, to which capercaillie and black grouse can also be added. The second group consists of roe deer and hare, which prefer more open, fragmented landscapes. Changes in both groups correspond to habitat changes visible in palynological data and written sources. In all three periods, both groups occur together, whilst their relative prevalence increases in the post-crusade periods. In Livonia, acknowledging the sample is skewed by Viljandi, the quantity of hare increases from 5% of the wild mammal total to 47% in the medieval and 65% in the post medieval period, echoed by trends in roe deer from 1.4% in the pre-crusade to 2.5% in the medieval. In Prussia, 4% hare and 1.5% roe deer in the pre-crusade period shifts to 7% hare and 36% roe deer in the medieval, increasing to 25% hare and 40% roe deer in the post-medieval. This changing prevalence coincides with increased deforestation and habitat fragmentation within the associated territories.

However, there is evidence for regional variability reflecting the enduring presence of woodland. In Prussia, this is particularly marked in the broad frontier region with the Grand Duchy of Lithuania, the southern belt of the 'Great Wilderness'. Comparatively high diversity is also evident in the faunal assemblage recovered from the castle at Klaipėda which

has been linked to the castle's territory representing a frontier landscape (Žulkus and Daugnora 2010). Here, remains of auroch or bison have been found in 16th century contexts, whilst the last documented presence of aurochsen is near Augustów in the 17th century (Bocherens et al. 2015). Both areas lie within the eastern Prussian frontier zone where the mosaic of wetlands and woods has traditionally limited significant settlement growth and communications; Schrötter's maps of east Prussia and Colberg's map of the Augustów voivodeship indicate the persistence of substantial albeit heavily fragmented corridors of woodland in this region by the early 19th century. In Livonia, biodiversity broadly increases towards the south, with an absence of wild red deer and aurochsen in Estonia by the crusading period (Paaver 1965: 235-242). No data was available from the southern Livonian borderland with Samogitia and Lithuania, but it is expected that levels of biodiversity were high in this largely depopulated region, comparable to the eastern Prussian frontier. It is therefore possible to conclude that the process of reduction in biodiversity in Livonia had already begun in the Iron Age, during the so-called 'stronghold period' of population expansion and the emergence of an elite hunting culture. This is also evident in neighbouring Lithuania, where during the period of state formation wild species make up 10-15% of settlement assemblages, and as much as 25% from hillforts reflecting the development of an aristocratic hunting culture and regulated fur exploitation (Girininkas and Daugnora 2013: 579).

5.2.2. The Emergence of a Fishing Industry

The combined osteological and isotopic data, alongside written sources, point to the development of a local fishing industry following the crusades. The proliferation of cod, herring and later, varieties of carp, can be attributed to the cultural and commercial changes

which sees the rise of the Hanse, the merchant confederation that is arguably stimulated by the Baltic Crusades. Aquaculture involving the breeding of cyprinids (mainly common carp) is also associated with religious institutions at this time (including monasteries and the houses of the Teutonic Order), although the extant evidence is tentative and largely derived from post-medieval sources (Bonow et al. 2016). The main function of fish ponds was the provision of fresh fish as a luxury food for these high-status communities, rather than intensive farming serving a broader market.

5.3. How does the impact of the Baltic Crusades compare to other examples of conquest, regime change and colonisation?

The Teutonic Order's officials were overly concerned with the management of natural resources which fundamentally underpinned their sovereignty and security. This is exemplified by the meticulous granting of access to animals, plants, water and land in the charters or *Handfesten* that structured settlements and defined power relations within the conquered territories. Given the apparent micromanagement of the landscape and provisioning systems within the theocracy's territories after the crusades, it is interesting to note that trends in faunal exploitation are broadly comparable to other examples of regime change (see section 2.1). Within a hierarchical political and trading structure that spanned the theocracy's lands, strategies of exploitation became tailored to local contexts, and intensification seems to have been pronounced in areas which experienced a significant influx of migrants, combined with changes in types of fodder. Here there is evidence for slight changes in livestock size which may reflect 'improvements', comparable to the impact of Roman migrants. However, in contrast to the introduction of a Roman economic system in Britain that endured only for as long as the Roman administration itself, the appropriation and

reorganisation of existing economic systems following the Baltic Crusades persisted into the post-medieval period. The emphasis on grain production and urban provisioning ensured the primacy of cattle rearing, already prevalent in neighbouring urbanised regions. This draws attention to the priorities of the Teutonic Order, which did not involve direct intervention in animal husbandry regimes. Instead, its officials focused on maximising the production of grain, more so in Prussia than Livonia over the course of the 14th century. The Finnish trends are also comparable, and there is a tentative correlation between sites dominated by Swedish migrants and different types of livestock. Interestingly, the decrease in sheep size from the medieval to post-medieval periods in Prussia may also have occurred in the context of prioritising cattle (Makowiecki et al. 2018). The presence of specialised butchers replicating standardised cuts with cleavers also resonates with both Roman and Norman cultures. Where the native population remained largely intact there is evident continuity in husbandry.

The introduction of a new elite stratum in the eastern Baltic faintly echoes the more expressive Norman cultural package visible in England after the Conquest, but whilst the theocracy recruited from the aristocratic class, its members were obliged to subscribe to a corporate code of behaviour rooted in a monastic paradigm. Conspicuous consumption was reflected in access to high quality food, imported luxuries, the limited use of fishponds, the grandmaster's park at Stuhm and the use of exotics and rarities in gift exchange. Over time, the upper echelons of the Baltic theocracy increasingly adopted the trappings of secular authority. The differences are even more striking when comparing the theocracy with contemporary sites of the Lithuanian grand dukes and nobility, where wild mammals make up a substantially higher percentage of faunal assemblages into the 16th century, with a highly stratified hunting culture attested in written sources (Girininkas and Daugnora 2013: 580). In summary, the trends in faunal exploitation following the Baltic Crusades are comparable to

other examples of conquest and regime change, articulated through the variables of the elite class, migrants and native communities.

