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Between the Danube and the Deep Blue Sea: Zooarchaeological Meta-Analysis Reveals Variability in the Spread and Development of Neolithic Farming across the Western Balkans

David Orton*, Jane Gaastra† and Marc Vander Linden†

The first spread of farming practices into Europe in the Neolithic period involves two distinct ‘streams’, respectively around the Mediterranean littoral and along the Danube corridor to central Europe. In this paper we explore variation in Neolithic animal use practices within and between these streams, focusing on the first region in which they are clearly distinct (and yet still in close proximity): the western Balkans. We employ rigorous and reproducible meta-analysis of all available zooarchaeological data from the region to test hypotheses (a) that each stream featured a coherent ‘package’ of herding and hunting practices in the earliest Neolithic, and (b) that these subsequently diverged in response to local conditions and changing cultural preferences.

The results partially uphold these hypotheses, while underlining that Neolithisation was a complex and varied process. A coherent, stable, caprine-based ‘package’ is seen in the coastal stream, albeit with some diversification linked to expansion northwards and inland. Accounting for a severe, systematic bias in bone recovery methodology between streams, we show that sheep and goats also played a major role across the continental stream in the earliest Neolithic (c.6100-5800 BC). This was followed by a geographically staggered transition over c.500 years to an economy focused on cattle, with significant levels of hunting in some areas – a pattern we interpret in terms of gradual adaptation to local conditions, perhaps mediated by varying degrees of cultural conservatism. Subsequent westward expansion carried with it elements of this new pattern, which persisted through the middle and late Neolithic.

Keywords: Neolithic; zooarchaeology; meta-analysis; western Balkans; neolithisation

Introduction

The spread of Neolithic farming practices across Europe from Anatolia and the eastern Mediterranean during the 7th to 5th millennia BC has long been understood to involve two ‘streams’: one westward around the Mediterranean littoral; the other north through the Balkans to the Pannonian Plain and on to central Europe following river corridors, principally the Danube (e.g. Bocquet-Appel et al. 2009). These have been referred to as ‘maritime’ and ‘continental’ streams respectively – a shorthand that we shall follow here. Each of these is defined by its own suite of pottery forms – in the earliest instance the maritime impressed-ware (Impresso) and continental Starčevo-Körös-Criș (SKC) groups. These distinct ceramic complexes developed and diversified through time in the spread of both streams: the former developing into Cardial ware; the latter eventually giving rise to the Linearbandkeramik (LBK) phenomenon that subsequently spread from the Plain across the majority of central and eastern Europe. The two streams eventually recombined in the territory of what is now France during the 5th millennium BC (see Vander Linden 2011).

Much of the debate surrounding the spread of the Neolithic through Europe has centred upon rates of spread and/or the relative roles of migration vis-à-vis indigenous adoption (e.g. Bocquet-Appel et al. 2012, Fort 2015). Important as the latter question clearly is, in this paper we focus less upon the on who and more upon the what in this process: how coherent were the sets of farming practices transmitted across Europe, and how amenable to subsequent adaptation and innovation? While the concept of a single monolithic Neolithic ‘package’ has been widely discredited (e.g. Thomas 2003, Çilingiroğlu 2005), the various practices traditionally associated with the Neolithic do very often appear to have spread together, and indeed in many cases certain technologies are likely to have been functionally dependent upon each other.
Moreover, in Europe it may be possible to speak of Neolithic packages, in the plural — in the sense that different variants of farming practices and associated technologies existed and perhaps spread independently. While ceramic typology may be the most immediately visible marker of the two streams of Neolithisation noted above, and indeed was the basis upon which they were originally identified, there is also widespread evidence for associated differences in lithic technology (e.g. Biagi & Starnini 2010) and in subsistence practices (e.g. Coward et al. 2008; Conolly et al. 2011). Different studies have stressed the respective roles of cultural preferences (e.g. Colledge et al. 2005) and of adaptation to differing environments (e.g. Conolly et al. 2012) in structuring the observed variation, though in fact both are likely to have played a role (e.g. Manning et al. 2013a). The key questions that concern us here are (a) whether the two streams can be seen as the spread of distinct, coherent, ‘packages’ of practices in the initial Neolithic, and (b) if so, to what extent these packages were subject to subsequent divergence and diversification in response to environmental conditions, changing cultural preferences, and/or local innovations.

We use the western Balkans as our case study. This is the first region in which the maritime and continental streams are clearly visible — along the eastern Adriatic littoral and in the middle Danube basin respectively — and one of very few cases in which they can be observed in close proximity. In both cases the full suite of Neolithic practices is apparently adopted more-or-less simultaneously across large areas from c.6100 BC (Biagi et al. 2005; Forenbaher et al. 2013; Whittle et al. 2002), with subsequent phases of expansion into new territory and infilling of upland areas (Vander Linden et al. 2014), making this an ideal region in which to compare dynamics of establishment and development of farming practices across streams. Surprisingly, there has been little previous systematic attempt to compare Neolithic subsistence practices between and within these two zones (although see McClure 2013) — indeed they are frequently lumped together in continental-scale analyses (Colledge et al. 2005; Coward et al. 2008; Manning et al. 2013a).

**Aims and hypotheses**

Our aims are twofold. Firstly we set out to explore the questions outlined above in the context of the western Balkans, by testing the following hypotheses:

1. A distinctive, coherent Early Neolithic package existed within each zone (Adriatic and continental) in terms of farming practices as well as ceramic forms.
2. Subsequent divergence occurred within each zone as subsistence practices were adapted to local conditions and changing cultural preferences.

We do this in the context of animal use, i.e. herding and hunting practices, by reference to a comprehensive dataset of published and unpublished zooarchaeological results. This is the first strand in an interdisciplinary project that will ultimately combine zooarchaeological, archaeobotanical, lithic, ceramic, and landscape-use datasets (see Vander Linden et al. 2013).

Secondly, we aim to contribute to the zooarchaeological literature an account of the methodological problems posed by supra-regional meta-analysis and a demonstration of possible solutions. We argue for a transparent, reproducible approach to both data and methods.

