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Phylogeographic structure of the pygmy shrew: revisiting the roles of southern and northern refugia in Europe.

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ABSTRACT

Southern and northern glacial refugia are considered paradigms that explain the complex phylogeographic patterns and processes of European biota. Here, we provide a revisited statistical phylogeographic analysis of the pygmy shrew *Sorex minutus* Linnaeus, 1766 (Eulipotyphla, Soricidae) examining the genetic diversity, genetic differentiation and demographic history in the Mediterranean peninsulas and in Western and Central Europe. The results showed support for genetically distinct and diverse phylogeographic groups consistent with southern and northern glacial refugia, as expected from previous studies, but also identified geographical barriers concordant with glaciated mountain ranges during the Last Glacial Maximum (LGM), early diversification events dated between the Upper Pleistocene and Lower Holocene for the main phylogeographic groups, and recent (post-LGM) patterns of demographic expansions. This study is the most comprehensive investigation of this species to date, and the results have implications for the conservation of intraspecific diversity and the preservation of the evolutionary potential of *S. minutus*.

KEYWORDS: mitochondrially encoded cytochrome *b* – glacial refugia – historical demography – Last Glacial Maximum – mammals – postglacial colonisation.

INTRODUCTION

During the Quaternary glaciations, species in Europe were restricted to glacial refugia at glacial maxima (Bilton *et al.*, 1998; Taberlet *et al.*, 1998; Hewitt, 2000; Stewart & Lister, 2001; Pazonyi, 2004; Sommer & Nadachowski, 2006). As glaciers retreated, a broad range of recolonisation patterns emerged, as evidenced by palaeontological, biogeographic and phylogeographic studies on various taxa, resulting in the complex contemporary patterns of endemism, species richness and biodiversity hotspots observed across Europe. While population contraction and lineage diversification within southern glacial refugia in the Mediterranean peninsulas during the Last Glacial Maximum [LGM; 19-26.5 thousand years ago (KYA) (Clark *et al.*, 2009)], and subsequent northward postglacial recolonisation of Europe have been accepted and recognised since the 1990s (Bilton *et al.*, 1998; Taberlet *et al.*, 1998; Hewitt 2000), the concept of northern glacial refugia also became a paradigm to explain the complex phylogeographic patterns and processes of European biota (Stewart & Lister, 2001; Pazonyi 2004; Sommer & Nadachowski, 2006). Fossil records and phylogenetic analyses revealed that many species of flora and fauna could have survived during the LGM in the Carpathian Basin (Stewart & Lister, 2001; Pazonyi, 2004; Sommer & Nadachowski, 2006; Stojak *et al.*, 2015) and in the Dordogne region (Steward *et al.*, 2010), and glacial refugia could also be located in Crimea (Marková, 2011) or in the Russian Plain (Banaszek *et al.*, 2012). Nowadays, locations of southern and northern glacial refugia during the LGM are hotspots of genetic diversity (Petit *et al.*, 2003; Stojak *et al.*, 2016).

The Eurasian pygmy shrew *Sorex minutus* Linnaeus, 1766 (Eulipotyphla, Soricidae) (Hutterer, 1990) has been used as a phylogeographic model species for understanding the effects of the glaciations in Europe and the colonisation history during the Pleistocene and postglacial times (Bilton *et al.*, 1998: McDevitt *et al.*, 2010; Vega *et al.*, 2010a, b). However, little is still known about the phylogeographic structure, genetic diversity and structure, and demographic history of this small mammal within these regions due to the limited number of samples from Mediterranean peninsulas. An expanded phylogeographic study of the pygmy shrew is therefore important for the understanding and further development of biogeographic models of glacial refugia and postglacial recolonization, for depicting areas with high intraspecific genetic diversity, for establishing conservation measures of rear-edge populations, and for the preservation of the evolutionary potential of species, particularly in the face of climate and anthropogenic change (Deffontaine *et al.*, 2005; Provan & Bennett, 2008; Stojak *et al.*, 2019; Stojak & Tarnowska, 2019).

