

1 **Diverse responses of common vole (*Microtus arvalis*) populations to Late**  
2 **Glacial and Early Holocene climate changes – evidence from ancient DNA**

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41 *Holocene*

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43 Traditionally, the harsh climatic conditions during the Last Glacial Maximum (LGM) period  
44 have been considered the cause of local extinctions and major faunal reorganizations that took  
45 place at the end of the Pleistocene. Recent studies have shown, however, that many of these  
46 events were associated with abrupt climate changes during the so-called Late Glacial and the  
47 Pleistocene/Holocene transition. Here we used ancient DNA to investigate the impact of those  
48 changes on common vole (*Microtus arvalis*) populations in Europe. The common vole is a  
49 temperate rodent species widespread in Europe. The genetic diversity of modern populations  
50 and the fossil record suggests that the species may have survived cold episodes, like Last Glacial  
51 Maximum, not only in the traditional Mediterranean glacial refugia, but also at higher latitudes  
52 in so-called cryptic northern refugia located in Central France, the northern Alps as well as the  
53 Carpathians. However, the course of post glacial recolonization and the impact of the Late  
54 Glacial and Early Holocene climate changes on the evolutionary history of the common vole

55 remains unclear. To address this issue we analysed mtDNA cytochrome *b* sequences from more  
56 than a hundred common vole specimens from 30 paleontological sites scattered across Europe.  
57 Our data suggests that populations from the European mid- and high latitudes suffered a local  
58 population extinction and contractions as a result of Late Glacial and Early Holocene climate  
59 and environmental changes. The recolonization of earlier abandoned areas took place in the  
60 Middle to Late Holocene. In contrast at low latitudes in Northern Spain there was a continuity  
61 of vole population. This indicates different responses of common vole populations to Late  
62 Glacial climate and environmental changes across Europe and corroborates the hypothesis that  
63 abrupt changes, like those associated with Younger Dryas and the Pleistocene/Holocene  
64 transition, had a significant impact on populations at the mid- and high latitudes of Europe.

## 65 **1. Introduction**

66 The period following the LGM (Last Glacial Maximum) was characterised by a number of  
67 climate changes that deeply transformed terrestrial ecosystems (Cooper et al., 2015; Feurdean  
68 et al., 2014; Stuart, 2015). Since 18.5 ka there was a slow and gradual improvement of the  
69 climate followed by rapid warming at around 14.7 ka which led to expansion of boreal forests  
70 in many regions of Europe and marked the beginning of Bølling/Allerød Interstadial  
71 (corresponding to Greenland Interstadial 1; GI-1). This warm period was followed by the abrupt  
72 world-wide cooling called Younger Dryas (YD) that took place between ca. 12.7 – 11.7 ka  
73 (corresponding to Greenland Stadial 1; GS-1) and led to short-term re-expansion of steppe-  
74 tundra environments. Finally, around 11.7 ka the onset of Holocene was marked with a  
75 contraction of cold-adapted species and the emergence of forests. In Europe as a result of these  
76 oscillations many species adapted to cold and dry steppe, both large and medium size like  
77 reindeer (*Rangifer tarandus*) (Sommer et al., 2013), saiga antelope (*Saiga tatarica*)  
78 (Nadachowski et al., 2016), arctic fox (*Alopex lagopus*) (Dalén et al., 2007) and small like  
79 collared lemmings (*Dicrostonyx torquatus*) (Palkopoulou et al., 2016) or even *Pliomys*

80 *coronensis* (= *P. lenki*, priority discussed by Terzea, 1983) (Cuenca-Bescós et al., 2010) an  
81 Iberian endemic were extirpated. Temperate and woodland species in general re-expanded over  
82 the region.

83 The common vole (*Microtus arvalis*) is at present one of the most common rodents in  
84 continental Europe (apart from areas such as Scandinavia and southernmost parts of Iberian,  
85 Italian and Balkan peninsulas where it is absent). It lives in well-drained open habitats, from  
86 lowlands to mountain pastures at elevations up to c. 3,000 m, being often abundant in cultivated  
87 fields and is regarded as an agricultural pest (Pardiñas et al. 2017). The earliest fossil record of  
88 this species is from Western Europe at Hundersheim (Maul and Markova, 2007) and  
89 Meisenheim 1 in Germany (van Kolfschoten, 1990) and Dobrkovice II (Fejfar, 1965) and  
90 Stránská skála cave in the Czech Republic (Kučera et al., 2009), all dated to ca. 0.6 – 0.5 Ma.  
91 During Last Glacial (ca. 119 ka – 11.7 ka) (Rasmussen et al., 2014) this species was common  
92 and widespread in both milder interstadials and cooler stadials (including the LGM), being the  
93 constant component of small mammal assemblages across almost the whole of Western  
94 (Chaline, 1972; López-García et al., 2017; Rhodes et al., 2018; Royer et al., 2016),  
95 Mediterranean (Bañuls-Cardona et al., 2017; Berto et al., 2017; Cuenca-Bescós et al., 2009,  
96 2010; López-García et al., 2014, 2013, 2011, 2010; Luzi et al., 2017; Luzi and López-García,  
97 2019; Nadachowski, 1984; Popov, 2018) and Central (Horáček and Ložek, 1988; Horáček and  
98 Sánchez-Marco, 1984; Jánossy, 1986; Luzi et al., 2019; Nadachowski, 1982, 1989; Pazonyi,  
99 2004; Socha, 2014) Europe. Surprisingly in the Eastern European Plain (Ukraine and European  
100 parts of Russia) *M. arvalis* was extremely rare or absent (Markova, 1982; Rekovets and  
101 Nadachowski, 1995; Rekovets and Nesin, 1993).

