Diverse responses of common vole (*Microtus arvalis*) populations to Late Glacial and Early Holocene climate changes — Evidence from ancient DNA

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The harsh climatic conditions during the Last Glacial Maximum (LGM) period have been considered the cause of local extinctions and major faunal reorganizations that took place at the end of the Pleistocene. Recent studies have shown, however, that in addition many of these ecological events were associated with abrupt climate changes during the so-called Late Glacial and the Pleistocene/Holocene transition. Here we used ancient DNA to investigate the impact of those changes on European populations of temperate vole species (*Microtus arvalis*). The genetic diversity of modern populations and the fossil record suggests that the species may have survived cold episodes, like LGM, not only in the traditional Mediterranean glacial refugia but also at higher latitudes in cryptic northern refugia located in Central France, the northern Alps as well as the Carpathians. However, the details of the post-glacial recolonization and the impact of the Late Glacial and Early Holocene climate changes on the evolutionary history of the common vole remains unclear. To address this issue, we analysed mtDNA cytochrome *b* sequences from more than one hundred common vole specimens from 36 paleontological and archaeological sites scattered across Europe. Our data suggest that populations from the European mid- and high latitudes suffered a local population extinction and contraction as a result of Late Glacial and Early Holocene

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climate and environmental changes. The recolonization of earlier abandoned areas took place in the Mid- to Late Holocene. In contrast, at low latitudes, in Northern Spain there was a continuity of common vole populations. This indicates different responses of common vole populations to climate and environmental changes across Europe and corroborates the hypothesis that abrupt changes, like those associated with Younger Dryas and the Pleistocene/Holocene transition, had a significant impact on populations at the mid- and high latitudes of Europe.

1. Introduction

The period following the Last Glacial Maximum was characterised by a number of climate changes that deeply transformed terrestrial ecosystems (Cooper et al., 2015; Feurdean et al., 2014; Stuart, 2015). From *ca.* 19.0 ka there was a slow and gradual warming of the climate followed by a more rapid temperature increase at around 14.7 ka which led to the expansion of boreal forests in many regions of Europe and marked the beginning of Bølling/Allerød Interstadial (corresponding to Greenland Interstadial 1; GI-1). This warm period was followed by the abrupt worldwide cooling called Younger Dryas (YD) that took place between *ca.* 12.7−11.7 ka (corresponding to Greenland Stadial 1; GS-1) and led to short-term re-expansion of steppe-tundra environments. Finally, at around 11.7 ka the onset of Holocene was marked with a contraction of cold-adapted species and the emergence of forests. In Europe as a result of these oscillations many species adapted to cold and dry steppe, both large and medium sized like reindeer (*Rangifer tarandus*) (Sommer et al., 2013), saiga antelope (*Saiga tatarica*) (Nadachowski et al., 2016), arctic fox (*Alopex lagopus*) (Dalén et al., 2007) and small like collared lemmings (*Dicrostonyx torquatus*) (Palkopoulou et al., 2016) became locally extinct. Temperate and woodland species, on the other hand, generally re-expanded over the region.

The common vole (*Microtus arvalis*) is at present one of the most common rodents in continental Europe (apart from areas such as Scandinavia and southernmost parts of the Iberian, Italian and Balkan peninsulas where it is absent). It lives in well-drained open habitats, from lowland to mountain pastures at elevations up to *ca.* 3000 m, being often abundant in cultivated fields and is regarded as an agricultural pest (Pardiñas et al., 2017). The earliest fossil record of this species is from Western Europe at Hundsheim (Maul and Markova, 2007), Miesenheim 1 in Germany (van Kolfschoten, 1990), Dobrkovice II (Fejfar, 1965) and Stránská skála cave in the Czech Republic (Kučera et al., 2009), all dated to *ca.* 0.6−0.5 Ma. During the Last Glacial (*ca.* 119 ka − 11.7 ka) (Rasmussen et al., 2014) the species was common and widespread in both milder interstadials and cooler stadials (including the LGM), being a constant component of small mammal assemblages across almost the whole of Western Europe (Chaline, 1972; López-García et al., 2017; Rhodes et al., 2018; Royer et al., 2016), Mediterranean Europe (Bañuls-Cardona et al., 2017; Berto et al., 2017; Cuenca-Bescós et al., 2009; López-García et al., 2014, 2013; 2011, 2010; Luzi et al., 2017; Luzi and López-García, 2019; Nadachowski, 1984; Popov, 2018) and Central Europe (Horáček and Ložek, 1988; Horáček and Sánchez-Marco, 1984; Jánossy, 1986; Luzi et al., 2019; Nadachowski, 1982, 1989; Pazonyi, 2004; Socha, 2014). Surprisingly in the Eastern European Plain (Ukraine and European parts of Russia) *M. arvalis* was extremely rare or absent (Markova, 1982; Rekovets and Nadachowski, 1995; Rekovets and Nesin, 1993).

Based on the distribution of modern genetic diversity and supported by the continuous fossil record, it has been suggested that the common vole, together with other species, survived the Last Glacial Maximum not only in traditional Mediterranean refugia but also in so called cryptic northern refugia located at higher latitudes (Fink et al., 2004; Pedreschi et al., 2019; Stewart et al., 2010; Stewart and Lister, 2001; Stojak et al., 2015; Tougard et al., 2008). Central France, the Alpine region and the Carpathians have been indicated as possible locations of such refugia (Fink et al., 2004; Heckel et al., 2005; Stojak et al., 2016; Tougard et al., 2008). However, the detailed trajectories of post glacial recolonization of the common vole remain unknown. The impact of the YD cooling and environmental changes associated with the Pleistocene to Holocene transition are unclear. Sympatric rodent species such as the field vole (*Microtus agrestis*) suffered a drastic population reduction during the YD which may have led to turnover in all of its European populations (Herman and Searle, 2011). More recently a detailed study of Central European populations of the common vole revealed a signal of genetic continuity since the LGM, although the start of population growth was estimated as *ca.* 9−8 ka suggesting that they may also have suffered a bottleneck near the Pleistocene/Holocene transition (Stojak et al., 2015).

Here we used the genetic data obtained from common vole remains originating from post-LGM and Holocene palaeontological sites across Europe to gain a more detailed insight into the post-glacial history of the species and to elucidate the impact of climate changes on its populations.

2. Material and methods

2.1. Material

A total of 321 samples (molars and mandibles) from 36 palaeontological sites across Europe were selected for genetic analysis (Supplementary Table B1). The time range of the collected samples covered the post-LGM and Holocene periods, roughly between 20.0 and 0.5 ka. All samples were morphologically described as *Microtus arvalis*, *M. arvalis/agrestis* or *Microtus* sp.