**Background**

**Meta-analysis of subsistence data**

Meta-analyses of Neolithic zooarchaeological data can largely be grouped into (a) regional studies reviewing data from a single broad cultural phenomenon or geographical region (e.g. Bartosiewicz 2005; Greenfield 2008a; Mlekuž 2005; Orton 2012; Radović 2011; Tagliacozzo 2005); and (b) continental or semi-continental scale analyses comprising multiple cultural groups and geographic regions (e.g. Bökönyi 1974a; Conolly et al. 2011; Manning et al. 2013a; 2013b). The latter are able to address the ‘big picture’ but at the expense of detail and contextualisation: density of coverage is typically limited — due both to relative invisibility of bone reports in local publications and to the necessity of employing strict quality control — while much intra-regional variation is inevitably collapsed into broader groupings. Operating on an intermediate scale, similar to that of Arbuckle et al. (2014), the present study hopes to achieve the best of both worlds — permitting meaningful comparison between two distinct archaeological phenomena whose apparent divergence has continental-scale implications, while retaining the comprehensive coverage and detailed comparisons typical of regional-scale syntheses.

**The Neolithic of the western Balkans**

The Neolithics of the continental and Adriatic zones within our study region appear to follow two distinct trajectories in terms of settlement and material culture. In most of the continental zone the early Neolithic is represented by the Starčevo/Körös/Criş (SKC) phenomenon, appearing in the river valleys of central Serbia by the end of the 7th millennium BC and widespread on the Pannonian Plain by the start of the 6th (Whittle et al. 2002). Sites are typically composed of clusters of pits — some of them possible dwellings — with only sporadic evidence for houses per se, pointing towards short-lived occupations and relatively mobile lifeways (Bailey 2000: 57; Tringham 2000: 40–41). To the south of the Danube-Aegean watershed, by contrast, the Anzabegovo-Vršnik culture of Macedonia is characterised by small but apparently more permanent sites featuring rectilinear architecture (Naumov 2013).

SKC sites are replaced by the Vinča culture from c.5500 cal. BC across most of the zone, with the Butmir group emerging in upland central Bosnia around the same time and the Sopot culture in the Sava valley perhaps slightly later (Perić 1995; Obelić et al. 2004, Vander Linden et al. 2014, Burić 2015). Settlements of all three groups typically consist of rectilinear wattle-and-daub houses and vary considerably in size and longevity — some appear to have had occupations running into centuries and could have...
supported hundreds of residents at their greatest extents (Tripković 2013, Hofmann 2015). Tells and more extensive settlements are both represented, some of the former featuring enclosure ditches.

Along the coast, early Neolithic sites are known from the very end of the seventh millennium BC and belong to the Impressed Ware (Impresso) cultural group, which extends up the Adriatic from the late seventh millennium to c.5500 cal BC (Forenbaher et al. 2013). Along the eastern Adriatic the Impresso is known mainly from cave sites (particularly to the south), with the vast majority of open-air sites known from the broader coastal regions of central and northern Dalmatia (Zadar and Šibenik regions). Open air sites are of modest size, e.g. Pokrovnik at 3ha, and contain rectilinear houses of wattle-and-daub (Marijanović 2009). Occasional construction elements such as terrace or boundary walls are also known (Legge and Moore 2011).

The Adriatic middle Neolithic is characterised by the Danilo culture complex, which dates from c.5500/5300 to c.4900/4800 cal BC and is known from both cave and open air settlements, with the earliest dated sites located in Istria and the Trieste Karst (e.g. Pupićina) where there is no preceding Impresso. Open air Danilo settlements contain rectilinear wattle-and-daub houses (c.4 x 4m) with floors of packed earth or clay, sometimes with stone foundations (Forenbaher & Vujnović 2013; Legge & Moore 2011; Marijanović 2012). Finally, the late Neolithic Hvar culture of Dalmatia and its hinterland c.4900/4800 to c.4000 cal BC (Forenbaher et al. 2013) is known from both cave and flat open-air sites, again featuring rectilinear houses with packed earthen floors (Podrug 2010). In Istria and the Trieste Karst the late Neolithic is characterised by the northern ‘Vlaška’ variant of the Danilo complex, persisting in these regions until c.4300 cal BC.

Materials and methods

The dataset

This study is based upon a database of all published zooarchaeological taxonomic data for Neolithic sites in the western Balkans, plus several as-yet unpublished assemblages studied by the authors or kindly supplied by colleagues. The western Balkans are here defined as those areas lying between 41.0–46.5˚N and 13.5–24.5˚E and to the east of the Adriatic. The Neolithic is determined to end at 4500 cal BC. In total, this dataset includes 321,348 specimens from 143 phases at 95 sites, spread across nine countries with a variety of archaeological traditions. Interventions range from individual test pits to large open-area excavations, encompassing caves, open-air flat sites, and tells. Recovery methodology varies from hand-collection to 100% wet-sieving, but is often unspecified. Data are drawn from 82 publications in nine languages, published between 1958 and 2016 and contributed to by 41 faunal analysts. Phase-level sample sizes (by fragment count) vary from 14 to 32,097, and specimens are identified to 139 different taxonomic categories, many of which overlap.

The challenges that this diversity raises — common to almost any zooarchaeological meta-analysis — require explicit attention, and the approach taken here is built upon principles of transparency and reproducibility (see Marwick 2016). We include as supplementary information both our entire starting dataset and the code (using R Statistical Software v.3.2.0; R Core Team 2015) for all stages of analysis – available at http://eprints.whiterose.ac.uk/104121/. This allows our analysis to be reproduced exactly, perhaps with additional data, or to be repeated with different quality control parameters, statistical methods, and/or levels of taxonomic/chronological aggregation.

Chronological resolution

The dataset was divided into early, middle, and late Neolithic periods, with cut-offs chosen to fit approximate cultural transitions in both parts of the study region (Table 1). Since radiocarbon dates are only available for a subset of sites, allocation to periods was often based upon relative chronology. Where multiple phases at a site fall within the same period these were merged. Site phases which could not be assigned with reasonable confidence to a given period were omitted.

Geographical groupings

Sites were divided firstly into coastal and continental groups and secondly into geographical/topographical zones within these, to allow exploration of divergence within the former (Figure 1).

The Adriatic ‘stream’ is thus split into:

- The coastal/island zone of southern Dalmatia and Montenegro
- The Ravni Kotari plain and Kvarner Gulf
- Northern Istria and the Trieste Karst
- The Dinaric Alps (Herzegovina and Montenegro)

While the continental ‘stream’ is divided into:

- The upper Vardar valley region and Ovče Pole (northern FYR Macedonia)
- The Morava, Toplica, Kolubara, and Mlava valley systems (Central Serbia)
- The Iron Gates region (Danube Gorges)
- Southern Transylvania (Mureş Valley)
- The Pannonian Plain (Banat, Bačka, Srem, eastern Slavonia and southern Hungary)
- The Sava valley upstream of the Plain.
- The upper Bosna valley (central Bosnia)

Site types

Due to the nature of the landscape and the history of research, the Adriatic zone contains a predominance of cave sites while continental sites are overwhelmingly open-air. To avoid conflating site-type differences with inter-regional variation, cave sites are marked as such throughout.