102 Based on the distribution of modern genetic diversity and supported by the continuous  
103 fossil record, it was suggested that the common vole, together with other species, survived the  
104 Last Glacial Maximum not only in traditional Mediterranean refugia but also in so called cryptic

105 northern refugia located at higher latitudes (Fink et al., 2004; Pedreschi et al., 2019; Stewart et  
106 al., 2010; Stewart and Lister, 2001; Stojak et al., 2015; Tougard et al., 2008). Central France,  
107 the Alpine region and the Carpathians were indicated as possible locations of such refugia (Fink  
108 et al., 2004; Heckel et al., 2005; Stojak et al., 2016; Tougard et al., 2008). However, the detailed  
109 trajectories of post glacial recolonization of the common vole remain unknown. The impact of  
110 the Younger Dryas cooling and environmental changes associated with the Pleistocene to  
111 Holocene transition are unclear. Sympatric rodent species such as the field vole (*Microtus*  
112 *agrestis*) suffered a drastic population reduction during the YD which probably led to the  
113 replacement of all European populations (Herman and Searle, 2011). More recently a detailed  
114 study of Central European populations of common voles revealed a signal of genetic continuity  
115 since LGM, although the start of population growth was estimated as ca. 9-8 ka suggesting that  
116 they may also have suffered a bottleneck near the Pleistocene to Holocene transition (Stojak et  
117 al., 2015).

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

## 122 **2. Material and Methods**

### 123 **Material**

124 A total of 321 samples (molars and mandibles) from 36 palaeontological sites across  
125 Europe were selected for genetic analysis (Supplementary Table B.1). The time range of the  
126 collected samples covered the Late Glacial and Holocene periods. All samples were  
127 morphologically described as *Microtus arvalis*, *M. arvalis/agrestis* or *Microtus* sp.

128 **██████** *DNA extraction*

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

136 **██████** *Multiplex amplification and sequencing*

137         In the case of 18 samples a fragment of mtDNA cytochrome b gene coding sequence was  
138 amplified using ten primer pairs in two multiplex PCR reactions (Supplementary Table B.2) as  
139 it was described in Palkopoulou et al. (2016). Purified PCR products were converted into  
140 double-indexed sequencing libraries (Kircher et al., 2012) and sequenced at MiSeq Illumina  
141 Platform (300 cycles, paired-end).

142 **██████** *Library preparation, target enrichment and sequencing*

143         Most of the samples were processed using the target enrichment approach  
144 (Supplementary Table B.3). Double-indexed sequencing libraries from genomic DNA were  
145 conducted following the protocol in Meyer & Kircher (2010) with few modifications. We  
146 applied a double-barcoding approach to minimise sequencing errors. Illumina adapters  
147 contained additional unique 7-bp sequences (barcodes) as it was described in Rohland et al.  
148 (2014). The second barcodes were introduced with indexing primers P5 and P7 (Kircher et al.,  
149 2012). Indexing PCR was performed using AmpliTaq Gold 360 Master Mix (Applied  
150 Biosystems) with the 19 amplification cycles. PCR products from three independent  
151 amplifications were pooled, purified using magnetic beads and concentrated to 40 µl. Target  
152 enrichment of mtDNA was performed as it was described in Horn (2012). Bait was prepared  
153 using modern DNA of the common and field vole. Complete mitochondrial genomes were

154 amplified as several overlapping fragments (see Supplementary Table B.4 for primer details).  
155 After purification, PCR products were sonicated at Covaris S220 to an average fragment length  
156 of 200 bp and enzymatically modified (Horn 2012). Two rounds of hybridization were  
157 performed, each 20-22 h long. Four samples were pooled in one reaction, differing from each  
158 other with indices and barcodes. Post-capture PCR were performed after each of hybridizations  
159 using Herculase II Fusion Polymerase (Agilent) and 10 to 15 cycles. Amplified products were  
160 purified, quantified, pooled in equimolar proportions and sequenced at NextSeq Illumina  
161 platform (150 cycles, paired-end, MidOutput kits).

#### 162 ██████ *Sequence data processing*

163 Raw Illumina reads were first demultiplexed based on index sequences using bcl2fastq  
164 Conversion Software v2.20 (Illumina) and barcoded reads were split into separate files using  
165 script Sabre (<https://github.com/najoshi/sabre>). AdapterRemoval v2 (Schubert et al., 2016) was  
166 used to trim adapter sequences and to collapse paired-end reads. Merged reads were aligned to  
167 reference mitochondrial genome of *M. arvalis* (NC\_038176.1) using the mem algorithm in *bwa*  
168 *0.7.17* (Li and Durbin, 2010). Only reads longer than 30 bp and with mapping quality over 30  
169 were retained and duplicates were removed applying SAMtools package. Consensus sequences  
170 were called using BCFtools package. In the case of samples processed using a multiplex PCR  
171 approach, after collapsing paired reads, sequences of primers were removed from amplicon  
172 sequences using *trim.seqs* command from the mothur (Schloss et al., 2009) and later the  
173 consensus from two replicates were compared and a final consensus called as in Stiller et al.,  
174 (2009).

#### 175 ██████ *Data validation*

176 MapDamage v.2 (Ginolhac et al., 2011) was used to check for damage pattern  
177 characteristic for ancient DNA and to estimate sequencing read length. To evaluate whether age  
178 assigned to sequences is congruent with its divergence from the root (RTT; Root-to-tip

179 divergence) we used TempEst 1.5.1 (Rambaut et al., 2016). As the input to TempEst 1.5.1 we  
180 used a best phylogeny chosen from 20 ML runs in RAxML (Stamatakis, 2014), using  
181 GTRGAMMA substitution model.

## 182 ██████ *Phylogenetic analyses*

183 In the phylogenetic reconstructions we used a 1,053 bp fragment of mtDNA cytochrome  
184 *b*. First, because all the extant samples were sequenced only for this fragment, Second, because  
185 in the majority of the samples, sequenced for the whole mtDNA, we observed regions where  
186 two different sequences were present. This was most probably the result of sequencing of  
187 nuclear sequences of mitochondrial origin (pseudogenes/*numts*) along with real mitochondrial  
188 sequences (Triant and DeWoody 2008). We did not notice this problem within cytochrome *b*.  
189 In order to determine phylogenetic position of Late Glacial and Holocene common voles we  
190 reconstructed a Bayesian phylogeny using Beast 1.8.4 (Drummond et al., 2012). For the  
191 reconstruction we used sequences of 829 extant common voles gathered from previous studies  
192 (Braaker and Heckel, 2009; Haynes et al., 2003; Heckel et al., 2005; Martínková et al., 2013;  
193 Stojak et al., 2016, 2015; Tougaard et al., 2008), 23 sequences from radiocarbon dated specimens  
194 from Orkney (Martínková et al., 2013) ), 38 sequences obtained earlier from two Polish sites -  
195 Oblazowa cave (western entrance) and the rock-overhang in Cisowa Rock sites (Lemanik et al.,  
196 submitted) and newly generated sequences from palaeontological specimens. |The phylogeny  
197 was reconstructed as in earlier studies (Stojak et al., 2015, 2016). We used a SDR06 model  
198 (Shapiro et al., 2006) in which data is partitioned into two partitions (first and second codon  
199 positions are linked and the third one is separated). A HKY +  $\Gamma$  substitution model was used  
200 for both partitions. We set the tip dates option on and each sequence that came from ancient  
201 individual had the age assigned based on its stratigraphic position or radiocarbon date  
202 (Supplementary Table B.3). We used an uncorrelated relaxed lognormal clock and a flexible  
203 Bayesian SkyGrid tree prior. We set substitution rates to the fixed value of 3.27E-7