2.2. DNA extraction

Genomic DNA was extracted at the Laboratory of Paleogenetics and Conservation Genetics, Centre of New Technologies, University of Warsaw dedicated to ancient DNA analyses and following protocols that reduce the probability of contamination with modern DNA. Single teeth were rinsed with sterile demineralized water in 2 ml Eppendorf tubes and crushed with sterile tips into smaller pieces. DNA was extracted using the protocol optimised to retrieve short DNA fragments (Dabney et al., 2013). A negative control was included in every batch of DNA extraction and processed further.

2.3. Multiplex amplification and sequencing

In the case of 18 samples a fragment of mtDNA cytochrome *b* gene coding sequence was amplified using ten primer pairs in two multiplex PCR reactions (Supplementary Table B2) as described in Palkopoulou et al. (2016). Purified PCR products were converted into double-indexed sequencing libraries (Kircher et al., 2012) and

sequenced using Illumina MiSeq Platform (300 cycles, paired-end).

2.4. Library preparation, target enrichment and sequencing

Most of the samples were processed using the target enrichment approach (Supplementary Table B3). DNA extracts were converted into double-indexed sequencing libraries following the protocol of Meyer and Kircher (2010) with minor modifications (Baca et al., 2019). We applied a double-barcoding approach to minimise sequencing errors. Illumina adapters contained additional unique 7-bp sequences (barcodes) as described in Rohland et al. (2014). The barcodes were introduced with indexing primers P5 and P7 (Kircher et al., 2012). Indexing PCR was performed using AmpliTaq Gold 360 Master Mix (Applied Biosystems) with the 19 amplification cycles. PCR products from three independent amplifications were pooled, purified using magnetic beads and concentrated to 40 μl. Target enrichment of mtDNA was performed as described in Horn (2012). Bait was prepared using modern DNA of the common and field vole. Complete mitochondrial genomes were amplified as several overlapping fragments (see Supplementary Table B4 for primer details). After purification, PCR products were sonicated using Covaris S220 to an average fragment length of 200 bp and enzymatically modified (Horn, 2012). Two rounds of hybridization were performed, each 20−22 h long. Four samples were pooled in one reaction, differing from each other with index and barcode sequences. Post-capture PCR were performed after each of hybridizations using Herculase II Fusion Polymerase (Agilent) with 10−15 cycles. Amplified products were purified, quantified, pooled in equimolar ratios and sequenced using Illumina NextSeq platform (150 cycles, paired-end, MidOutput kits).

2.5. Sequence data processing

Raw Illumina reads were first demultiplexed based on index sequences using bcl2fastq Conversion Software v2.20 (Illumina) and barcoded reads were split into separate files using the script Sabre (https://github.com/najoshi/sabre). AdapterRemoval v2 (Schubert et al., 2016) was used to trim adapter sequences and to collapse paired-end reads. Merged reads were mapped to a reference mitochondrial genome of *M. arvalis* (NC_038176.1) using the BWA-MEM algorithm in *bwa 0.7.17* (Li and Durbin, 2010). Only reads longer than 30 bp and with mapping quality over 30 were retained and duplicates were removed using the SAMtools package. Consensus sequences were called using the BCFtools package. In the case of samples processed using a multiplex PCR approach, after collapsing of paired-end reads, primer sequences were trimmed from amplicon sequences using the *trim.seqs* command from the mothur package (Schloss et al., 2009) and later the consensuses from two replicates were compared and a final consensus called as per Stiller et al. (2009).

2.6. Data validation

MapDamage v.2 (Ginolhac et al., 2011) was used to check for damage pattern characteristic of ancient DNA and to estimate sequencing read lengths. To evaluate whether age assigned to sequences is congruent with its divergence from the root (RTT; Root-to-tip divergence) we used TempEst 1.5.1 (Rambaut et al., 2016). As the input to TempEst 1.5.1 we used a best phylogeny chosen from 20 ML runs in RAxML (Stamatakis, 2014), using the GTRGAMMA substitution model.

2.7. Phylogenetic analyses

In the phylogenetic reconstructions we used a 1053 bp fragment of mtDNA cytochrome *b*. First, because all the extant samples were sequenced only for this fragment and second, because in the majority of the samples, sequenced for the whole mtDNA, we observed regions where two different sequences were present. This was probably due to the sequencing of nuclear sequences of mitochondrial origin (pseudogenes/*numts*) along with real mitochondrial ones (Triant and DeWoody, 2008). We did not find this problem within fragment encompassing cytochrome *b*. In order to determine phylogenetic position of post-LGM and Holocene common voles we reconstructed a Bayesian phylogeny using Beast 1.8.4 (Drummond et al., 2012). For the reconstruction we used sequences of 829 extant common voles gathered from previous studies (Braaker and Heckel, 2009; Haynes et al., 2003; Heckel et al., 2005; Martínková et al., 2013; Stojak et al., 2016, 2015; Tougard et al., 2008), 23 sequences from radiocarbon dated specimens from Orkney (Martínková et al., 2013), 41 sequences obtained earlier from two Polish sites - Obłazowa cave (western entrance) and the rock-overhang in the Cisowa Rock sites (Lemanik et al., 2020) and newly generated sequences from palaeontological specimens. The phylogeny was reconstructed as in earlier studies (Stojak et al., 2015, 2016). We used a SDR06 model (Shapiro et al., 2006) in which data is separated into two partitions (first and second codon positions are linked and the third one is separated). A HKY + Γ substitution model was used for both partitions. We set the tip dates option on and each sequence that came from an ancient individual had the age assigned based on its stratigraphic position or radiocarbon date (Supplementary Table B3). We used an uncorrelated relaxed lognormal clock and a flexible Bayesian SkyGrid tree prior. We set substitution rates to the fixed value of 3.27E-7 substitutions/site year^{-1} as determined earlier by Martínková et al. (2013). Four MCMC chains were run for 200 million generations each with parameters sampled every 20,000 generations. Convergence of the chains and Effective Samples Size was checked in Tracer 1.7.1 (Rambaut et al., 2018). Tree files were combined using *logcombiner* and a Maximum Clade Credibility tree was summarized using *treeannotator* (Drummond et al., 2012).