Database structure and content

Database structure is modelled on Conolly (2012), consisting of linked tables for site, phase, and taxon, plus a look-up table of taxonomic categories (taxa). The latter is taken
<table>
<thead>
<tr>
<th>Period</th>
<th>Date range (cal. BC)</th>
<th>Adriatic cultural groupings</th>
<th>Continental cultural groupings</th>
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<td>Impresso</td>
<td>Starčevo-Körös-Criş</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Anzabegov-Vršnik</td>
</tr>
<tr>
<td>Middle Neolithic</td>
<td>c.5500/5400–5000</td>
<td>Danilo</td>
<td>Early Vinča (A–B)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Early Danilo-Vlaška</td>
<td>Early Butmir (Kakanj)</td>
</tr>
<tr>
<td>Late Neolithic</td>
<td>c.5000–4500</td>
<td>Early/Classic Hvar</td>
<td>Late Vinča (C–D)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Later Danilo-Vlaška</td>
<td>Sopot, Butmir</td>
</tr>
</tbody>
</table>

Table 1: Broad period categories used here, with approximate date ranges and main cultural groupings. Ranges based on Borić 2009; Forenbaher et al. 2013; McClure et al. 2014; Orton 2012; Vander Linden et al. 2014, Whittle et al. 2002.

Figure 1: Sites included in analysis, coloured by regional groupings. Numbers match table 2. Produced using R package raster (Hijmans 2015).

from Conolly with new categories added as required. Each individual taxon record, the smallest unit of data, represents all occurrences of a given taxon in a given site-phase. Data are restricted to taxonomic abundance by fragment count (Number of Identified Specimens, NISP), as one of the few forms of zooarchaeological data to be routinely and consistently reported. In the first instance all vertebrate specimens were entered using taxonomic categories from the original publications, including indeterminate specimens and those identified to broad categories such as ‘medium mammal’, ‘small carnivore’, or ‘fish’.

**Taxonomic coverage**

Fish, birds, reptiles, amphibians, and ‘micromammals’ (conventionally, taxa smaller than hedgehog and unlikely to have been consumed or otherwise used by humans) are often treated as specialisms within zooarchaeology, and only sporadically included alongside the main ‘macromammals’—often at lower taxonomic resolution. Moreover, where these groups are omitted from reports it is rarely clear whether they were absent or simply not studied. All categories other than macromammals are thus excluded here.

**Size-class data and partial identifications**

While size-class data is potentially informative, there is little consistency in reporting: one analyst’s ‘medium mammal’ might be another’s ‘large mammal’ (cf. Reynard et al. 2014), while many reports simply omit specimens not identified to taxon. Our analysis is thus restricted to specimens identified at least to genus level. A similar principle applies to specimens identified as one or other of two morphologically similar genera (e.g. ‘cattle/red deer’). At individual sites a strong case can be made for allocating such specimens to each possible taxon according to the ratio of positively identified specimens. This is likely to introduce inter-site biases, however, since in many cases
such partially identified specimens are subsumed under e.g. ‘large mammal’ and hence excluded from analysis. Accordingly, we exclude such ambiguous identifications throughout the dataset.

In several cases, multiple species from a single genus are represented in the dataset, along with indeterminate specimens – e.g. Martes martes (pine marten), Martes foina (beech marten), and Martes sp. In such cases data were combined at genus level. The grouping table used to combine these taxa is included with the data.

**Sheep and goats**
A special case is presented by ‘Ovis/Capra’, a common category due to the notorious difficulty of separating domestic sheep and goat remains (Boessneck 1969; Halstead et al. 2002; Rowley-Conwy 1998; Zeder & Lapham 2010; Zeder & Pilaar 2010). While many reports include separate categories for positively identified sheep (Ovis aries) and goats (Capra hircus) alongside the ubiquitous ‘sheep/goat’, reported rates of identification to species vary. This situation could be handled by (a) treating all sheep and goats together; (b) excluding indeterminate Ovis/Capra and only analysing positively identified specimens; or (c) using the latter to allocate the former between taxa pro rata.

Sheep and goats are distinct species typically managed in different ways within a given economy, and should thus ideally not be lumped (e.g. Balasse & Ambrose 2005). The alternatives are worse, however. Option (b) would grossly but inconsistently underestimate the importance of sheep and goats vis-à-vis other taxa, in many cases removing them altogether. Option (c) would give undue influence to often very small samples of positively identified specimens and introduce significant inter-observer bias, not least due to publication of new diagnostic criteria during the decades represented in our dataset. Due to the asymmetrical nature of identification criteria (Halstead et al. 2002; Zeder & Lapham 2010), and to biases linked to factors such as age (Mallia 2015; Zeder & Pilaar 2010), there is little reason to believe that definitively speciated specimens are representative of the overall sheep/goat ratio. Moreover, in our dataset an arbitrary division would have to be made for assemblages where only ‘sheep/goat’ are reported. We are therefore forced to fall back upon treating all sheep and goats as a single group.

**Wild/domestic uncertainty**
Three taxa are present here in both wild and domestic form: cattle/aurochs (Bos taurus/B. primigenius), pigs (Sus scrofa), and dogs/wolves (Canis familiaris/C. lupus), with many reports also listing indeterminate categories: Bos sp., Sus sp., or Canis sp. The same options apply here as for Ovis/Capra: (a) combining wild and domestic; (b) omitting indeterminate specimens; or (c) allocating the latter between categories according to the ratio of definitively wild and domestic specimens. Each option has inherent problems. The first might be acceptable for cattle and dogs – each dominated by domestic specimens – but not for pigs, both forms of which occur in appreciable numbers at many sites. Wild and domestic pigs represent very different subsistence practices, much more so even than sheep and goat, and cannot reasonably be conflated. Option (b) would again introduce significant inter-observer bias due to varying degrees of confidence. Option (c) was chosen here. Since specimen-level wild/domestic distinction is primarily a matter of size, there is less scope for the complex identification biases of sheep and goats. That said, our approach is likely slightly to overestimate numbers of wild pigs, since these are more frequently mature and measurable.