204 substitutions/site year<sup>-1</sup> as determined earlier by Martínková et al. (2013). Four MCMC chains  
205 were run for 200 million generations each with parameters sampled every 20,000 generations.  
206 Convergence of the chains and Effective Samples Size was checked in Tracer 1.7.1 (Rambaut  
207 et al., 2018). Tree files were combined using *logcombiner* and a Maximum Clade Credibility  
208 tree was summarized using *treeannotator* (Drummond et al., 2012).

### 209 [REDACTED] *Demographic analyses*

210 More detailed analyses aimed at the reconstruction of regional population dynamics were  
211 undertaken for two regions, Central Europe and Spain. Constructing both datasets, we choose  
212 only ancient sequences obtained from radiocarbon dated layers or from layers constrained with  
213 two dated layers. Sequences of present-day individuals were chosen from broadly the same area  
214 as the ancient ones. Based on palaeontological and genetic data obtained here we proposed a  
215 number of scenarios that could lead to the observed temporal pattern of genetic diversity of  
216 common voles in both locations (Supplementary Data A1.2). We tested the support for these  
217 scenarios using an Approximate Bayesian Computation approach (Beaumont et al., 2002). The  
218 analyses including coalescent simulations, model choice and pseudo-observed datasets (PODs)  
219 analyses were performed in BaySICS v. 1.9.7.9.5 software (Sandoval-Castellanos et al., 2014).  
220 First, we performed pilot coalescent simulations to optimise parameters and choose a proper set  
221 of summary statistics (SuSt). The priors of effective population size ( $N_e$ ) had an exponential  
222 distribution in pilot simulations to better screen a sample range. In the final simulations we  
223 replaced these priors with uniform distributions based on 95% credible intervals of  $N_e$  posterior  
224 distributions. The age of samples, as well as times of demographic changes, were also set as  
225 uniform priors. We set the generation time of species to 1 per year and mutation rate to 32.7%  
226 per million years (Myr<sup>-1</sup>) following Martínková et al. (2013). Other parameters such as  
227 transition/transversion bias, gamma shape parameter and nucleotide frequency were set based  
228 on calculations in MEGA X (Kumar et al., 2018). One and two million simulations were run in

229 the pilot and the final analysis respectively. Selection of informative SuSt were carried out in  
230 the pilot simulations. For final analyses we chose the SuSt where the distribution was useful in  
231 distinguishing between scenarios (Lagerholm et al., 2014). In the analyses of the Central  
232 European dataset we used number of haplotypes, segregating sites, pairwise differences,  
233 nucleotide diversity, gene diversity for two statistical groups and Fst and pairwise differences  
234 between those groups. In the analyses of the Spanish dataset, we used segregating sites, pairwise  
235 differences, nucleotide diversity and Tajima's D for three statistical groups and pairwise  
236 differences between those groups. The scenario comparison was performed using Bayes factor  
237 (BF) for every pair of scenarios. The consistency of the model likelihoods and BFs were  
238 assessed by applying the procedure with 20 different acceptance proportions, from 0.0025% to  
239 0.5% as in Smith et al. (2017). We also performed the PODs analyses to estimate the probability  
240 of corrected model selections. We compared 1,000 PODs with two million final simulations.

241 To reconstruct changes in effective female population size in common voles we used the  
242 Bayesian SkyGrid method (Gill et al., 2013). First, Bayesian phylogeny was inferred using  
243 Beast 1.8.4 using similar parameters as for the initial tree but applying a strict clock.. Two  
244 MCMC chains were run for 50 million generations each with parameters sampled every 5,000  
245 generations. Convergence and Effective Samples Size was checked, and Bayesian SkyGrid was  
246 reconstructed in Tracer 1.7.1 from two combined logfiles.

#### 247 **■** *Radiocarbon dating*

248 Most of the samples obtained for genetic analyses were teeth, too small for radiocarbon  
249 dating (<10mg) thus in most cases we had to rely on stratigraphic dating. To improve  
250 stratigraphic information available for the sites from which the analysed specimens originated  
251 we obtained radiocarbon dates for six sites that lacked absolute dating. layer from sites where.  
252 Dating was performed in Poznan Radiocarbon Laboratory (Poznań, Poland) and in Beta  
253 Analytics (Miami, USA). In addition, we attempted to date the 10 largest vole mandibles (40 –

254 100 mg) which yielded DNA sequences. Dating was performed in the Centre of Applied Isotope  
255 Studies at the University of Georgia (Athens, USA). Radiocarbon ages were calibrated with  
256 Oxcal 4.2 (Ramsey and Lee, 2013) using IntCal13 (Reimer et al., 2013) calibration curve.

### 257 **3. Results**

#### 258 **Sequencing results, age assignment and data validation**

259 We recovered mtDNA cytochrome *b* sequence from 143 specimens from 24 sites dated  
260 to Late Glacial and Holocene periods. 97 specimens were identified as common voles (*M.*  
261 *arvalis*), 41 as field voles (*M. agrestis*), and two each as narrow-headed voles (*L. gregalis*) and  
262 European pine vole (*M. (Terricola) subterraneus*). Ages were assigned to genetic sequences  
263 based on stratigraphic information available for a particular site (Table 1, Appendix A,  
264 Supplementary Tables B.3 and B.5).