2.8. Demographic analyses

More detailed analyses aimed at the reconstruction of regional population dynamics were undertaken for two regions, the Western Carpathians and Northern Spain. While constructing both datasets, we choose only ancient sequences obtained from radiocarbon dated layers or from layers constrained with two dated layers. Sequences of present-day individuals were chosen from broadly the same area as the ancient ones. Based on palaeontological and genetic data obtained here we proposed a number of scenarios that could lead to the observed temporal pattern of genetic diversity of the common vole in both locations. We tested the support for these scenarios using an Approximate Bayesian Computation approach (Beaumont et al., 2002). The analyses including coalescent simulations, model choice and pseudo-observed dataset (PODs) analyses were performed in BaySICS v. 1.9.7.9.5 software (Sandoval-Castellanos et al., 2014). First, we performed pilot coalescent simulations to optimise parameters and choose a proper set of summary statistics (SuSt). The priors of effective population size (N_e) had an exponential distribution in pilot simulations to better screen a sample range. In the final simulations we replaced these priors with uniform distributions based on 95% credible intervals of N_e posterior distributions. The age of samples, as well as times of demographic changes, were also set as uniform priors. We set the generation time of species to 1 per

year and mutation rate to 32.7% per million years (Myr^{-1}) following Martínková et al. (2013). Other parameters such as transition/transversion bias, gamma shape parameter and nucleotide frequency were set based on calculations in MEGA X (Kumar et al., 2018). One and two million simulations were run in the pilot and the final analysis respectively. For the final analyses we chose the SuSt where the distribution was useful in distinguishing between scenarios (Lagerholm et al., 2014). In the analyses of the Central European dataset we used number of haplotypes, segregating sites, pairwise differences, nucleotide diversity, gene diversity for two statistical groups and Fst and pairwise differences between those groups. In the analyses of the Spanish dataset, we used segregating sites, pairwise differences, nucleotide diversity and Tajima's D for three statistical groups and pairwise differences between those groups. The scenario comparison was performed using Bayes factor (BF) for every pair of scenarios. The consistency of the model likelihoods and BFs were assessed by applying the procedure with 20 different acceptance proportions, from 0.0025% to 0.5% as in Smith et al. (2017). We also performed the PODs analyses to estimate the probability of corrected model selections. We compared 1000 PODs with two million final simulations.

To reconstruct changes in effective female population size of common vole we used the Bayesian SkyGrid method (Gill et al., 2013). Bayesian phylogeny was inferred using Beast 1.8.4 with similar parameters as for the initial tree but applying a strict clock. Two MCMC chains were run for 50 million generations each with parameters sampled every 5000 generations. Convergence and Effective Samples Size was checked, and Bayesian SkyGrid was reconstructed in Tracer 1.7.1 from two combined logfiles.

2.9. Radiocarbon dating

Most of the samples obtained for genetic analyses were teeth, too small for radiocarbon dating (<10 mg) thus in most cases we had to rely on stratigraphic dating. To improve stratigraphic information available for the sites from which the analysed specimens originated we obtained radiocarbon dates for six sites that lacked absolute dating. Dating was performed in Poznan Radiocarbon Laboratory (Poznań, Poland) and in Beta Analytics (Miami, USA). In addition, we attempted to date the 10 largest vole mandibles (40−100 mg) which yielded DNA sequences. Dating was performed in the Centre of Applied Isotope Studies at the University of Georgia (Athens, USA). Radiocarbon ages were calibrated with Oxcal 4.2 (Ramsey and Lee, 2013) using IntCal13 (Reimer et al., 2013) calibration curve.

3. Results

3.1. Sequencing results, age assignment and data validation

We recovered mtDNA cytochrome *b* sequence from 142 specimens from 31 sites dated to the post-LGM and Holocene. Ninety-seven specimens were identified as common vole (*M. arvalis*), 41 as field vole (*M. agrestis*), and two each as narrow-headed vole (*Lasiopodomys gregalis*) and European pine vole (*M. (Terricola) subterraneus*). In the first instance ages were assigned to genetic sequences based on stratigraphic information available for a particular site (Table 1, Appendix A, Supplementary Tables B3 and B5).

We used two approaches to validate the assigned ages of the obtained sequences. First, we checked for damage patterns characteristic for ancient DNA sequences. We found that 16 samples, generated using the targeted enrichment approach, either have no damage, or very low levels of damage, at the ends of DNA molecules (below 10%). In the case of eight of those specimens this maybe the

result of their relatively recent age (Late Holocene) although the remaining eight come from older layers and the lack of DNA damage suggests that they have been introduced from younger levels. Second, we checked whether the ages assigned to genetic sequences were congruent with their divergence from the root of the tree. We found that five samples had a particularly high divergence from the root of the tree, more than expected according to their associated dates suggesting that they were substantially younger. As a result of both validation procedures, we removed ten genetic sequences from our dataset (Supplementary Table B3). These two approaches only detect extreme cases of material being analysed that was much younger than suggested by their stratigraphic provenance and smaller scale mixing would not be detected. To avoid drawing conclusions based solely on the stratigraphic dating we obtained direct radiocarbon dates for ten available common vole mandibles which represent different mtDNA lineages (Table 1).

Due to the very small sample size of the material to be dated (mostly less than 100 mg) the radiocarbon dating laboratory was not able to provide C:N ratios of the extracted collagen. However, the collagen yields were relatively high (≥2%), and the obtained dates, with one exception, fit well with the stratigraphy of the sites from which they originated (Appendix A).

3.2. Distribution of common vole mtDNA diversity during the post-LGM and Holocene

The Bayesian phylogeny reconstructed with ancient and modern common vole specimens revealed six mtDNA lineages with moderate to high posterior probability values (Fig. 1). They correspond to Eastern, Balkan, Central, Italian, Western-North (WN) and Western-South (WS) mtDNA lineages which were described previously and make up the present-day mtDNA diversity of the species (Stojak et al., 2016, 2015; Tougard et al., 2008) (Figs. 1 and 2A).

The geographic distribution of mtDNA lineages during the post-LGM period was similar to that of the present-day with the exception of Central Europe. Most of the specimens from sites in Central Europe, and specifically from the Western Carpathians, yielded the Central mtDNA lineage (47 specimens). This lineage today is found in more western areas such as modern Switzerland, Germany, the Netherlands and Denmark. Only five individuals were assigned to the Eastern mtDNA lineage which is the only one found in present-day Central and Eastern Europe (Fig. 2). Two sites dated to post-LGM, including Rejtek I rock-shelter from the Pannonian Basin and Muierilor cave in Romania, only included individuals belonging to the Eastern lineage (two and one specimens, respectively). At others sites the Eastern lineage co-occurred with the Central lineage and was always in a minority. One individual from Bivak cave in Hungary belonged to the Balkan lineage. Our Central European Holocene record is more limited although we found both Eastern and Central lineages in the Early Holocene. However, the Mid-Holocene only included individuals from the Eastern lineage (Fig. 2B, Supplementary Table B3).