Six reports list only Sus sp. In five Adriatic cases we allocate these remains entirely to domestic pig, based on the rarity of wild pig at sites from the same region and period. In the final case – Opovo, Serbia – wild pigs are shown to dominate by Diagnostic Zones (DZ, an alternative quantification technique) but subsumed with domesticates by NISP. Rather than omit the site, we apply the wild:domestic ratio from the DZ data to the NISP count for pigs.

**Questionable identifications**
Records of unlikely species must be tackled individually. A few sites list Equus caballus (horse), not thought to have been present in either wild or domestic form during the Balkan Neolithic. These are likely either to be intrusive or to represent Equus hydruntinus (wild ass), which maintained a relict population in part of our region until at least the 5th millennium (Crees & Turvey 2014). They are subsumed here under Equus sp.

Fallow deer (Dama dama) are not considered native to early/mid Holocene Europe apart from a few relict populations around the Mediterranean, with their subsequent spread attributed to humans (Masseti & Vernesi 2014). They are reported from two sites in our dataset, Vinča and Opovo (Dimitrijević 2006; Russell 1993). The former are antlers which might have been imported and are excluded from analysis (see below). The latter are postcranial specimens that would represent some of the earliest Holocene evidence for Dama in temperate Europe. Given their paucity in comparison to other cervids at Opovo (4 of 5964), and the isolated nature of this find, we take the conservative option of excluding them.

Three Asiatic mouflon (Ovis orientalis) specimens are reported from Na Breg (Ivkovska 2009). Since this species is not believed native to the Balkans, they are assumed here to be unusually large domestic sheep and subsumed under ‘Ovis/Capra’ – ibex is also possible but less likely given the site’s topographical location. Finally, a single elk/moose (Alces alces) specimen is reported from Tumba Madžari in Macedonia (Moskalevska & Saner 1989), where we exclude it as either misidentified or residual. Moose persisted into historical periods in central Europe (Schmölder & Zachos 2006) but there is extremely limited evidence for Holocene moose in the study region, although five specimens are reported from late Epipalaeolithic Cuina Turcului in the Iron Gates (Boldemey 1973).

**Antlers**
Antler finds may derive either from hunting or from collection of shed antler for working, potentially causing overrepresentation of cervids. Where antler numbers are
reported, these are subtracted from the NISP counts used here.

**Partial reporting**
Quantitative data are sometimes only provided for a subset of macro-mammalian taxa, perhaps alongside an ‘other’ category and/or list of unquantified taxa. We include such assemblages insofar as key metrics (see below) can be reliably calculated. At Alsónyék–Kanizsa-dűlő (Nyerges 2013), for example, the ‘other’ category may include dogs, birds, and fish as well as minor wild mammalian taxa, preventing calculation of %wild but permitting e.g. %cattle. At Pokrovnik minor wild species are listed (Moore 2007b) but not quantified, while relative proportions of major taxa by phase are given only as percentages (Legge & Moore 2011). Since both phases clearly meet our size cut-off, %cattle etc. are calculated, but %wild omitted. Assemblages with such partial reporting are excluded from correspondence analysis.

**Recovery methodologies**
The effects of recovery methodology on assemblage composition are well known, with larger species being systematically overrepresented in assemblages recovered without extensive sieving (e.g. Payne 1972; Shaffer 1992, Quittmyr 2004). Excluding assemblages with unsatisfactory or unknown recovery would remove c.70–80% of site-phases from our dataset depending on criteria. Instead, we include assemblages regardless of recovery methodology, but explicitly assess its impact upon the results. Assemblages are graded on a four-point scale: (0) no sieving or sieving only on experimental basis, (1) limited systematic sieving, (2) extensive systematic sieving, and (3) 100% sieving. These categories are inevitably fuzzy given that they reflect percentage of sediment sieved, wet vs. dry sieving, and aperture size, and that descriptions of recovery protocols are often cursory. Broadly speaking, a score of 2 indicates that around half or more of excavated sediment was sieved through a 10mm or smaller mesh.

**Sample-size**
A minimum NISP cut-off of 200 was applied after lumping phases into our chronological periods, and after excluding certain taxa/elements as set out above.

**Analyses**
Firstly, we use a number of simple metrics to assess variation in animal use between and within the Adriatic and continental zones.

1. The percentage of NISP contributed by wild taxa (%wild).
2. The abundance of (a) pig, (b) cattle, and (c) sheep/goat, as a percentage of the total of these three taxa (respectively, %pig, %cattle, %caprines).

Secondly, we analyse variation between assemblages via correspondence analysis (using R package ca; Nenadić & Greenacre 2007) with the same groupings and sample size cut-off as set out above. A common tool in zooarchaeological meta-analyses (e.g. Bartosiewicz 2005; Mlekuž 2005; Manning et al. 2013a), CA has the benefit of considering all aspects of variation in taxonomic composition simultaneously, but loses the transparency of the simple metrics.

**Results**
After lumping by our three periods, 98 assemblages from 81 sites meet the criteria for inclusion (**Table 2**). **Table 3** breaks this down by zone, period, and site type. Given that it spans a larger land area, it is unsurprising that the continental zone has a larger overall sample size. Adriatic data are most abundant in the ‘early’ period and drop off in ‘late’, while continental assemblages are scarcest in the ‘middle’ Neolithic. In neither case is it clear to what extent this reflects actual settlement/population density vis-à-vis research bias. Cave sites make up 69% of Adriatic assemblages, but in the continental zone there is only the site of Peștera Cauce, Transylvania.

**Relative taxonomic abundances**
**Figure 2** shows the four main taxonomic metrics by zone and period, with colours indicating sub-regions. The same data are plotted spatially in **Figure 3**, while **Figure 4** summarises the data for domestic species using ternary axes. Starting with the early Neolithic, all metrics apart from %pigs show a clear difference between the two zones: while the Adriatic has almost consistently low percentages of wild taxa and a domestic fauna consisting of at least 75% caprines (Odmut excepted – see below), the continental zone is much more varied.

Remarkable uniformity is observed along the Adriatic coast from Montenegro to southern Istria and between site types, although the caves of the southernmost coast have more evidence of hunting in this period than the open-air sites further north. A narrow majority of continental assemblages also have %wild below 20%, but the remainder are distributed continuously from 20% to c.75%. Diversity is even more apparent for continental domestic fauna: while %pig is always below 20%, %caprines ranges from 7–86% and %cattle from 4–93%, forming a continuous spectrum from caprine-dominated to cattle-dominated domestic faunas. There is clearly a geographical element here: hunting is most important in the Iron Gates and on the Pannonian Plain, and least important in Macedonia and Transylvania; caprines dominate in Macedonia and to some extent the Plain, but are less important in the Iron Gates and variable elsewhere. Some regions also exhibit considerable internal variability in both %wild and the balance of domestic taxa.