6. Conclusions

The trends outlined in the largest inter-regional zooarchaeological study in north-eastern Europe contribute a new understanding to the cultural transformations resulting from the conquest of the eastern Baltic region and the reorganisation of native territories into Christian theocratic polities. The Baltic Crusades resulted in dramatic and complex cultural changes which would be expected to have a strong resonance in the use of animals for primary and secondary products. The management of the landscape was re-organised, new markets emerged and connected with newly created hinterlands and provisioning networks, particularly towns and the houses of the ruling theocracy, a monetised economy developed, and the population grew, partly due to an influx of migrants into towns and, in Prussia, into the countryside. Noticeable changes can be related to the behaviour of the elite class that made up the new regime, with political and economic restructuring accentuating earlier trends in husbandry and provisioning, alongside the presence of migrants who introduce new stock, agrarian practices and technologies. The role of the horse changed with the abandonment of its use in public funerary rituals, but local stock continued to be used alongside a small percentage of larger animals bred for military purposes. A local fishing industry developed after the crusades, stimulated by new markets, although fishing remained under the Teutonic Order's control. There was a gradual, overall decline in diversity, but wild species remained available and perhaps even abundant in the denser woods and wetlands of east Prussia and Livonia. These trends reflect the nature of the relationships between the incoming and native populations in the eastern Baltic, providing a vital window on adaptation

and resilience in the context of conquest and multicultural encounters. Future data ought to reinforce the general trends highlighted in this study, but will also demonstrate local variability which characterises the composite societies of medieval Livonia and Prussia.

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Datasets related to this article can be found at https://figshare.com/s/3743c9aa37a894a402f3.

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Figures

Figure 1a: Map showing sites referred to in this study in the eastern Baltic region in the current geopolitical situation.

Figure 1b: Map showing sites referred to in this study in Estonian counties, Latvian and Lithuanian provinces.

Figure 1c: Map showing sites referred to in this study in Polish provinces (font sizes differ for readability).

Figure 1d: Map showing the territorial boundaries of Prussia from c. 1400 (aft. Biskup et al. 2009, with the Kulmerland aft. Poliński 2003, map 2), and Livonia c. 1450 (aft. Benninghoven 1963), including the outline of the Danish Duchy of Estonia which was created during the crusading period and sold to the Teutonic Order in 1346.

Figure 2: The diachronic representation of cattle, pigs and caprines in Livonia and Prussia, shown as relative %, calculated from an average of the %ages from different sites (NISP >1000; values in Table 1).

Figure 3a: Diachronic changes in the estimated withers height ranges of cattle (Pre-Crusade: N=93 Medieval: N=156 Post-Medieval: N=332).

Figure 3b: Diachronic changes in the estimated withers height ranges of caprines (Pre-Crusade: N=35 Medieval: N=72 Post-Medieval: N=135).

Figure 3c: Diachronic changes in the estimated withers height ranges of pigs (Pre-Crusade: N=185 Medieval: N=103 Post-Medieval: N=86) and wild boar (darker boxes) (Pre-Crusade: N=272 Medieval: N=112 Post-Medieval: N=87) in Prussia. For further details see Makowiecki et al. 2018.

Figure 4: Estimated horse withers height ranges and outliers in the Baltic crusader states, sub-divided into the Slavic Pre-Crusade Kulmerland (N=98), Pre-Crusade Prussia (N=73), Pre-Crusade Estonia (N=13), Medieval Prussia (N=19), Medieval Estonia (N=24), Medieval Latvia (N=13), Post-Crusade Prussia (N=51) And Post-Medieval Estonia (N=4). Estimates based on May's (1985) corrected factors of Kiesewalter and Vitt (aft. Johnstone 2004, 156).

Figure 5: The diachronic representation of terrestrial wild mammals in Livonia and Prussia, sub-divided into those primarily exploited for meat and those for fur, with beavers (exploited for both) included as a separate category. Calculated from an average of the %ages from different sites.

Figure 6: Principal Component Analysis (PCA) of the data represented as loading plots, sub-divided by region and phase. The markers represent individual sites in relation to the loading plots. A: Pre-Crusade Period; B: Medieval Period; C: Post-Medieval Period.

Figure 7: Relative changes in mammal species diversity from the pre-crusade to post-medieval periods in Livonia and Prussia, calculated using Simpson's (1949) index from assemblages >1000 NISP (a) and >100 NISP (b) (values in Table 1). The diversity values are represented as ranges for each period and region, with average and median values indicated. Higher values indicate a greater diversity of species represented within assemblages. In the case of Gniew and Staświny (Prussia), assemblages from the same locality but derived from different sites have been compared. In the case of Gdańsk with multiple phases from individual sites, the final phase has been used.

Table 1 (dataset stored on figshare): NISP values used in this study, with sites sub-divided between regions and time periods of analysis: pre-crusade Livonia (a), Prussia (b), medieval Livonia (c), Prussia (d), post-medieval Livonia (e) and Prussia (f), birds (g) and fish (h). For comparative purposes, pre-crusade sites, which existed in a different geopolitical setting, are situated within the two post-crusade medieval territories. Please see Supplementary Table and References.