In Western Europe we found the WN lineage from sites in France (Coulet des Roches), Belgium (Trou Al'Wesse) and the UK (Bridged Pot). An Italian lineage was present in the northern Italian site of Riparo Tagliente (Verona province). A divergent haplotype of this lineage was also found in Ljubićeva pećina (Istria, Croatia), where the Eastern lineage is present today. In Spain, both in post-LGM and Holocene periods, all individuals belonged to the WS lineage. At the two Spanish sites, El Portalón and El Mirador, we found a highly divergent branch of the WS lineage that separated between 35 and 40 ka ago. This lineage was found in both, the Late Pleistocene and Holocene layers, but is not present in the modern population.

Table 1
Radiocarbon dates obtained from Late Pleistocene common vole mandibles.

No	UGAMS#[a]	Sample ID	Country	Site	Layer	mtDNA lineage[b]	Starting material (mg)	Collagen yield (%)	^{14}C age	Calibrated (BP) (95.4% range)		
										lower	upper	median
1	43,306	MI376	Czechia	Býčí skala	8c	CEN	42	7.9	9860 ± 30	11,316	11,211	11,249
2	43,307	MI378	Czechia	Býčí skala	8c	CEN	56	4.4	8820 ± 25	10,120	9704	9853
3	43,311	MI1337	Slovakia	Muráň cave	3/4	CEN	40	7.8	12,110 ± 30	14,112	13,827	13,988
4	43,312	MI1359	Belgium	Trou Al'Wesse	4b	WN	91	2.9	24,750 ± 60	28,968	28,565	28,770
5	43,313	MI1368	Belgium	Trou Al'Wesse	12	WN	57	3.3	25,850 ± 60	30,428	29,706	30,078
6	43,314	MI1371	UK	Bridget Pot cave		WN	70	4.8	9670 ± 30	11,199	10,870	11,125
7	43,315	MI2136	Spain	El Miron	306	WS	63	2.5	13,220 ± 30	16,051	15,737	15,890
8	43,308	MI659	Spain	El Mirador	MIR49	WS	110	5.9	8040 ± 25	9020	8779	8983
9	43,309	MI1285	Spain	El Portalón	P1	WS	88	4.1	17,420 ± 40	21,235	20,835	21,019
10	43,310	MI1286	Spain	El Portalón	P1	WS	48	2	16,560 ± 40	20,158	19,793	19,984

[a] AMS Laboratory code.
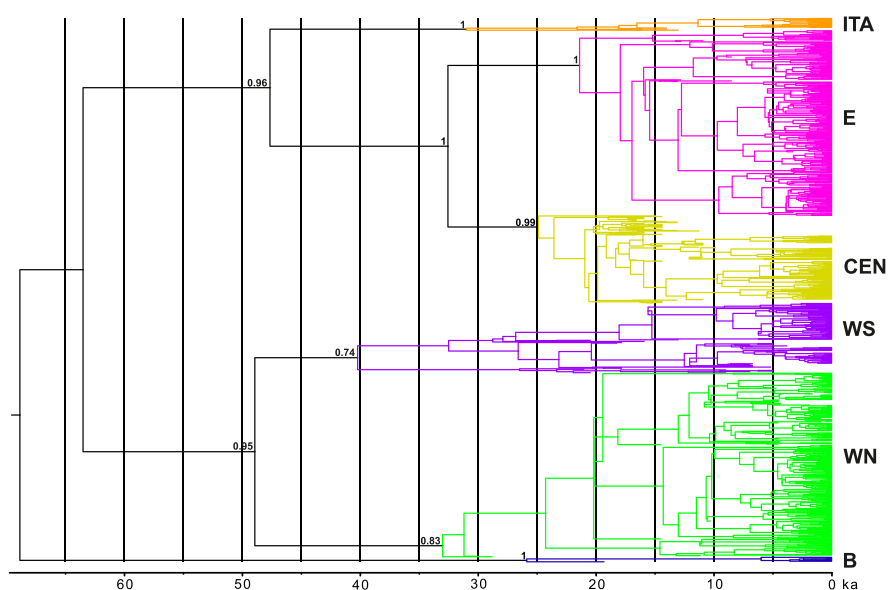[b] CEN − Central; WN − Western-North; WS − Western-South.

Fig. 1. Bayesian phylogeny of the post-LGM, Holocene and extant common voles from Europe. Maximum Clade Credibility tree, based on 1053 bp mtDNA cytochrome *b* fragment, summarized from 9000 trees sampled from 720 million MCMC generations. Numbers at nodes indicates posterior clade probabilities of the major lineages: B - Balkan, ITA − Italian, CEN − Central, E − Eastern, WN − Western-North, WS − Western-South.

3.3. Reconstruction of regional evolutionary histories

The number of sequences obtained for two regions, the Western Carpathian area and Northern Spain, enabled more detailed demographic inferences to be made.

The Western Carpathian dataset comprises 152 sequences, 73 from extant and 79 from ancient specimens (Supplementary Table B6). We used approximate Bayesian computations (ABC) to investigate the genetic support for four demographic scenarios that might have led to the temporal pattern of genetic diversity observed in the Western Carpathian area (Fig. 3). To test whether the observed pattern was not caused only by genetic drift the first scenario assumed a constant population size since the LGM until present (model A). The second scenario was that the post-LGM common vole population went through a bottleneck around the YD or the Pleistocene/Holocene transition (model B) as proposed by Stojak et al. (2015). A third possibility was that the post-LGM population was composed of individuals that diverged some time ago, then came into contact during the post-LGM and then went through a bottleneck (model C). Finally, a fourth scenario was that

Central Europe was inhabited by two populations, the one present during the post-LGM went extinct and was replaced by the second around the Pleistocene/Holocene transition (model D).

The ABC model choice analysis supported the scenario assuming complete population replacement (model D) with a likelihood ranging from 0.709 to 0.851 (with an average 0.775, Supplementary Table B7) depending on the acceptance proportion that was used in the analysis. The Bayes Factors indicate substantial support for model D as opposed to A and strong and very strong support for model D compared to that given to B and C, respectively (Supplementary Table B7). Additionally, the PODs analysis indicated that the probability of choosing the right scenario were 0.974, 0.943, 0.809, 0.929 for models A, B, C, and D respectively which means that the analysis has high statistical power.