In the middle Neolithic the continental picture becomes more coherent, and the contrast to the Adriatic starker. While there is still considerable variation in contribution of wild taxa, the continental domestic fauna is now almost uniformly cattle-focused (the exception being the one remaining Macedonian site, Anzabegovo IV). The contribution of pigs increases slightly, to a median of around 10%. These changes may be partly due to geographical biases, with few assemblages in this period from Macedonia and the Pannonian Plain, although in the latter case those few do show a shift toward cattle. Likewise,
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<th>Period</th>
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<td>Adriatic</td>
<td>Karst</td>
<td>cave</td>
<td>Middle</td>
<td>347</td>
<td>Radović 2011</td>
</tr>
<tr>
<td>78</td>
<td>Vela pec (Istria)</td>
<td>Adriatic</td>
<td>Karst</td>
<td>cave</td>
<td>Late</td>
<td>220</td>
<td>Radović 2011</td>
</tr>
<tr>
<td>79</td>
<td>Vela spila (Korčula)</td>
<td>Adriatic</td>
<td>Southern coast</td>
<td>cave</td>
<td>Early</td>
<td>206</td>
<td>Radović 2011</td>
</tr>
<tr>
<td>79</td>
<td>Vela spila (Korčula)</td>
<td>Adriatic</td>
<td>Southern coast</td>
<td>cave</td>
<td>Middle</td>
<td>346</td>
<td>Radović 2011</td>
</tr>
<tr>
<td>80</td>
<td>Vela spila (Ločinji)</td>
<td>Adriatic</td>
<td>Central coast</td>
<td>cave</td>
<td>Early</td>
<td>368</td>
<td>Pilaar Birch in press</td>
</tr>
<tr>
<td>81</td>
<td>Zemunica</td>
<td>Adriatic</td>
<td>Southern coast</td>
<td>cave</td>
<td>Early</td>
<td>283</td>
<td>Radović 2011</td>
</tr>
<tr>
<td>82</td>
<td>Zingari</td>
<td>Adriatic</td>
<td>Karst</td>
<td>cave</td>
<td>Middle</td>
<td>227</td>
<td>Bon 1996</td>
</tr>
</tbody>
</table>

Table 2: Summary of sites and phases included in analysis, after lumping phases according to our periods.

<table>
<thead>
<tr>
<th>Early</th>
<th>Middle</th>
<th>Late</th>
<th>TOTAL</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adriatic Cave</td>
<td>6</td>
<td>8</td>
<td>6</td>
</tr>
<tr>
<td>Adriatic Open</td>
<td>5</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Continental Cave</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Continental Open</td>
<td>34</td>
<td>11</td>
<td>22</td>
</tr>
<tr>
<td><strong>TOTAL</strong></td>
<td><strong>35</strong></td>
<td><strong>11</strong></td>
<td><strong>23</strong></td>
</tr>
</tbody>
</table>

Table 3: Numbers of included assemblages by period, region, and site type.

The typical ratio of cattle to caprines appears to increase substantially in central Serbia. The earliest assemblage from the Bosna valley, Obre I (actually spanning the early/middle Neolithic cut-off) does not stand out clearly from other continental regions, with %wild and %cattle on the median but relatively high %caprines and almost no pigs.

Adriatic assemblages show an increase in diversity into the middle Neolithic, largely related to cave sites from the karst of northern Istria and Trieste (initial and early Danilo-Vlaška), some of which feature %wild above 50% and relatively abundant pigs and cattle. Although classified here as middle Neolithic, these sites represent the first spread of the Neolithic into this northern region. One open-air site from the Ravni Kotari plain – Smilčić – also has a rather more 'continental' assemblage, with more than 50% cattle, although there are some doubts about the quality of excavation and curation (S. Radović, pers. comm.).

Moving into the late Neolithic, there is little clear change in the continental zone, although the contribution
of pigs increases again with concomitant decreases in %cattle at some sites. Coverage is more extensive than in the middle Neolithic, making the contrast with the early sites more convincing, although there are no data from Macedonia. A cluster of sites with fairly high %wild is apparent on the southern Pannonian Plain, the Iron Gates, and the Kolubara valley (i.e. modern-day northern Serbia, Vojvodina, and the Romanian Banat). These assemblages are all attributed to the Vinča culture but the same trend is not seen at Vinča sites to the south in the Morava and Mlava valleys of central Serbia, nor at Sopot sites to the west (Hermanov Vinograd on the Plain and a cluster of three sites upstream on the Sava) or the Butmir sites of the Bosna valley: it appears to be a specific regional phenomenon coterminous neither with cultural nor topographical groupings.

Cattle are generally dominant, although two assemblages have unusually high %caprines: Peștera Cauce is perhaps unsurprising as a high-altitude cave site, but the Vinča settlement of Vitkovo in southern Central Serbia is
Figure 3: Relative contributions of main domesticates (pie charts) and of wild species (greyscale symbols), split by period. Dots represent open-air sites; triangles represent caves. Produced using R packages `raster` and `mapplots` (Gerritsen 2014; Bivand & Lewin-Koh 2015).
anomalous (Bulatović 2011; 2012). The outlying cluster of Sopot sites in the Sava valley have lower %cattle than average (a consistent c.50%) while the two Butmir sites on the Bosna fall towards the upper end of %cattle observed within the main (i.e. Vinča) group.

The late Neolithic Adriatic picture is obscured by low overall sample size and lack of open-air sites from the coastal plain, but generally appears consistent with previous periods. The exception is Lisići, a highly idiosyncratic site on the upper Neretva in central Bosnia and Herzegovina, close to the watershed between the two zones. A coastal site in terms of its Hvar pottery (Benac 1958), it stands out with the highest %wild (95%) of any assemblage in either zone. The complete absence of domestic caprines here seems suspicious: given that the fauna were not studied by an experienced archaeozoologist (Benac 1955) it is possible that some of the 38 reported chamois specimens might actually be sheep or goat. Likewise, there may be domestic pigs among the 105 ‘wild pig’ specimens. Whatever the status of these specimens, however, the site would nonetheless stand out from other Adriatic assemblages in terms of contribution of both cattle and wild fauna. Given Lisići’s unique location and the fact that no nearby sites are likely to be excavated in future – the valley having been artificially flooded in 1953 – this assemblage would benefit from reanalysis.