In this study, we explored the evolutionary history and phylogeographic structure of *Sorex minutus* using a statistical phylogeography approach (Knowles & Maddison, 2002; Knowles, 2009). Here, we emphasise the genetic diversity and structure within and among refugia, the inference of geographical barriers and the demographic history of *S. minutus*, which are aspects that have not been studied in detail previously. Specifically, we asked the following questions: 1) What are the geographical distribution and genetic diversity patterns of the genealogical lineages of *S. minutus*? 2) Is there significant population genetic structure across the geographic range of *S. minutus*? 3) What is the historical demography of *S. minutus* in Europe? Our results showed support for distinct and genetically diverse lineages, geographical barriers concordant with glaciated mountain ranges during the LGM, and recent (post-LGM) population expansions with contemporary contact areas. The results presented here have implications for the long-term conservation of intraspecific diversity and the preservation of the evolutionary potential of *S. minutus* in the face of modern climate change.

MATERIALS AND METHODS

Study species

Sorex minutus is common over most of its distribution but is rarely dominant and it occurs in a wide range of terrestrial habitats with adequate ground cover and in relatively damp areas, including swamps, grasslands, heaths, sand dunes, woodland edge, rocky areas, shrubland and montane forests (Hutterer, 1990, 2016; Churchfield, 1990; Churchfield & Searle, 2008). It is found from southern and western Europe to much of central and northern Europe, Ireland and the British Isles, and Siberia to Lake Baikal in the east (Hutterer, 1990, 2016). It is found from sea level up to 2260 m (in the Alps), but its distribution becomes patchy and limited to higher altitudes in southern Europe where it occurs with some degree of geographical isolation and differentiation, while in central and northern parts of Europe and in Siberia it is more abundant and populations are more connected and widespread (Hutterer, 1990, 2016).

Samples and molecular methods

A total of 671 mitochondrially encoded cytochrome *b* (*MT-CYB*) DNA sequences of *S. minutus* from Europe and Siberia were used for this study (Fig. 1B; see Supplementary information Table S1). DNA sequences were obtained from samples collected from the wild following ethical guidelines (Sikes, Gannon & the Animal Care and Use Committee of the American Society of Mammalogists, 2011), or from museums, and from published GenBank data (including AB175132: Ohdachi *et al.*, 2006; AJ535393 – AJ535457: Mascheretti *et al.*, 2003; GQ272492 – GQ272518: Vega *et al.*, 2010a; GQ494305 – GQ494350: Vega *et al.*, 2010b; and JF510376 – JF510321: McDevitt *et al.*, 2011). In addition, four *MT-CYB* sequences of *S. volnuchini*, which was used as an outgroup (Fumagalli *et al.*, 1999), were incorporated into the analysis (including AJ535458: Mascheretti *et al.*, 2003).

Genomic DNA from wild and museum samples was extracted using a commercial kit (Qiagen). Partial (1110 bp) *MT-CYB* sequences were obtained by PCR using two primer pairs that amplified approximately 700 bp of overlapping fragments, or using five primer pairs (for museum samples with highly degraded DNA) that amplified approximately 250 bp of overlapping fragments (Vega *et al.*, 2010a). PCR amplification was performed in a 50 μl final volume: 1X Buffer, 1 μM each primer, 1 μM dNTP's, 3 mM $MgCl_2$ and 0.5 U Platinum Taq Polymerase (Invitrogen), with cycling conditions: 94°C for 4 min, 40 cycles at 94°C for 30 s, 55°C for 30 s and 72°C for 45 s, and a final elongation step at 72°C for 7 min. Purification of PCR products was done with a commercial kit (Qiagen) and sequenced (Macrogen and Cornell University Core Laboratories Center).

Phylogenetic analysis

DNA sequences were edited by eye in BioEdit version 7.0.9.0 (Hall, 1999), contigs were made from forward and reverse sequences also in BioEdit, and sequences were aligned using ClustalX version 2.0 (Larkin *et al.*, 2007). A haplotype data file was obtained using DnaSP version 5.10.1 (Librado & Rozas, 2009). Newly obtained haplotypes were deposited in GenBank (Accession Numbers: MN840358 - MN840484, Supplementary information Table S1).

The model of evolution that best fitted the molecular data (haplotypes) was searched using jModelTest version 2.1.10 (Darriba *et al.*, 2012) using the Bayesian Information Criterion value. The substitution model supported was the General Time Reversible (GTR) with specified substitution types (A–C=0.4250, A–G=23.5124, A–T=1.6091, C–G=1.8671, C–T=17.2314, G–T=1.0000), proportion of invariable sites (0.6044), gamma shape parameter (0.2816) and nucleotide frequencies (A=0.2777, C=0.3076, G=0.1416, T=0.2731).