To investigate the history of the population from Northern Spain we used a subset of our dataset comprising 58 cytochrome *b* sequences, 30 from extant and 28 from ancient specimens (Supplementary Table B8). All sequences belonged to the WS mtDNA lineage suggesting no major change in the population of common voles during that time. To check for more subtle changes
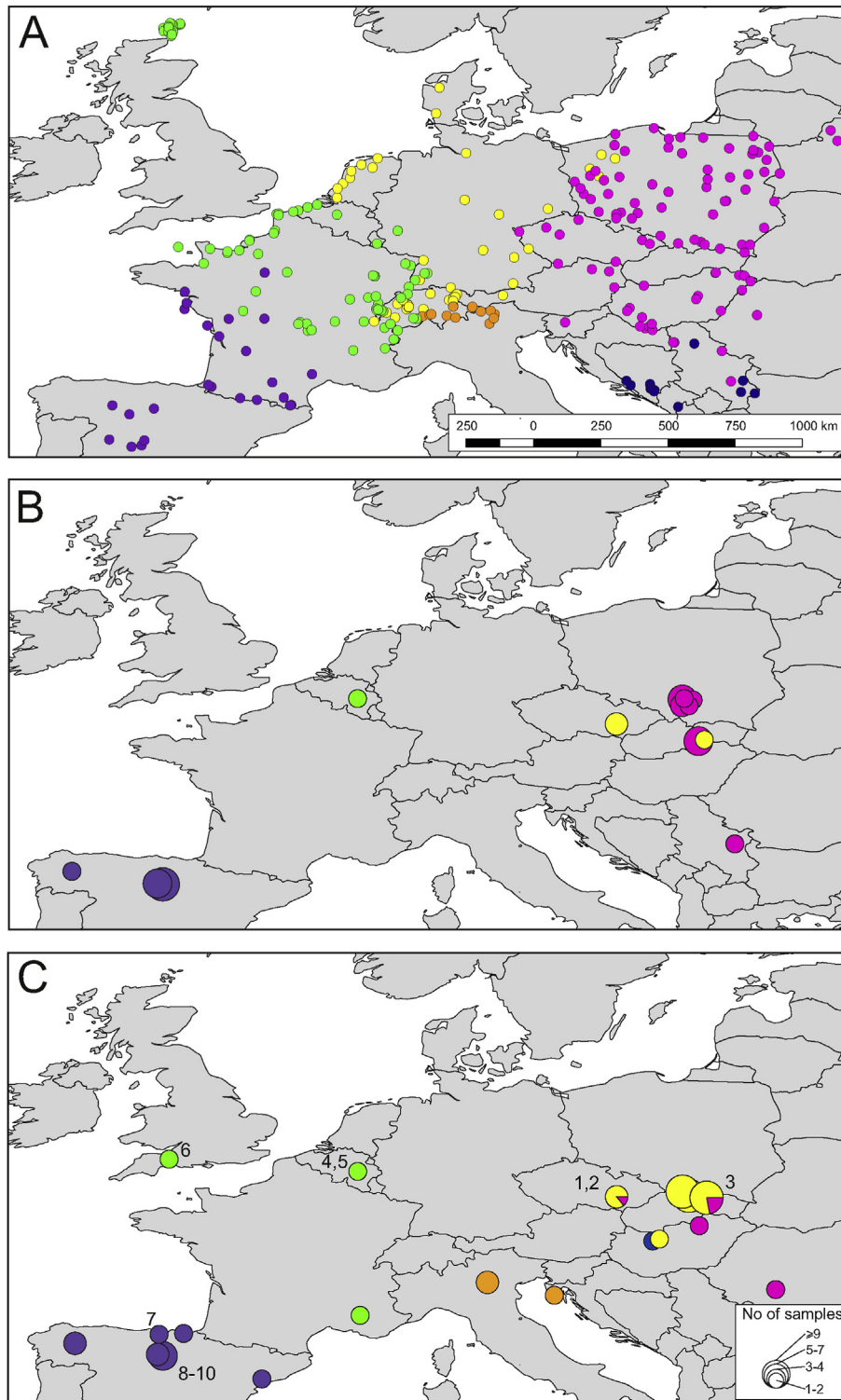
Fig. 2. Distribution of mtDNA diversity of common vole in Europe. A – modern, B – Holocene, C – post-LGM. Colour correspond to mtDNA lineages (pink – Eastern; yellow – Central; orange – Italian; green – Western-North; violet – Western-South; navy blue – Balkan). Numbers on panel C indicates site of origin of radiocarbon dated specimens and correspond to these in Table 1.

that did not involve lineage replacement we used Bayesian SkyGrid analysis which revealed modest changes of effective population size of the Spanish population through the last 30,000 years.

The highest effective population size was found to be at the end of LGM around 20−19 ka and decreased towards the Holocene with a minimum in the Early-to Mid-Holocene followed by a slight recovery up to the present day (Fig. 4). Additionally, we tested support for the four demographic scenarios using the ABC approach (Fig. 5). The first scenario assumed a constant vole population size through time (Model A). The second one (Model B) assumed the
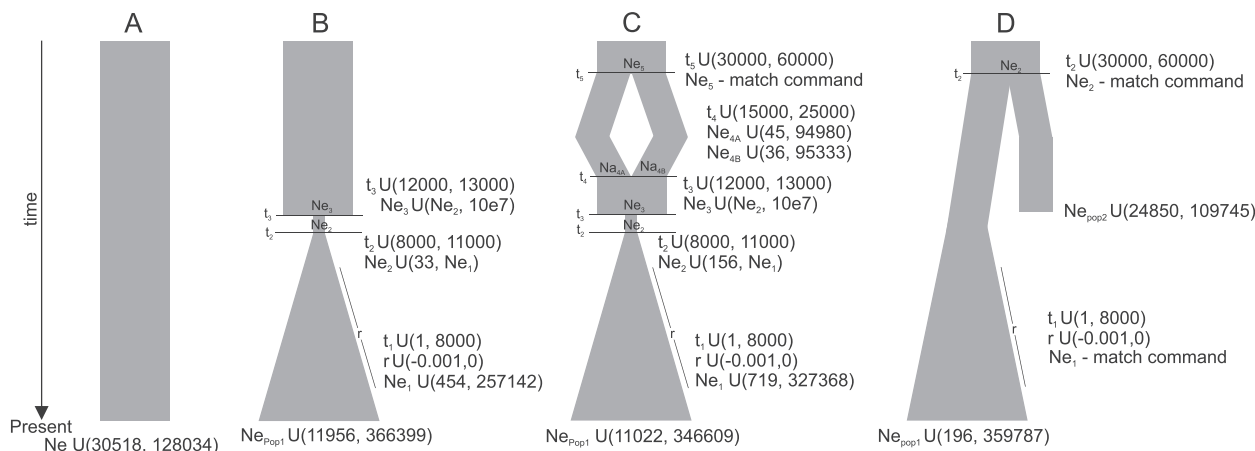
Fig. 3. Schematic representation of demographic scenarios (A−D) for the Western Carpathian common vole population tested using ABC approach. The priors that describes each scenario are given. t_x − timing of the event; Ne_x − effective population size at the time t_x; r − growth rate.

bottleneck event during the post-LGM period followed by re-expansion at the onset of the Holocene. This model was used to test whether there was an impact of the YD on population from Spain. Model C was based on the SkyGrid reconstruction of effective population size and the fossil record and assumed that the highest population size at the end of the LGM was followed by population decline between 20 and 10 ka and since the Early Holocene the population size remained constant. Finally, model D assumed population decrease between 20 and 12 ka and was used to test whether we were able to detect any change in effective population size.