Correspondence Analysis

Figure 5 shows correspondence analysis (CA) results for assemblages with quantitative data for all taxa. Odmut is excluded since its unusually high percentage of ibex (34%) resulted in a score of almost −20 on Dimension 2, obscuring variation between other sites. The scores for the most common taxa (Figure 5a, points in black) reveal a tri-polar situation similar to that observed for Europe more widely by Manning et al. (2013a; 2013b), with the first two dimensions clearly separating (a) domestic cattle and pigs, (b) domestic sheep and goats, and (c) the main terrestrial wild animals. Including the latter as separate taxa (albeit with small carnivores lumped) rather than combining them into a single ‘terrestrial wild’ category following Manning et al. reveals additional details.

Our CA results show that, across the western Balkans, pig specimens identified as wild tend to occur with deer while those identified as domestic co-occur with cattle. Geometric morphometrics (GMM) has recently cast doubt over traditional metrical separation between wild and domestic pigs in the region, suggesting the existence of a ‘large-domestic’ population alongside the expected large-wild and small-domestic groups (Evin et al. 2015). Our results concur with new isotopic data (Balasse et al. 2016) indicating that this ‘large-domestic’ group represents functionally wild, hunted animals, regardless of ancestry.

Wild cattle plot close to their domestic counterparts. Given that size distinction in this case is less clear, with wild cattle rarely forming a clearly distinct group (Bartosiewicz et al. 2006; Wright & Viner-Daniels 2015), there is a worrying possibility of widespread misidentification. Alternatively a genuine correlation may have existed between cattle herding and cattle hunting. The position of domestic dog amongst the main wild taxa is also interesting, and might perhaps be linked to their potential role in hunting.

Plotting CA scores for individual assemblages (Figure 5b–c) tells a similar story to the basic metrics discussed above. In the early Neolithic, Adriatic sites cluster around the sheep/goat pole while continental assemblages are distributed between all three poles. More specifically, Macedonian and Transylvanian sites plot along an axis from sheep/goat to cattle/pig, while Iron Gates sites mostly fall toward the wild end of the cattle/pig-wild axis. Central Serbian and Pannonian Plain sites are widely dispersed.

In the middle Neolithic, southern and central Adriatic sites mostly remain close to the sheep/goat pole (excepting Smilčić; see above), while northern karstic caves are split between the latter and the wild pole. Apart from Anzabegovo in Macedonia, continental sites are restricted to the cattle/pig-wild axis – mostly at the former end. The same broad pattern applies in the late Neolithic, with the
addition of the Adriatic wild outlier of Lisičići and the two caprine-rich continental outliers noted above: Peštera Cauce and Vitkovo. Bosna and Sava valley sites all plot at the cattle/pig pole, while Central Serbian and Plain sites are again spread along the cattle/pig-wild axis.

Influence of sample size

It has been suggested elsewhere that systematic relationships may exist between sample size and taxonomic composition of southeast European Neolithic faunal assemblages, e.g. that unusually high %wild is typically a feature of smaller assemblages and/or that dominance of caprines increases with sample size (Bartosiewicz 2007, 297–298; Bonsall et al. 2013, 156–158). In order to test for such effects, Figure 6 plots %wild, %cattle, and %caprines against log(NISP) for each of the two geographical zones in our study. In the continental zone, no significant relationships exist. In the Adriatic zone there indeed appears to be a negative correlation between sample size and %wild, although this is fairly weak (Pearson’s $r = -0.378$, Spearman’s $\rho = -0.556$) and only just significant at 5% ($p = 0.043$, based on Pearson’s): while the largest assemblages have few wild specimens, smaller assemblages cover the full spectrum. Splitting by sub-region, only the karst sites show a clear intra-group trend, and even this is heavily influenced by a single unusually large assemblage.

Insofar as a relationship does exist across the zone as a whole, there are two likely reasons. Firstly, one might expect short-term camps a priori to have both high levels of hunting and limited sample sizes; conversely, NISP at large and/or long-term settlements – which in the Adriatic

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**Figure 5:** Correspondence analysis results: (a) taxon scores, with major taxa highlighted; (b–d) assemblage scores by period. Circles represent open-air sites; triangles represent caves.
region are generally associated with little hunting – is to a considerable degree a factor of excavation extent and hence varies widely, with some very large cases. Secondly, thorough bone recovery will increase sample size for a given excavated volume and might also be expected to decrease \%\text{wild} depending on the species typically hunted at a given site (red deer and wild pig, for example, being amongst the larger species in the region). Overall, there is little reason to think that sample size is influencing \%\text{wild}, rather than both NISP and composition being influenced by site type and location. Recovery effects are explored in detail below.

**Influence of recovery strategy**

Before interpreting these results further it is crucial to consider effects of recovery strategy. The distribution of our recovery classes (Table 4) shows a clear bias between the two main zones, with 81% of Adriatic assemblages...
subject to reasonably thorough sieving compared to just 24% in the continental zone (excluding those for which strategy is unreported). The caprine:cattle ratio is particularly vulnerable to recovery effects, given the obvious size difference between these taxa. The potential effect on %\textit{wild} is less certain due to the range of taxa and body sizes represented within both wild and domestic categories, but given the numerical importance of red deer and wild pig (both large taxa) amongst the former it is plausible that lack of sieving could have inflated %\textit{wild} in a similar way to %\textit{cattle}.

Figure 7 shows the same data as Figure 4, but with points coloured by recovery methodology. Figure 8 shows (a) domestic faunal composition and (b) CA results for all periods in the same way. In all cases it appears at first glance that recovery has had a dramatic effect on assemblage composition. In fact zone and recovery confound one another, making it difficult to infer their relative influence. The few well-sieved continental assemblages do fall closer to the Adriatic norm of more caprines and fewer cattle and wild animals, while the few poorly sieved Adriatic assemblages fit better with the continental group. Within the early and middle Neolithic the continental data show an apparent relationship between recovery and %\textit{wild}.

Recovery alone cannot fully explain the observed trends, however. Firstly, since the full range of variation observed within the continental early Neolithic for all four metrics is present even within the unsieved fraction, the reduction in diversity into later periods must be accounted for by other factors. Secondly, even the sieved assemblages in the continental early Neolithic show more variation in caprine:cattle ratio than the Adriatic group, and lower average %\textit{caprines}. Comparison between zones is most problematic for the middle Neolithic, due to lack of thoroughly sieved assemblages and low reporting rate in the small sample. The only continental site with reasonably thorough sieving reported is Anzabegovo in Macedonia. Nonetheless, the retraction of diversity in continental cattle:caprines ratios requires explanation, while even relatively limited sieving at Nin in the Adriatic zone produced a higher %\textit{caprines} than any continental site apart from Anzabegovo. The lack of recovery information from several northern Adriatic sites is also problematic, since some of these have comparatively low %\textit{caprines}.