The phylogenetic relationships among *MT-CYB* haplotypes of *S. minutus* were inferred by Bayesian analysis and by generating a parsimony phylogenetic network. The Bayesian analysis was done using MrBayes version 3.2.7 (Ronquist *et al.*, 2012) with two independent runs (10 million generations and 5 chains each), a sampling frequency every 1000 generations and temperature of 0.1 for the heated chain, and checking for convergence in Tracer version 1.7.1 (Rambaut *et al.*, 2018). Trees were summarized after a burn-in value of 2500 to obtain the posterior probabilities of each phylogenetic branch. The main phylogenetic groups (phylogroups) were identified based on monophyly of the haplotypes, and were named based on the geographical origin of the samples. The phylogenetic network was done using PopART version 1.7 (http://popart.otago.ac.nz) implementing a median-joining algorithm.

Sequence polymorphism indices and diversity values, including the number of haplotypes (*H*), polymorphic (segregating) sites (*S*) and parsimony informative sites (*P*), haplotype diversity (*Hd*), nucleotide diversity (π), and average number of nucleotide differences (*k*), were estimated using DnaSP. This was done for the whole data set (ingroup), for the main phylogroups, and also for other relevant geographic groups, including island populations and continental samples.

Population genetic structure

Pairwise genetic differentiation values (F_{ST}) between all pairs of phylogroups and other relevant geographic groups, and an Analysis of Molecular Variance (AMOVA) were calculated using Arlequin version 3.11 (Excoffier *et al.*, 2005). Ten thousand nonparametric permutations were performed to generate a random distribution to test the significance of the pairwise F_{ST} values and covariance components of the AMOVA, and $\alpha = 0.05$ was set as the threshold for statistical significance.

With samples assigned to phylogroups and with the samples' geographical coordinates, the geographic midpoints (i.e. mid-geographic location between two or more coordinates) of the phylogroups were calculated using the Geographic Midpoint Calculator (available at http://www.geomidpoint.com/). The geographic midpoints were used to obtain the pairwise geographic distances among phylogroups with the Geographic Distance Matrix Calculator version 1.2.3 (by PJ Ersts, available at http://biodiversityinformatics.amnh.org/open_source/gdmg.) A Mantel test was used to evaluate the relationship between matrices of pairwise geographic distances and genetic differentiation values (Slatkin's linearised pairwise F_{ST} as $D = F_{ST}/(1-F_{ST})$; Slatkin, 1995). Despite criticisms, the Mantel test is still a widely used and can be a powerful statistical approach to analyse sequence data to test evolutionary hypotheses (Diniz-Filho *et al.*, 2013). Due to the very low (or absence of) genetic variation in the Orkney islands, DNA sequences originating from there were pooled to avoid issues with pairwise F_{ST} calculations.

Geographic barriers were computed using Barrier version 2.2 (Manni *et al.*, 2004). This approach implements Monmonier's maximum difference algorithm to find edges (boundaries) on a Voronoi tessellation associated with the highest rate of change in genetic distances among samples interconnected by a geometric network (i.e. Delaunay triangulation) (Manni *et al.*, 2004). A barrier highlights the geographic areas where a genetic discontinuity is found, and where samples on each side of the barrier are genetically more similar than samples taken on different sides of the boundary. Pairwise genetic distances were estimated using continental samples only, limiting the data set in the geometric network calculation to one sample per locality, and computing a maximum of 10 barriers.

Historical demography

A strict molecular clock was compared to the uncorrelated lognormal relaxed molecular clock (Drummond *et al.*, 2006). Coalescent constant population size and Bayesian skyline demographic models (Drummond *et al.*, 2005) were compared to identify the best-fitting pattern of changes in the pygmy shrew population. For model selection, path sampling and stepping-stone sampling (Baele *et al.*, 2013), based on four independent MCMC chains (1000 steps of 100,000 generations each, following a 10 million generations burn-in period), were used for calculating the log Marginal Likelihoods Estimates (MLEs) for each model. MLEs were used to calculate Bayes Factors (BFs) for each comparison between tested models to determine the best-fitting one (Kass & Raftery, 1995). The best-fitting models were then used to estimate the Time of divergence from the Most Recent Common Ancestor (TMRCA) and Bayesian Skyline Plots (BSP) (see below). The 95% Highest Posterior Density (HPD) was included in the TMRCA and BSP estimations.