The analysis failed to reject constant population size as a best supported model (Supplementary Table B9). However, it has been shown that in cases of large, rodent-like populations ABC usually fails to detect population declines or bottlenecks of magnitude smaller than 95% (Mourier et al., 2012).

4. Discussion

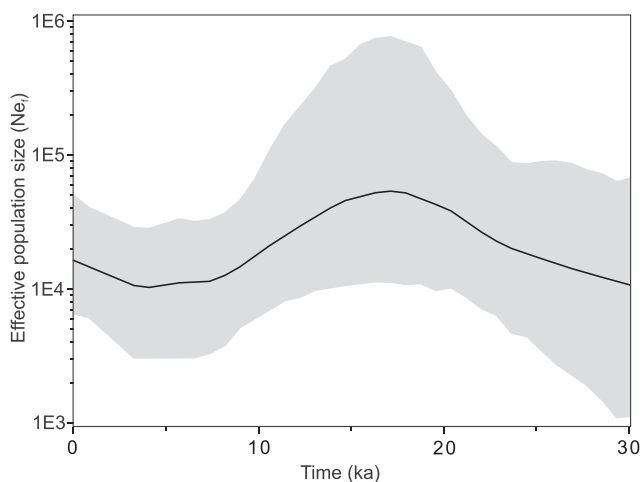Late Pleistocene evolutionary histories of species are usually

Fig. 4. Bayesian reconstruction of female effective population size changes through time for common voles from Northern Spain. Median estimate of Ne_f (solid line) and associated 95% HPD interval (grey area).

reconstructed based on the fossil record or on the distribution of genetic diversity in modern populations. Both these approaches, although powerful, have limitations. On their own they may lead to incomplete or even incorrect conclusions. The use of ancient DNA enables the direct estimation of genetic diversity in past populations and may reveal demographic processes which are otherwise unavailable.

4.1. Evolutionary history of common voles in the Western Carpathians

The temporal distribution of genetic diversity in the Western Carpathian area is consistent with a population replacement around the Pleistocene/Holocene transition. The evidence for this comes from 55 specimens from layers dated to the post-LGM and Early Holocene periods that yielded a Central mtDNA lineage which was replaced by a population belonging to the Eastern lineage. The age of the three Central lineage specimens was further confirmed by direct radiocarbon dating the specimens themselves yielding Late Glacial and Early Holocene dates (Table 1). We used an ABC approach to test whether the more probable is the scenario of complete replacement of the Central population by the Eastern (in this case the few Eastern individuals found in the same layers as Central ones were in fact of different ages, or were the result of material mixing at the site) or whether the scenario existed in which Western Carpathians was inhabited by individuals belonging to both the Central and Eastern mtDNA lineages during the post-LGM and was followed (between 12 and 8 ka) by the Central one becoming extinct while the Eastern one survived spreading throughout the region (Fig. 3). The ABC analysis supported the population replacement scenario. The alternative scenario where selective extinction of the Central lineage occurred would require that the individuals belonging to different mtDNA lineages differ in ecological plasticity or that Eastern lineage had some advantageous adaptations that allowed it to gradually outcompete individuals from Central lineage. Several recent studies suggested that the spatial distribution of the present-day mtDNA diversity of a range of mammals, including common voles, is correlated with specific environmental and climatic features (McDevitt et al., 2012; Tarnowska et al., 2016; Stojak et al., 2019). This suggests that distinct populations of one species may differ in their adaptations to certain climatic and environmental conditions. Therefore, we cannot completely rule out the possibility that individuals from the
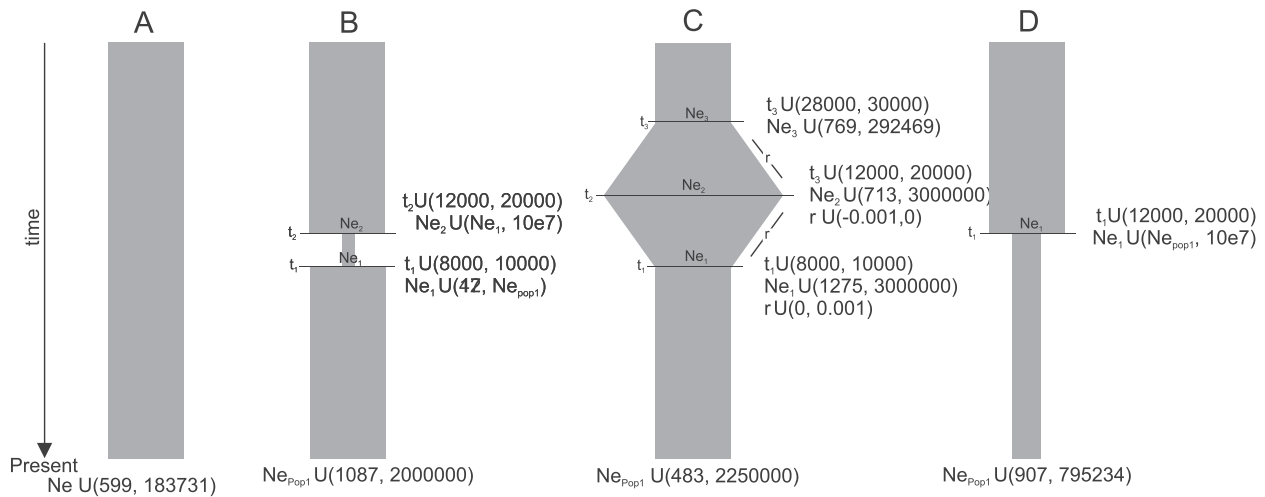
Fig. 5. Schematic representation of demographic scenarios for Spanish common vole tested using the ABC approach. The priors that describes each scenario are given. t_x — timing of the event; Ne_x — effective population size at the time t_x; r — growth rate.