Discussion

We can now revisit our two hypotheses concerning the spread and development of early farming practices in the western Balkans. First, we predicted that the Adriatic and Continental zones would each exhibit a coherent, distinct pattern of animal exploitation in the earliest Neolithic, as components of respective ‘Neolithic packages’.

\begin{table}[h]
\begin{tabular}{|c|c|c|c|c|c|}
\hline
Zone & Period & None & Limited & Frequent & 100\% & Unknown \\
\hline
\textbf{Adriatic}  &  &  &  &  &  &  \\
\textbf{Early} & 1 & 1 & 1 & 6 & 2 \\
\textbf{Middle} & 0 & 1 & 0 & 6 & 4 \\
\textbf{Late} & 1 & 0 & 0 & 4 & 2 \\
\textbf{TOTAL} & 2 & 2 & 1 & 16 & 8 \\
\hline
\textbf{Continental}  &  &  &  &  &  &  \\
\textbf{Early} & 18 & 1 & 4 & 3 & 9 \\
\textbf{Middle} & 4 & 3 & 1 & 0 & 3 \\
\textbf{Late} & 10 & 5 & 3 & 2 & 3 \\
\textbf{TOTAL} & 32 & 9 & 8 & 5 & 1 \\
\hline
\end{tabular}
\caption{Numbers of included assemblages by period, region, and recovery standards.}
\end{table}
Second, we suggested that a subsequent divergence in practices would be observable in each region as subsistence regimes were adapted to local conditions and emerging cultural preferences. Neither hypothesis was entirely borne out.

Within the Adriatic zone, the early Neolithic data do support the idea of a coherent incoming set of practices based around caprine herding, with limited use of other domesticates and very little hunting. There is a remarkable similarity in assemblage composition amongst both cave and open air sites from Montenegro to southern Istria (i.e. our southern and central coast regions) albeit with slightly more evidence for hunting in cave assemblages. Radiocarbon data indicate rapid Neolithic expansion across this region, although it has been suggested that this initially entailed the spread of pottery use and caprine herding with other typically Neolithic practices developing later (Forenbaher et al. 2013, 596; cf. Forenbaher & Miracle 2005). Any subsequent consolidation of Neolithic lifeways does not appear to have affected

<table>
<thead>
<tr>
<th>Figure 7: Distributions of key metrics for assemblages by period and geographical zone, coloured by recovery class. Produced using R package beeswarm.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Early</td>
</tr>
<tr>
<td>% wild</td>
</tr>
<tr>
<td>Adriatic Continental</td>
</tr>
<tr>
<td>% caprines</td>
</tr>
<tr>
<td>Adriatic Continental</td>
</tr>
<tr>
<td>% cattle</td>
</tr>
<tr>
<td>Adriatic Continental</td>
</tr>
<tr>
<td>% pigs</td>
</tr>
<tr>
<td>Adriatic Continental</td>
</tr>
</tbody>
</table>

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Figure 8: (a) Ternary plot for main domesticates across all assemblages, coloured by recovery class. Produced using R package ggtern. (b) Correspondence analysis scores across all assemblages, coloured by recovery class.
the zooarchaeological record, with the early pattern proving remarkably stable throughout the Neolithic.

With the subsequent expansion of Neolithic practices to northern Istria and the Friese karst in our ‘middle Neolithic’ period, we see a very different pattern. Many of the cave sites in this group feature much more evidence for hunting and a lower contribution of caprines vis-à-vis cattle and especially pigs. This pattern would make sense either as an adaptation to the more mountainous, subalpine environment, or perhaps as a reflection of seasonal pastoral use of caves (Bonsall et al. 2013). An alternative, or complementary, explanation might involve the influence of pre-existing Mesolithic populations on Neolithic subsistence practices given the high density of Mesolithic sites in the region, although debate continues regarding the lack of Mesolithic radiocarbon dates from the early 6th millennium BC, immediately prior to the appearance of Neolithic sites (Biagi & Spataro 2001; Bonsall et al. 2013, 150–151; Forenbaher et al. 2013; Forenbaher & Miracle 2005; Mlekuž et al. 2008). In this case a subsequent consolidation of Neolithic practices may perhaps be observed, with late Neolithic northern assemblages shifting back some way toward the caprine-dominated profile seen to the south.

The other direction of expansion in the Adriatic zone is inland, up the river valleys into the Dinaric Alps. Cave sites of inland Montenegro and southern and western Herzegovina with early Neolithic (i.e. Impresso) ceramics have been argued to represent piecemeal adoption of Neolithic technologies by local Mesolithic populations (Forenbaher & Miracle 2005). Unfortunately, early Neolithic zooarchaeological data are only available from Odmut – technically in the Danube catchment but featuring Impresso pottery in its earliest Neolithic level – where the incorporation of small numbers of livestock into a previously exclusively wild fauna does support this hypothesis, as does analysis of the material culture (Cristiani & Borić 2016).

The only studied inland Adriatic faunal assemblage from Herzegovina is late-Neolithic Lisičići (see above). We cannot rule out that this is a specialised hunting site within a more balanced regional economic system, but even in this case (and allowing for possible identification errors) it is without parallel amongst the more coastal sites, including caves. Insofar as Lisičići does represent a highly specialised late Neolithic economy in the upper Neretva, the paucity of Neolithic (and absence of Mesolithic) archaeological, ecofactual, and chronological data from this area makes it hard to discern whether this purely reflects adaptation of Neolithic practices to the subalpine environment.

Moving to the continental zone, the most striking trend is the reduction in variability of domestic faunas over time. Although confounded by geographical coverage to a small extent, at least between the early and middle periods, this trend is visible even within the larger sub-regions. This is the opposite of the hypothesised pattern, in which a coherent initial farming ‘package’ is subsequently adapted to variable local conditions. One explanation might be that our 600-year ‘early Neolithic’ period has actually captured the process of adaptation from a caprine-based to a more cattle-focused animal economy, and that the observed variability is thus really diachronic rather than synchronic. To test for this, dated continental sites were plotted on an absolute chronological scale (Figure 9). Multiple ‘early’ Neolithic phases at individual sites which were combined above have been separated here, and the sample size cut-off applied to individual site-phases.