265 We used two approaches to validate the assigned ages of the obtained sequences. First,  
266 we checked for damage patterns characteristic for ancient DNA sequences. We found that 16  
267 samples, generated using the targeted enrichment approach, either have no damage, or very low  
268 levels of damage, at the ends of DNA molecules (below 10%). In the case of eight of those  
269 specimens this maybe the result of their relatively recent age (Late Holocene) although the  
270 remaining eight come from older layers and the lack of DNA damage suggests that they have  
271 been introduced from younger levels. Second, we checked whether the ages assigned to genetic  
272 sequences were congruent with their divergence from the root of the tree (Root-to-Tip analysis,  
273 RTT). We found that five samples had a particularly high divergence from the root of the tree,  
274 more than expected according to their associated dates suggesting that they were substantially  
275 younger. As a result of both validation procedures, we removed ten genetic sequences from our  
276 dataset (Supplementary Table B.3). These two approaches only detect extreme cases of material  
277 being analysed that was much younger than suggested by their stratigraphic provenance and  
278 smaller scale mixing would not be detected. To avoid drawing conclusions based solely on the

279 stratigraphic dating we obtained direct radiocarbon dates for ten available common vole  
 280 mandibles which represent different mtDNA lineages (Table 1).

281 Table 1. Radiocarbon dates obtained from Late Pleistocen common vole mandibles.

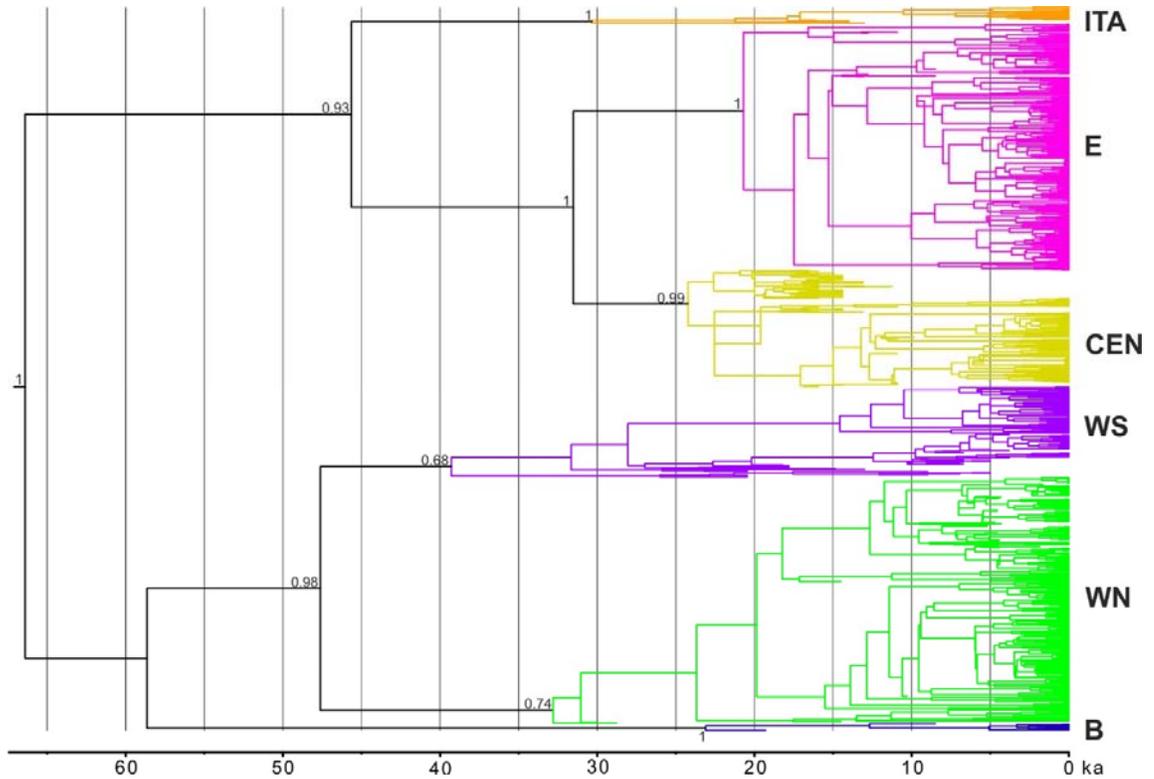
No	UGAMS#	Sample ID	Country	Site	layer	mtDNA lineage*	starting material (mg)	Collagen yield (%)	<sup>14</sup> C age	Calibrated	
										lower	upper
1	43306	MI376	Czechia	Býčí skála	8c	CEN	42	7.9	9,860 ± 30	11,316	11,2
2	43307	MI378	Czechia	Býčí skála	8c	CEN	56	4.4	8,820 ± 25	10,120	9,7
3	43311	MI1337	Slovakia	Muráň cave	3/4	CEN	40	7.8	12,110 ± 30	14,112	13,8
4	43312	MI1359	Belgium	Trou Al'Wesse	4b	WN	91	2.9	24,750 ± 60	28,968	28,5
5	43313	MI1368	Belgium	Trou Al'Wesse	12	WN	57	3.3	25,850 ± 60	30,428	29,7
6	43314	MI1371	UK	Bridget Pot cave		WN	70	4.8	9,670 ± 30	11,199	10,8
7	43315	MI2136	Spain	El Miron	306	WS	63	2.5	13,220 ± 30	16,051	15,7
8	43308	MI659	Spain	El Mirador	MIR49	WS	110	5.9	8,040 ± 25	9,020	8,7
9	43309	MI1285	Spain	El Portalón	P1	WS	88	4.1	17,420 ± 40	21,235	20,8
10	43310	MI1286	Spain	El Portalón	P1	WS	48	2	16,560 ± 40	20,158	19,7

282 \*- CEN – Central; WN – Western-North; WS – Western-South

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

### 287 **Distribution of common voles mtDNA diversity during Late Glacial and Holocene**

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



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**Figure 1. Bayesian phylogeny of the Late Glacial, Holocene and extant common voles from Europe.**

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Maximum clade credibility tree, based on 1,053 bp mtDNA cytochrome *b* fragment, summarized from 9,000 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. The phylogenetic tree is available from TreeBase project no. NNNNNN.