Eastern lineage gradually replaced the Central ones as a result of their better adaptations to Late Glacial and Early Holocene environments.

Regardless of the details of this process it seems that the final replacement took place in the Early Holocene. This is confirmed by the Central lineage specimens present in the Early Holocene layers in Peskö cave (SE Slovakia) and Býčí skala (in the Moravian karst) (Horáček and Ložek, 1988; Horáček and Sázelová, 2017; see also Appendix A) and especially by the two directly dated Central lineage specimens from the latter site which yielded ages of 9.8 and 11.2 ka BP, respectively (Table 1). The Early Holocene replacement is consistent with the previous estimations that an increase in the population size of the Eastern lineage started at *ca.* 10−8 ka (Stojak et al., 2015).

In line with these findings are the results from the reconstruction of the faunal succession for the northern parts of the Carpathian Basin which showed a slight decrease of common vole abundance around the YD with another drastic decrease around the Boreal period (Pazonyi, 2004). This suggests that the extinction of Central lineage in the Western Carpathians may have taken place as a result of environmental rearrangements during the Preboreal period.

The primary habitat of the common vole is grassland. Central Europe during the Early and Middle Holocene was covered with a dense forest over vast areas as revealed by many pollen diagrams (see e.g. Mitchell, 2005). Although the recent palaeovegetation reconstructions showed continuous presence of patches of open land in the Western Carpathians and adjacent areas throughout Late Glacial and Holocene (Abraham et al., 2016; Kuneš et al., 2015; Trondman et al., 2015) the proportion of open landscapes had fallen significantly around 9−8 ka in many regions (Abraham et al., 2016; Jamrichová et al., 2017; Kuneš et al., 2015). At this time the climate became wetter (Feurdean et al., 2014; Jamrichová et al., 2017) and the semi-open pine forests dominating the Early Holocene were replaced by more diversified plant communities with spruce forests and mixed oak woodlands amongst others (Abraham et al., 2016; Kuneš et al., 2015; Pokorný et al., 2015). Thus, the extirpation of the Central lineage may have been caused by a drastic loss of suitable habitats.

4.2. Evolutionary history of common voles in Western Europe and the British Isles

Two radiocarbon dated specimens from Trou Al'Wesse (Belgium) yielded a pre-LGM ages. They belonged to the WN lineage although they diverged earlier than the coalescence of the extant populations (Fig. 1). This suggests that population continuity existed in the region throughout the last 30 ka rather than there being a turnover, even if the population decreased in numbers as a result of the LGM. Although the genetic evidence is still very limited this is concordant with the cryptic northern refugium hypothesis (Stewart and Lister, 2001). The other interesting case is the single specimen from Bridged Pot cave dated to the Early Holocene. At present there are no common voles in the British Isles with the exception of the Orkney Isles, where they have been introduced by humans *ca.* 5000 years ago (Martínková et al., 2013). *Microtus arvalis* has not been considered to be part of the British fauna of the Last Glacial and only the field vole has been identified in the fossil record (Coard and Chamberlain, 1999; Currant and Jacobi, 2001) although there are problems distinguishing these two species based on dental characters (Navarro et al., 2018).

Recently, a number of common vole remains were identified using collagen fingerprinting from Pin Hole cave (Creswell Crags, UK) (Buckley et al., 2018). Although the deposits Pin Hole have been shown to be mixed (Stewart and Jacobi, 2015), this suggests that the common vole was present in the British Isles during the Late Pleistocene and/or early Holocene. The phylogenetic position of the individual from Bridged Pot cave suggests that it was a part of the continuous population of mainland Europe (Fig. 2). Given the age of the specimen (Table 1) the possible scenario explaining its presence in the British Isles may be that the common vole may have expanded to Britain during the Late Glacial warming and their local extinction was then caused by either YD cooling or the Holocene reforestation. The disappearance of the connection between the British Isles and continental Europe during the Early Holocene may have prevented the species' subsequent recolonization. In other small mammals inhabiting Britain today such as the field vole, bank vole (*Clethrionomys glareolus*), water vole (*Arvicola amphibius*) and pygmy shrew (*Sorex minutus*) the populations of these taxa, which colonized Britain during Late Glacial, retreated to fringes of the island possibly as a result of YD cooling (Brace et al., 2016; Searle

et al., 2009). Subsequent populations of all these species were able to recolonize Britain at the onset of the Holocene. This was not the case for the common vole. Recently Martínková et al. (2013) showed that recolonization of the northern areas of France and Belgium by the common vole was relatively late and started not earlier than 2000 years ago, long after the disappearance of land connecting the British Isles and mainland Europe.

4.3. Evolutionary history of common voles in Spain

In Spain, the distribution of genetic diversity through time and the reconstructed trajectory of population size changes suggest population continuity with a possible decrease around the Late Glacial and Early Holocene. The demographic reconstruction was mostly done using the stratigraphically dated sequences with only four being directly dated using radiocarbon dating, thus there is a level of uncertainty associated with this conclusion. However, the reconstructed trajectory fits well with the changes in the abundance of common vole remains observed on palaeontological sites across Northern Spain and Southern France. At the El Miron site (Cantabrian Cordillera) the maximum abundance of common vole falls between 27 and 15 ka, with the onset of Bølling-Allerød the decline is observed leading to a complete disappearance in the Early Holocene. Vole remains reappear in the Chalcolithic period at around 4 ka (Cuenca-Bescós et al., 2009). The same is seen at other sites like Antoliñako Koba (Biscay) (Rofes et al., 2015), Santimamiñe (Biscay) (Rofes et al., 2013) and on the Galician site Valdavara-1 (López-García et al., 2011). A similar pattern was found in South-Western France (Royer et al., 2016), suggesting similar population history throughout the whole range of the WS lineage. The trajectory of common vole populations seems to follow the general pattern of paleoenvironmental changes in Spain over the last 30 ka. During the LGM and post-LGM grasslands and steppe vegetation prevailed in Northern Spain providing the preferred habitat type of the common voles (Carrión et al., 2010; Fletcher et al., 2010). From ca. 15 ka oak (Quercus sp.) and pine (Pinus sp.) forests began to appear reaching a peak during the Early Holocene (Carrión et al., 2010). Thus, the loss of primary habitat due to an expansion of forests may be the cause of the observed population decrease. There is no clear change in paleoenvironmental records from the Middle Holocene onwards, however during that time a growing pressure of humans on the landscape has been recognized. The human activities, involving deforestation by burning, pastoralism and ploughing, were highly uneven, both spatially and temporarily, but clearly visible in palynological records of the Chalcolithic and Bronze Age (Carrión et al., 2010). It has been argued that human activities affected small mammal communities even earlier, from the Neolithic onwards (López-García et al., 2013). Thus, the slight recovery of population size observed on SkyGrid plot and in the fossil record may have been caused by an increase in human-maintained grasslands, the main present-day habitat of the common vole.