Taken as a whole the data show no clear diachronic trend, but this is partly due to interregional differences. The single largest group, from the Pannonian Plain, shows an overall reduction in %caprines in favour of cattle from c.5700 BC. Too few dated assemblages are available from Central Serbia or Transylvania for reliable assessment of diachronic trends in these regions but there is some suggestion of an earlier reliance on cattle, while two fairly early Iron Gates site shows a heavily cattle-based domestic economy from the outset. Interestingly, the first studied site from the Sava Valley group – Galovo at c.5700–5600 BC – already indicates a relatively high-cattle, low-caprine economy, matching its downstream contemporaries on the southern Plain. Finally, Macedonia is represented by successive phases at Anzabegovo, showing no notable change during this period or indeed beyond. There is little sign of an increase in %pigs within this period in any region. Turning to the contribution of hunting, the Pannonian Plain sites show a steady increase through time, while the two Iron Gates assemblages are dominated by wild taxa much earlier. Galovo again fits the trend for the Plain sites. All four Central Serbian and Transylvanian sites have limited hunting but none date from the latter half of the period, while Macedonia (i.e. Anzabegovo) again shows no change.

If one assumes that the economic system(s) from which farming practices reached the middle Danube – whether upstream from the south-east or from the south via Macedonia – were characterised by relatively high percentages of caprines and limited hunting, these results can most easily be interpreted in terms of staggered adaptation to the generally damper climate of the temperate central and northern Balkans – widely assumed to have favoured cattle and pigs over caprines (e.g. Bartosiewicz 2005, see also Connolly et al. 2012). In the rather more Mediterranean climate of Macedonia – as along the Adriatic coast – a caprine-based economy appears to persist into the middle Neolithic and quite probably beyond.

The question then becomes why the rate and timing of this adaptation should have been so varied within the continental zone. In the Iron Gates the apparently immediate adoption of a cattle– rather than caprine-focused domestic economy alongside continued large-scale hunting may reflect both the distinctive environment of this region and its well-documented Mesolithic–Neolithic continuity, with the pre-existing population perhaps selectively adopting the most suitable domesticates. Both arguments have also been made for the frequency of wild taxa and pigs in the northernmost Adriatic (see above). Apparent differences between the Pannonian Plain, Transylvania, and central Serbia are harder to explain. The late persistence
of a caprine-dominated economy on the Plain relative to adjacent areas has long been noted – though not previously demonstrated in such detail – with cultural conservatism invoked to explain this phenomenon for Körös sites in Hungary (Bartosiewicz 2007; Whittle 2005). The gradual increase in hunting shown here is consistent with the idea of an incoming Neolithic population that took many generations to develop the practical knowledge necessary intensively to exploit the local wild fauna – in marked contrast to areas such as the Iron Gates and perhaps the Trieste Karst.

Why, then, did this change toward the end of our 'early Neolithic' window, giving way to the much more uniform pattern of domestic fauna observed in the middle Neolithic? Unfortunately, the centuries around 5500 cal BC remain a relatively obscure period within central Balkan prehistory, coinciding both with the end of the SKC phenomenon and with a relative gap in the distribution of studied and dated faunal assemblages (Orton 2012, figure 8; see also Porčić et al. 2016; Vander Linden et al. submitted).

The cattle-dominated continental pattern continues through the middle and late Neolithic, including into new regions and environmental zones (i.e. the mountains of central Bosnia and the west of the Sava valley). While not uniformly split, we can see a greater overall emphasis on hunting in the Iron Gates and Plain relative to central Serbia and the Bosna and Sava valleys. These general regional variations divide not only between ceramic cultural groups (Sopot in the Sava valley, Butmir in the Bosna valley) but also across them (Vinča in Central Serbia, the Iron Gates and the Plain).

**Conclusions**

The conclusions of this paper relate in equal measure to the Neolithisation of the Balkans and to zooarchaeological methodology. Starting with the former, the data

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**Figure 9:** Key metrics for radiocarbon-dated continental sites in our 'early Neolithic' group, plotted on an absolute chronological scale and coloured by region. Date estimates and ranges calculated using R package *Bchron* (Parnell 2015), aided by *plyr* (Wickham 2011). Points represent medians and bars represent one-sigma (i.e. 68.27%) confidence intervals, based on (a) *BchronCalibrate* results for single dates, or (b) *BchronDensity* results for multiple dates.
provide partial support to our initial hypotheses. While early Neolithic faunal assemblages from the Adriatic zone reveal a highly coherent caprine-dominated, low-hunting pattern consistent with the idea of a uniform incoming ‘Neolithic package’, their continental contemporaries are characterised by considerable diversity from the outset of the Neolithic, at least to the limit of available chronological resolution.

In the Adriatic zone, subsequent adaptation was seen through the process of Neolithic expansion into new areas to the north and inland, while the ‘core’ area of the southern and central coastal sites retained the highly coherent early Neolithic pattern. The former could be interpreted in terms of adaptation to more upland environments, increased role of pre-existing foraging groups in the uptake of farming practices, or both – although Mesolithic–Neolithic continuity in the northern Istria/Trieste karst region remains disputed.

At first glance, the continental data show an unexpected trend of convergence over time, with early Neolithic diversity giving way to a reasonably consistent cattle-focused economy from c.5600 BC, albeit with varying levels of hunting. We suggest that this represents a staggered process of adaptation to local environmental conditions, with some regions (the Iron Gates, perhaps central Serbia) adopting a more cattle-focused system almost immediately while others, notably the Pannonian Plain, retained an emphasis on sheep and goat for almost half a millennium despite damp conditions widely assumed to have favoured cattle and pigs. Selective adoption by pre-existing forager populations might be invoked for the Iron Gates, with its documented late Mesolithic population and continued reliance on hunting, but is harder to sustain elsewhere. The timing of the eventual broader shift away from caprines and towards a more coherent regional economy is interesting, coinciding as it does with the under-researched SKC-Vinča transition and with the expansion of settlement further up the Sava Valley and into the Bosna.

Overall, our results reinforce the point that Neolithisation was a highly complex and varied process, suggesting that adaptation of Neolithic practices to local conditions could have been extremely fast in some cases and remarkably slow in others. Ongoing work under the aegis of the European Research Council project EUROFARM, funded under the European Union’s Seventh Framework Programme (FP/2007–2013; ERC Grant Agreement no. 313716), led by MVL and hosted by UCL. We thank all team members and project partners.

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Competing Interests

The authors declare that they have no competing interests.
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