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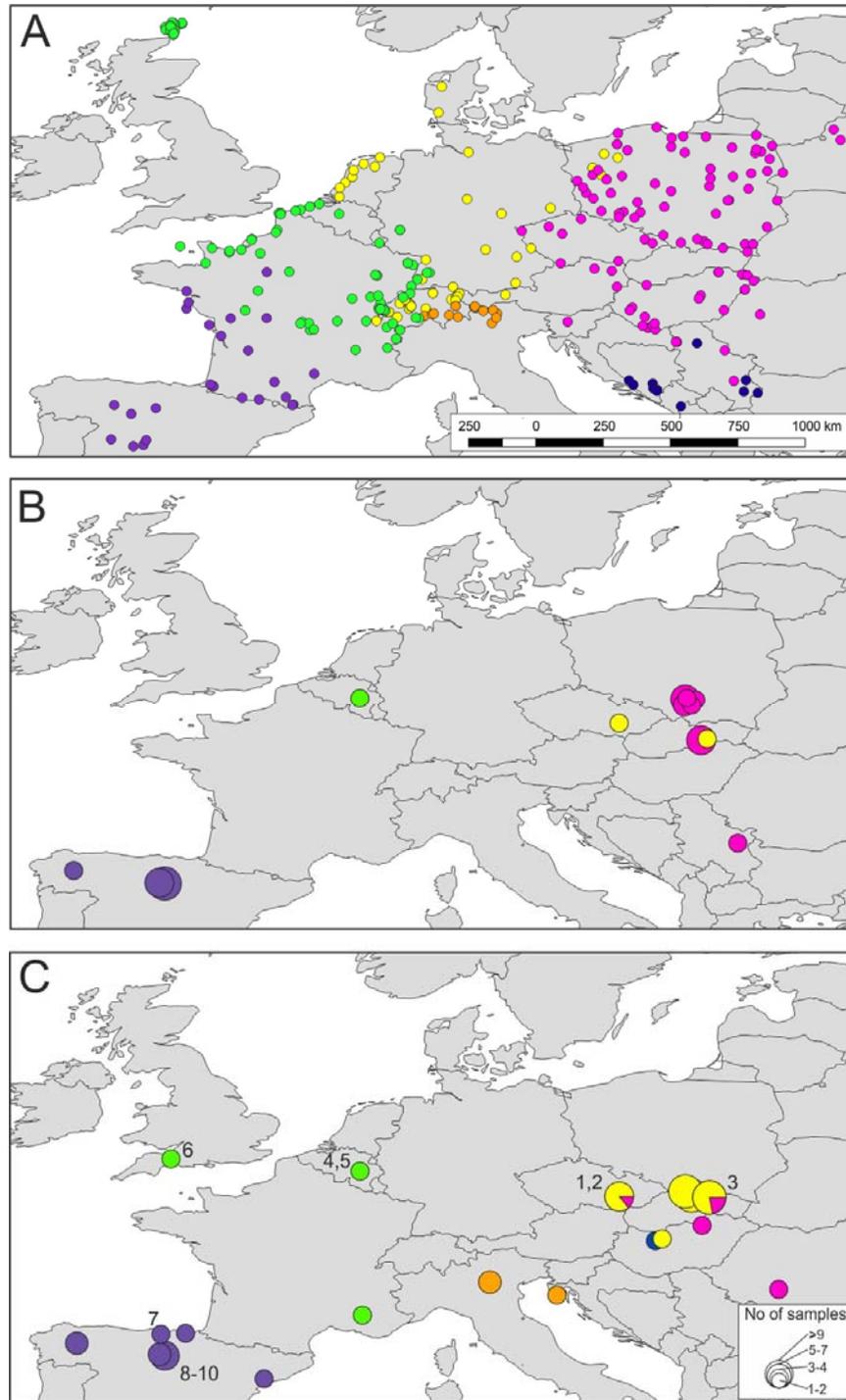
The geographic distribution of mtDNA lineages during the Late Glacial and Early Holocene period was similar to that of the present-day except for Central Europe. Most of the specimens from sites in Central Europe, and specifically from the Western Carpathians, yielded the Central mtDNA lineage (48 specimens). This lineage today is found more to the west in the territory of 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). Only two sites dated to Late Glacial Rejtek I. rock-shelter from the Pannonian Basin and Muierilor cave in Romania, only included individuals belonging to the Eastern lineage (two and one, respectively) on the others it co-occurred with Central lineage and was always in a minority One individual from Bivak cave in Hungary belonged to the

309 Balkan lineage. Our Central European Holocene record is more limited although we found both  
310 Eastern and Central lineages in the Early Holocene. However, the Mid-Holocene only included  
311 individuals from the Eastern lineage (Fig. 2B, Supplementary Table B.3).

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

320

321



**Figure 2. Distribution of mtDNA diversity of common vole in Europe.**

A – modern, B – Holocene, C – Late Glacial. 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.

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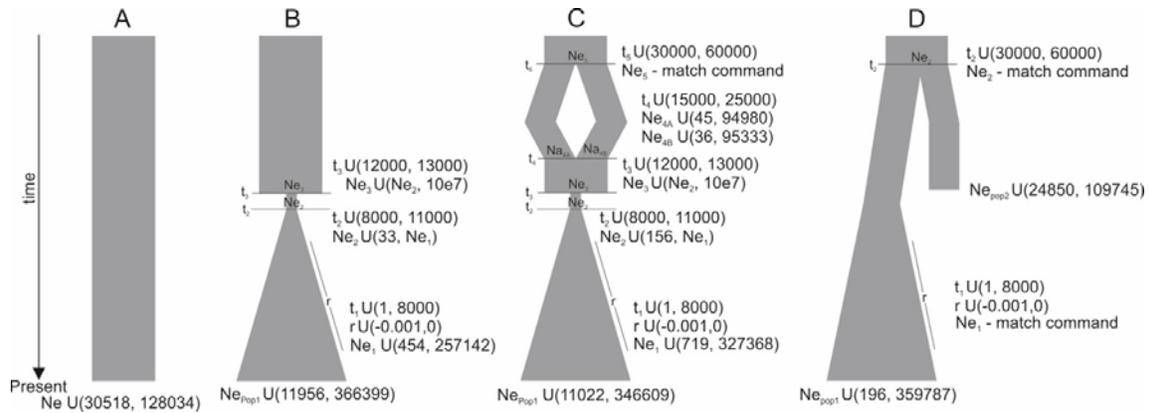
328 **█** *Reconstruction of regional evolutionary histories*

329       The number of sequences obtained for two regions, the Western Carpathian area and the  
330 Northern Spain, enabled the more detailed demographic inference.