4.4. The post-glacial history of common vole populations

The use of ancient DNA to investigate evolutionary histories of animals revealed that the Late Pleistocene was a highly dynamic period marked with numerous faunal turnovers (extinctions, regional extirpations and population replacements) most of which had not been recognized earlier from the fossil record (Baca et al., 2017). Most of these events were grouped in two distinct clusters. The first one was around ca. 37–28 ka (Greenland Interstadials 7–4) (Cooper et al., 2015). During that time the native European population of mammoths (M. primigenius) (lineage III) was replaced by a population coming from Asia (lineage I) (Palkopoulou al.,

2013; Fellows Yates et al., 2017). Also local populations of Ursus spelaeus were replaced by U. ingressus in the Ach valley (Germany) (Münzel et al., 2011). Population replacement was also recorded in the collared lemmings (Dicrostonyx torquatus) which was probably extirpated from Europe for some time between ca. 40 and 32 ka (Brace et al., 2012; Palkopoulou et al., 2016).

It was suggested that the Late Pleistocene faunal turnovers were mainly driven by the abrupt climate warmings of the Greenland Interstadials while the gradual changes like the LGM had milder effects on populations (Cooper et al., 2015). Although this was not always the case as exemplified by the two Europe-wide population replacements of cold-adapted collared lemming that took place between 23 and 20 ka BP which were not associated with any clearly recognisable climate changes. However, this LGM turnovers in the collared lemming (Brace et al., 2012; Palkopoulou et al., 2016) were correlated with the temporary disappearance of the mammoth (Brace et al., 2012; Nadachowski et al., 2018).

In this study we investigated the evolutionary history of the common vole during the post-LGM period which included the second cluster of extinctions and faunal turnovers (Cooper et al., 2015). During this period several cold-adapted species became extirpated from Europe (Puzachenko and Markova, 2019). Meanwhile temperate taxa expanded from their LGM refugia. Their expansion was disturbed by the short glacial re-advance of the YD. The impact of this cooling on temperate species has not yet been fully characterised although the YD has been shown to cause significant range reduction of large ungulates such as roe deer (Capreolus capreolus) (Sommer et al., 2009) and red deer (Cervus elaphus) (Sommer et al., 2008). It was also hypothesized as causing a severe population reduction of several rodents and a small carnivore in the British Isles (Brace et al., 2016; Searle et al., 2009). Among those species, the field vole (M. agrestis) experienced a Europe-wide bottleneck which apparently led to population replacement across the whole species' range. The demographic histories of field and common voles are frequently compared. These species, sympatric within most of their ranges, differ slightly in their habitat preferences. The common vole generally prefers drier locations to the field vole that prefers damper conditions (Jacob et al., 2014; Mathias et al., 2017). It was hypothesized that this difference in habitat preferences allowed common vole populations to endure cold and dry episodes, like the YD, relatively intact while of the field vole experienced drastic population reductions (Paupério et al., 2012).

However, our data suggests that the Late Glacial and the Early Holocene climate and environmental changes also affected common vole populations. At mid- and high latitudes in Central and Western Europe it led to local extinctions and population replacements.

In contrast to species that have been shown to suffer from YD cooling but were able to recover their populations across Europe at the advent of more favourable climatic conditions at the onset of the Holocene (Searle et al., 2009; Brace et al., 2016), the range of the common vole populations remained restricted, or their population densities were low, until the beginning of Middle Holocene, or even later, in the Western Europe.

The history of common vole populations at lower latitudes in Southern Europe was different. In Northern Spain we observed a population continuity throughout last 20 thousand years although the highest effective population size around the end of the LGM declined towards the Early Holocene and was followed by a slight recovery.

Altogether this suggest that, despite clear regional differences, the Early Holocene was a pivotal period for common voles across Europe during the last ca. 20 ka and that the main factor affecting populations of the species was habitat availability.

This study indicates that evolutionary histories of common vole populations were different across Europe and corroborate the hypothesis that abrupt changes, like those associated with the YD and the Pleistocene/Holocene transition had significant impact on populations at mid- and high latitudes of Europe.

Author contribution

M.B and A.N. conceived and supervised the study. M.B., D.P., K.B. performed laboratory experiments and analysed the data, K.D. performed ABC analyses. A.L., I. H., J.M.L-G, S.B.-C, P.P., E.D., E. C.-B., C. B., J. M. L., B. M., X. M. G. C.-B, M. K., Z. M., A. P., J.W., M.V.K., J.R.S., A.N. assembled paleontological materials and provided information on paleontological context, M.B., D.P., J.R.S and A.N. wrote the manuscript with the input from all the co-authors.

Data availability

DNA sequences obtained in this study were deposited in Gen-Bank under accession nos. MK748347-MK748442, MN537983. The phylogenetic tree is available from TreeBASE under accession no. 25268.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRediT authorship contribution statement

Mateusz Baca: Supervision, Conceptualization, Investigation, Formal analysis, Visualization, Writing - original draft, Writing - review & editing, Funding acquisition. **Danijela Popović:** Conceptualization, Investigation, Formal analysis, Writing - review & editing. **Katarzyna Baca:** Investigation. **Anna Lemanik:** Resources, Investigation. **Karolina Doan:** Formal analysis, Writing - original draft. **Ivan Horáček:** Resources, Writing - review & editing. **Juan Manuel López-García:** Resources. **Sandra Bañuls-Cardona:** Resources. **Piroska Pazonyi:** Resources. **Emmanuel Desclaux:** Resources. **Evelyne Crégut-Bonnoure:** Resources. **Claudio Berto:** Resources. **Jadranka Mauch Lenardić:** Resources. **Barbara Miękina:** Resources. **Xabier Murelaga:** Resources. **Gloria Cuenca-Bescós:** Resources. **Magdalena Krajcarz:** Resources. **Zoran Marković:** Resources. **Alexandru Petculescu:** Resources. **Jarosław Wilczyński:** Resources. **Monika Vlasta Knul:** Resources. **John R. Stewart:** Resources, Writing - review & editing. **Adam Nadachowski:** Conceptualization, Supervision, Resources, Writing - review & editing.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2020.106239.

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