TMRCAs for the ingroup (all *S. minutus* samples) and the phylogroups were estimated using BEAST version 2.5.2 (Bouckaert *et al.*, 2014). The following prior assumptions were: random starting tree, monophyletic groups (for the ingroup and the Irish phylogroups) (Drummond *et al.*, 2006) to calculate the evolutionary rate, and the GTR substitution model with four categories, gamma = 0.9680 and proportion of invariable sites = 0.4680 (from jModelTest using the full data set). The oldest record of *S. minutus* has been found in Podlesice and Mała Cave, Poland dated between 5.3 and 3.6 MYA (Early Pliocene;

Mammal Neogene 14) (Rzebik-Kowalska, 1998). Using this fossil information, a calibration point for the ingroup was set at 4.45 MYA (SD = 0.5 MY; 5.27 – 3.63 MYA) with a normal prior distribution. Due to the absence of dated fossils of pygmy shrews that can be assigned specifically to the main phylogroups, a second calibration was set for the node age of the Irish lineage at 0.006 MYA (SD = 0.0005 MYA; 0.00682 – 0.00518 MYA). This secondary calibration point, derived from a previous analysis and applied to our data set, was based on the inferred colonisation time of Ireland by *S. minutus* in the Neolithic using multiple genetic markers and fossil data (McDevitt *et al*., 2009, 2011). The trace files were analysed in Tracer, the tree information from the four runs were combined and resampled at a lower frequency (for a total of 10,000 trees) using LogCombiner, and the information was summarized using TreeAnnotator selecting Maximum clade credibility tree and median heights. The phylogenetic tree showing the TMRCAs was created using FigTree version 1.4.4 (http://tree.bio.ed.ac.uk/software/figtree/) with median and 95% HPD values based on those 10,000 trees.

Genetic evidence of population expansion for the phylogroups, island populations and continental samples was investigated using the R_2 test of neutrality (Ramos-Onsins & Rozas, 2002), based on the difference of the number of singleton mutations and the average number of nucleotide differences, and Fu's *Fs* (Fu, 1997), a statistic based on the infinite-site model without recombination that shows large negative *Fs* values when there has been a demographic population expansion. Both population expansion tests were carried out in DnaSP using coalescent simulations for testing significance (10,000 replicates).

Mismatch distributions (i.e. the distribution of the number of differences between pairs of haplotypes) were estimated for the phylogroups (and where N ≥ 10) to compare the demography of the populations with the expectations of a sudden population expansion model (Rogers & Harpending, 1992). For the phylogroups and continental samples that showed a unimodal mismatch distribution and significant population expansion, the time since the population expansion (t) was calculated as $t = \tau/2u$, where τ (tau) is the mode for the unimodal mismatch distribution, and u is the cumulative (across the sequence) probability of substitution (Schenekar & Weiss, 2011). The calculations were done using the MS Excel Mismatch Calculator (Schenekar & Weiss, 2011) with sequence length = 1110 bp, generation time = 1 year (Hutterer *et al.*, 2016), substitutions per site per million years (subst/Site/MY) = 0.551 (based on the average substitution rate across all sites 'clock.rate' results from BEAST) and cumulative substitutions/generation = 0.00062.

BSPs were calculated using BEAST based on the posterior distribution of effective population size through time from a sample of gene sequences. This was done for the phylogroups showing a unimodal mismatch distribution and significant signatures of recent population expansion (where N ≥ 10). The analysis was run for 100 million generations, sampled every 1000, using the best-fitting model.

RESULTS

Phylogenetic analysis

For the complete *S. minutus* data set (*N* = 671) (Fig. 1B), there were 424 haplotypes with 390 polymorphic sites of which 277 were parsimony informative (Table 1). We report 160 newly sequenced specimens of *S. minutus* from the Iberian (4) and Balkan (19) peninsulas and from Central and Northern Europe (137) from which 127 were new haplotypes. Also, there were three new sequences and haplotypes of *S. volnuchini*, from which two were from Turkey and one from the Crimean Peninsula.

The Bayesian phylogenetic analysis showed *S. minutus* as a monophyletic group and revealed six distinct lineages corresponding to their geographical origin (i.e. phylogroups) supported by high posterior probabilities (Fig. 2A). Samples from the Mediterranean peninsulas clustered in three distinct phylogroups, namely the Iberian, Italian and Balkan phylogroups. The Iberian group was represented with few DNA sequences (*N* = 6). It was geographically restricted to the Iberian Peninsula and included samples from Rascafría, Central Spain (Sierra de Guadarrama) and Picos de Europa, Northern Spain. The Italian phylogroup (*N* = 26) was mostly restricted to the north-central regions of the Italian peninsula; it included samples from the Apennines and the Alps in Italy, but also from

Switzerland, Slovenia, Southern and Eastern France near the border with Italy, Czech Republic and Germany. The Balkan phylogroup (*N* = 22) included samples mostly from the Balkan Peninsula and a few from further north in Central Europe. This phylogroup showed a weak north/south subdivision, with one clade containing samples from Switzerland, Austria, Slovakia, Czech Republic, Hungary and Montenegro, another clade containing samples from Serbia, Bosnia and Herzegovina and North Macedonia, plus other ungrouped basal samples from Montenegro, North Macedonia, Serbia and Turkey (East Thrace, Southeast Europe).