331       The Western Carpathian dataset comprise 152 sequences, 73 from extant and 79 from  
332 ancient specimens (Supplementary Table B.6). We used approximate Bayesian computations  
333 to investigate the genetic support for four demographic scenarios that might have led to the  
334 temporal pattern of genetic diversity observed in Central Europe (Fig. 3). We tested whether  
335 there was a constant population since the LGM until present (model A). The second scenario  
336 was that the post-LGM common vole population went through a bottleneck around the Younger  
337 Dryas or the Pleistocene/Holocene transition (model B). A third possibility was that the post-  
338 LGM population was composed of individuals that diverged some time ago, then came into  
339 contact during the Late Glacial and then went through a bottleneck (model C). Finally, a fourth  
340 scenario was that Central Europe was inhabited by two populations, the one present during the  
341 Late Glacial went extinct and was replaced by the second around the Pleistocene/Holocene  
342 transition (model D).

343       The ABC model choice analysis supported the scenario assuming complete population  
344 replacement (model D) with a likelihood ranging from 0.709 to 0.851 (with an average 0.775,  
345 Supplementary Table B.7) depending on the acceptance proportion that was used in the  
346 analysis. The Bayes Factors indicates substantial support for model D against A and strong and  
347 very strong support for models D as opposed to B and C, respectively (Supplementary Table  
348 B.7). Additionally, the PODs analysis indicated that the probability of choosing the right  
349 scenario were 0.974, 0.943, 0.809, 0.929 for models A, B, C, and D respectively which means  
350 that the analysis has high statistical power.

351



352

353

**Figure 3. Schematic representation of demographic scenarios (A-D) for the Western Carpathian common**

354

**vole population tested using ABC approach. The priors that describes each scenario are given.  $t_x$  – timing**

355

**of the event;  $Ne_x$  – effective population size at the time  $t_x$ ;  $r$  – growth rate.**

356

357

To investigate the history of population from Northern Spain we used a subset of our

358

dataset comprising 58 cytochrome *b* sequences, 30 from extant and 28 from ancient specimens

359

(Supplementary Table B.8). All sequences belonged to WS mtDNA lineage suggesting no

360

major change in the common voles' population during that time. To check for more subtle

361

changes that didn't involve lineage replacement we used Bayesian SkyGrid analysis which

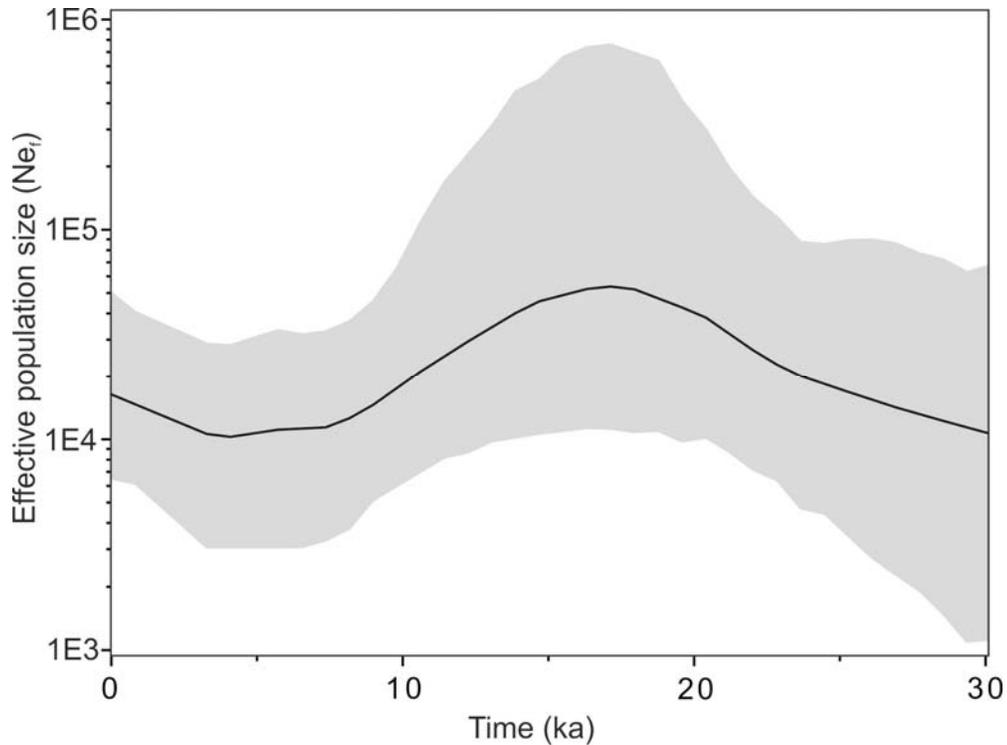
362

revealed modest changes of effective population size of the Spanish population through the last

363

30,000 years

364



365

366 **Figure 4. Bayesian reconstruction of female effective population size changes through time for common**  
 367 **voles from Northern Spain.**

368

Median estimate of  $N_{e_f}$  (solid line) and associated 95% HPD interval (grey area).

369

370 The highest effective population size was found to be at the end of LGM around 20 –

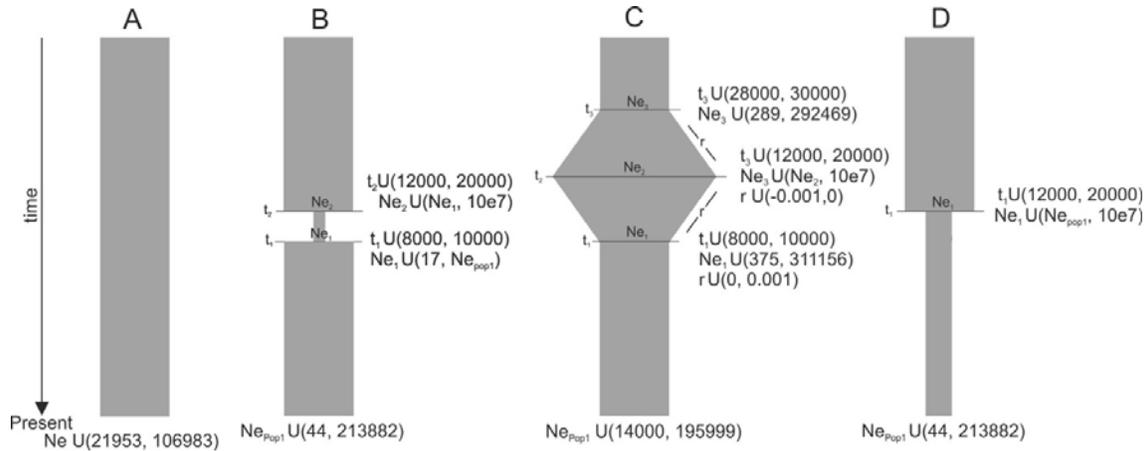
371 19 ka and decreased towards the Holocene with a minimum in the Early- to Mid-Holocene

372 followed with a slight recovery until the present day (Fig. 4). We investigated the support for

373 the four demographic scenarios resulting from the SkyGrid analysis using ABC approach (Fig.

374 5).

375



376

377 **Figure 5. Schematic representation of demographic scenarios for Spanish common voles tested using ABC**  
 378 **approach.**

379

380 The analysis failed to reject constant population size as a best supported model  
 381 (Supplementary Table B.9). However, this was expected as it has been shown that in cases of  
 382 large, rodent-like populations ABC usually fails to detect population declines or bottlenecks of  
 383 magnitude smaller than 95 % (Mourier et al., 2012).

384

#### 385 **4. Discussion**

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

#### 392 **Evolutionary history of common voles in the Western Carpathians**

393 The temporal distribution of genetic diversity in the Western Carpathian area is consistent  
 394 with the population replacement around the Pleistocene/Holocene transition. The evidence for

395 this comes from 48 specimens from layers dated to the Late glacial and Early Holocene periods  
396 that yielded a Central mtDNA lineage which was replaced by the population belonging to the  
397 Eastern lineage. The age of the three Central lineage specimens was further confirmed by the  
398 direct radiocarbon dating which yielded Late Glacial and Early Holocene dates (Table 1). Using  
399 an ABC approach we tested whether a more probable was scenario which assumed a complete  
400 replacement of the Central population by the Eastern one (in this case the few Eastern  
401 individuals found in the same layers as Central ones were in fact separated in time, or were the  
402 result of mixing at the site, or the combination of both). Alternatively, a scenario was considered  
403 where during the post-LGM period the Western Carpathians was inhabited by a population  
404 which consisted of individuals belonging to Central and Eastern mtDNA lineage and between  
405 12 and 8 ka one of them, namely the Central one, went extinct while the Eastern one survived  
406 and spread throughout the region (Fig. 3). The ABC analysis strongly supported the population  
407 replacement scenario. The alternative scenario where selective extinction of the Central lineage  
408 occurred would require that the individuals belonging to different mtDNA lineages differ in  
409 ecological plasticity or that Eastern lineage had some advantageous adaptations that allowed it  
410 to gradually outcompete individuals from Central lineage. Several recent studies suggested that  
411 the spatial distribution of the present-day mtDNA diversity of a range of mammals, including  
412 common voles, is correlated with specific environmental and climatic features (McDevitt et al.,  
413 2012, Tarnowska et al., 2016, Stojak et al., 2019). This suggests that distinct populations of one  
414 species may differ in their adaptations to certain climatic and environmental conditions.  
415 Therefore, we cannot completely rule out the possibility that individuals from the Eastern  
416 lineage gradually replaced the Central ones as a result of better adaptation to Late Glacial and  
417 Early Holocene environments.

418       Regardless the details of this process it seems that the final replacement took place in the  
419 Early Holocene. This is confirmed by the Central lineage specimens present in the Early

420 Holocene layers in Peskő cave (SE Slovakia) and Býčí skála site (Moravian karst) (Horáček  
421 and Ložek, 1988; Horáček and Sázelová, 2017; see also Appendix A) and especially by the two  
422 directly dated Central lineage specimens from the latter site which yielded ages of 9.8 and 11.2  
423 ka BP, respectively. The Early Holocene replacement is consistent with the previous  
424 estimations that an increase in the population size of the Eastern lineage started at ca. 10-8 ka  
425 (Stojak et al., 2015).

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

431         The primary habitats of the common vole is grassland. The Central Europe during the  
432 Early and Middle Holocene was covered with a dense forest present over vast areas as revealed  
433 by many pollen diagrams (see e.g. Mitchell, 2005). Although the recent palaeovegetation  
434 reconstructions showed continuous presence of patches of open land in the Western Carpathians  
435 and adjacent areas throughout Late Glacial and Holocene (Abraham et al., 2016; Kuneš et al.,  
436 2015; Trondman et al., 2015) the proportion of open landscapes had fallen significantly around  
437 9-8 ka in many regions (Abraham et al., 2016; Jamrichová et al., 2017; Kuneš et al., 2015). At  
438 this time the climate became wetter (Feurdean et al., 2014; Jamrichová et al., 2017) and the  
439 semi-open pine forests dominating in the early Holocene were replaced by more diversified  
440 plant communities with spruce forests, mixed oak woodlands and others (Abraham et al., 2016;  
441 Kuneš et al., 2015; Pokorný et al., 2015). Thus, the extirpation of the Central lineage could have  
442 been caused by the drastic loss of suitable habitats.

443

444 **█** *Evolutionary history of common voles in Western Europe and the British Isles*

445 Two radiocarbon dated specimens from Trou Al'Wesse (Belgium) yielded a pre-LGM  
446 ages. They belonged to the WN lineage although they diverged earlier than the coalescence of  
447 the extant populations (Fig. 1). This suggests that population continuity existed in the region  
448 throughout the last 30 ka rather than a turnover, even if it contracted as a result of the LGM.  
449 Although the evidence is still very limited this is concordant with the cryptic northern refugium  
450 hypothesis (Stewart and Lister, 2001). The other interesting case is the single specimen from  
451 Bridged Pot cave dated to the Early Holocene. At present there are no common voles in the  
452 British Isles with the exception of the Orkney Isles, where they have been introduced by humans  
453 ca. 5,000 years ago (Martínková et al., 2013). *Microtus arvalis* has not been considered to be  
454 part of the British fauna of the Last Glacial and only the field vole was identified in the fossil  
455 record (Coard and Chamberlain, 1999; Currant and Jacobi, 2001) however there are problems  
456 distinguishing these two species based on dental characters (Navarro et al., 2018).