There was also a well-supported and geographically widespread Western phylogroup (*N* = 283), which included samples from northern Spain (Cantabrian Mountain Range), Southern France and Andorra (i.e. the Pyrenees), western and central France (including Belle-Île), Ireland, the Orkney Islands, and western mainland Britain and offshore islands on the western coast of mainland Britain. Samples from Ireland formed an internal monophyletic lineage (i.e. the Irish phylogroup, *N* = 94) within the Western phylogroup. Notably, two samples from Navarra in northern Spain (ESNa0861 and ESNa1131; Accession Number JF510331) shared haplotypes with samples from Ireland (Hap_64). A monophyletic South Italian phylogroup (*N* = 4) was most closely related to the Western phylogroup than to the Italian phylogroup, and was geographically restricted to La Sila, Calabria in Southern Italy.

Samples from northern and central Europe and Siberia, namely the Northern phylogroup (*N* = 330), formed the most geographically widespread lineage and included samples ranging from Central France and Britain (excluding those within the Western phylogroup), across Central and Northern Europe to Lake Baikal in Siberia, but did not include samples from Southern Europe. Samples from mainland Britain belonging to the Northern phylogroup did not form an internal monophyletic cluster.

The phylogenetic network had a complex structure (Fig. 2B), but the haplotypes clustered into the same phylogroups detected with Bayesian phylogenetics and were distantly related from each other (> 10 mutational steps). The Western phylogroup had a star-like pattern and showed three most internal haplotypes; notably, Hap_61 was found in the Pyrenees with other Western haplotypes directly connected to it, Hap_94 was found on islands of the western coast of Scotland (Arran and Mull) with other Scottish and continental Western haplotypes directly connected to it, and Hap_64 included samples from Northern Spain and Ireland with other Irish haplotypes connected to it. The Northern phylogroup showed a star-like pattern with many reticulations and three most internal haplotypes separated from each other by few mutational steps. There was a weak geographical subdivision within the Northern phylogroup, where samples from Siberia, Eastern and Northern Europe were derived or most closely connected to samples from Central Ukraine (Hap_287), samples from Central Europe were derived or most closely connected to samples from The Netherlands (Hap_274), and all samples from Britain were derived or most closely connected to other samples from The Netherlands than to the other central haplotypes (Hap_90); however, the highly reticulated pattern of the inner haplotypes of the Northern phylogroup indicated that this geographical subdivision was weak.

Sequence polymorphism indices and diversity values for the phylogroups and other geographic groups are shown in Table 1. For the phylogroups, the haplotype diversity values were high (>90%), and the nucleotide diversity values were either half or almost half as much as the ingroup. Notably, the Northern phylogroup had the highest haplotype diversity values, followed by the Balkan phylogroup; however, the Balkan phylogroup had the highest nucleotide diversity values. The Irish phylogroup, which clustered within the Western phylogroup, showed slightly lower haplotype diversity than any other phylogroups.

The continental groups (Northern continental and Western continental) showed equivalent DNA polymorphism values as the main phylogroups, but the island groups showed different levels of DNA polymorphism (Table 1). There was low DNA polymorphism in islands of the Orkney Archipelago, with only 11 haplotypes in all Orkney Islands combined (*N* = 119), but all haplotypes were unique to these islands. There were eight haplotypes in Orkney Mainland (*N* = 44), from which seven were unique to this island (the largest island of the archipelago), there were two unique haplotypes in Orkney South Ronaldsay (*N* = 40), and there was only one haplotype in Orkney Westray (*N* = 33) also present in Orkney Hoy (*N* = 2) and Orkney Mainland. There were five haplotypes in Belle-Île (*N* = 5), and only one was present in the continent also belonging to the Western phylogroup. The British group (*N* = 91) showed high haplotype diversity but moderate nucleotide diversity values and had 80 haplotypes from which 77 were unique haplotypes not found elsewhere.