457 Recently, a number of common vole remains were identified using collagen  
458 fingerprinting from Pin Hole cave (Creswell Crags, UK) (Buckley et al., 2018). Although the  
459 deposits Pin Hole have been shown to be mixed (Stewart and Jacobi, 2015), this suggests that  
460 common voles were present on the British Isles during at least some of the Late Pleistocene  
461 and/or early Holocene. The phylogenetic position of the individual from Bridged Pot cave  
462 suggests that it was a part of the continuous population of mainland Europe. Given the age of  
463 the specimen (Table 1) the possible scenario explaining its presence in the British Isles may be  
464 that the common vole may had expanded to Britain during the Late Glacial warming and then  
465 the Younger Dryas cooling or the Holocene reforestation caused of their local extinction. The  
466 disappearance of the connection between the British Isles and continental Europe during the  
467 Early Holocene may have prevented the species' subsequent recolonization. A similar scenario  
468 was proposed for a range of small mammals inhabiting the British Isles today such as the field  
469 vole, bank vole (*Clethrionomys glareolus*), water vole (*Arvicola amphibius*) and pygmy shrew

470 (*Sorex minutus*) (Brace et al., 2016; Searle et al., 2009). Populations of all these species were  
471 able to recolonize the British Isles at the onset of the Holocene. This was not the case for the  
472 common vole. Recently Martinkova et al. (2013) showed that the recolonization of the northern  
473 areas of France and Belgium by the common vole was recent and started not earlier than 2,000  
474 years ago, long after the disappearance of land connecting the British Isles and mainland  
475 Europe.

#### 476 ██████ *Evolutionary history of common voles in Spain*

477 The distribution of genetic diversity through time and the reconstructed trajectory of  
478 population size changes suggest population continuity with a possible decrease around the Late  
479 Glacial and Early Holocene. The demographic reconstruction was done using mostly the  
480 stratigraphically dated sequences with only four being directly dated using radiocarbon dating,  
481 thus there is a level of uncertainty associated with this conclusion. However, the reconstructed  
482 trajectory fits well with the changes in the abundance of common vole remains observed on  
483 palaeontological sites across northern Spain and Southern France. At El Miron site (Cantabrian  
484 Cordillera) the maximum abundance of common vole falls between 27 and 15 ka, with the onset  
485 of Bølling-Allerød the decline is observed leading to a complete disappearance in the Early  
486 Holocene. Vole remains reappear in the Chalcolithic period at around 4 ka (Cuenca-Bescós et  
487 al., 2009). The same is seen at other sites like Antoliñako Koba (Biscay) (Rofes et al., 2015),  
488 Santimamiñe (Biscay) (Rofes et al., 2013) and on the Galician site Valdavara-1 (López-García  
489 et al., 2011). A similar pattern was found in South-western France (Royer et al., 2016),  
490 suggesting similar population history throughout the whole range of the WS lineage. The  
491 trajectory of common vole populations seems to follow the general pattern of  
492 paleoenvironmental changes in Spain over the last 30 ka. During the LGM and Late Glacial  
493 grasslands and steppe vegetation prevailed in Northern Spain providing the preferred habitat  
494 type of the common voles (Carrión et al., 2010; Fletcher et al., 2010). From ca. 15 ka oak

495 (*Quercus sp.*) and pine (*Pinus sp.*) forests began to appear reaching a peak during the Early  
496 Holocene (Carrión et al., 2010). Thus, the loss of primary habitat due to an expansion of forests  
497 may be the cause of the observed population decrease. There is no clear change in  
498 paleoenvironmental records from the Middle Holocene onwards, however during that time a  
499 growing pressure of humans on the landscape has been recognized (Carrión et al., 2010). The  
500 human activities, involving deforestation by burning, pastoralism and ploughing, were highly  
501 spatially and temporarily uneven but clearly visible in palynological records from the  
502 Chalcolithic and Bronze Age (Carrión et al., 2010). It has been argued that human activities  
503 affected small mammal communities from the Neolithic onwards (López-García et al., 2013).  
504 Thus, the slight recovery of population size observed on SkyGrid plot and in the fossil record  
505 may have been caused by an increased humanly maintained grasslands, the main present-day  
506 habitat of common voles.

#### 507 ██████ *The Post glacial history of common vole populations*

508       The use of ancient DNA to investigate evolutionary histories of animals revealed that the  
509 Late Pleistocene was a highly dynamic period marked with numerous faunal turnovers  
510 (extinctions, regional extirpations and population replacements) most of which had not been  
511 recognized earlier from the fossil record (Baca et al., 2017). Most of these events were grouped  
512 in two distinct clusters. The first one was around ca. 37-28 ka (Greenland Interstadials 7-4)  
513 (Cooper et al., 2015). During that time the native European population of mammoths (*M.*  
514 *primigenius*) (lineage III) was replaced by a population coming from Asia (lineage I)  
515 (Palkopoulou et al., 2013; Fellows Yates et al., 2017). In the Ach valley (Germany) local  
516 populations of *Ursus spelaeus* were replaced by *U. ingressus* (Münzel et al., 2011). Population  
517 replacement was also recorded in the collared lemmings (*Dicrostonyx torquatus*) which was  
518 probably extirpated from Europe for some time between ca. 40 and 32 ka (Brace et al., 2012;  
519 Palkopoulou et al., 2016).

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

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

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

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

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

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

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

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577 granting access to the collection.

## 578 **6. Author contribution**

579 M.B and A.N. conceived and supervised the study. M.B., D.P., K.B. performed laboratory  
580 experiments and analysed the data, K.D. performed ABC analyses. A.L., I. H., J.M.L.-G, S.B.-  
581 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.,  
582 J.R.S., A.N. assembled paleontological materials and provided information on paleontological  
583 context, M.B., D.P., J.R.S and A.N. wrote the manuscript with the input from all the co-authors.

## 584 **7. Data availability**

585 DNA sequences obtained in this study were deposited in GenBank under accession nos  
586 MK748347-MK748442.

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