Population genetic structure

The highest pairwise differentiation values were found between some southern phylogroups and island groups, while the lowest values were between phylogroups and islands groups that clustered within them (Supplementary information Table S2). There was higher percentage of variation among (73.5 %) than within (26.5 %) groups, and there was a significant population differentiation (F_{ST} = 0.7349, P < 0.0001). The Mantel test showed a nonsignificant relationship between pairwise geographic and genetic distances based on Slatkin's linearised F_{ST} (R_2 = 0.0095, P = 0.2935) (Supplementary information Fig. S1).

The barriers identified using the computational geometry approach reflected the genetic differentiation between *S. minutus* and *S. volnuchini*, and among the phylogroups within *S. minutus* (Fig. 1C). The first barrier separated *S. minutus* from *S. volunichini*. The nine following barriers coincided with the location of mountain ranges, including a barrier located in the north of the Balkan Peninsula, in the Alps and in the Pyrenees, which reflected the genetic subdivisions and lineages in *S. minutus*.

Historical demography

Comparison of BFs for each model indicated the Bayesian skyline demographic model as the best-fitting one (BF = 391), and the strict molecular clock was better than the uncorrelated lognormal relaxed molecular clock (BF = 23). The MLEs for the constant population size and Bayesian skyline demographic models using the strict molecular clock were -10960 and -10569, while using the uncorrelated lognormal relaxed molecular clock were -10907 and -10592, respectively. Therefore, the strict clock and Bayesian skyline demographic model were selected as the best-fitting according to BFs. The effective sample size (ESS) for all values was higher than 200.

All branches of the Bayesian genealogy (Fig. 3, Table 2) were well-supported (posterior probabilities PP ≥ 0.97), except for the clade containing all phylogroups excluding Iberian (PP = 0.05). Molecular dating analysis revealed that the ingroup and outgroup separated approximately 83.4 KYA, with lower and upper 95% HPD limits between 59.7 and 110.2 KYA (Fig. 3, Table 2). The diversification of S. minutus occurred approximately 31.8 KYA (95% HPD: 21.8 – 40.5 KYA) with the formation of the Iberian phylogroup, followed by the formation of the Balkan group 29.6 KYA (95% HPD: 21.8 – 40.5 KYA), while in Western, Central and Northern Europe, S. minutus continued its diversification with the Northern phylogroup forming 24.1 KYA (95% HPD: 16.4 – 33.1 KYA), the Italian phylogroup forming 15.3 KYA (95% HPD: 10.7 – 21.5 KYA), the South Italian phylogroup forming 12.8 KYA (95% HPD: 8.5 – 17.8 KYA), and the Western phylogroup forming 9.3 KYA (95% HPD: 6.7 – 12.6 KYA) (Fig. 3, Table 2). The TMRCA of the Balkan phylogroup was the earliest, dated back to 15.5 KYA (95% HPD: 9.7-22.7 KYA), followed by the Northern phylogroup, dated back to 11.8 KYA (95% HPD = 7.7-16.8 KYA), while the rest of the main phylogroups had TMRCAs dated approximately to about 6 and 9 KYA (Fig. 3, Table 2). Within the Western phylogroup, the TMRCA for the Irish clade dated back to 5.9 KYA (95% HPD: 4.9 – 6.9 KYA).

The population expansion tests (R_2 and Fu's *Fs*) showed significant departures from neutrality for the ingroup and several other phylogroups, except for the Balkan, Iberian and South Italian (Table 2). The population expansions were not an effect of the island samples belonging to these phylogroups, and continental samples analysed separately also demonstrated a similar pattern (Table 2). For the island groups, only the Irish and British groups showed signatures of recent population expansions (Table 2).

The mismatch distributions varied significantly among the phylogroups (Fig. 4A; Supplementary information Fig. S2). The ingroup showed a bimodal mismatch distribution, which reflected the pairwise comparisons within and among phylogroups in *S. minutus*. The Northern (and Northern continental), Italian, Western (and Western continental) and Irish phylogroups all had distinctly unimodal distributions with an almost perfect fit between observed and expected pairwise differences of a sudden population expansion model. All population expansions for the phylogroups were dated to the Holocene; the Italian and Northern phylogroups had the oldest times of expansion (>8.0 KYA), while the Irish showed a relatively recent population expansion dated to 1.6 KYA.

The BSP obtained for three phylogroups (Northern, Western and Irish) suggested that demographic expansions of these populations started approximately 5.0 KYA (Fig. 4B). BSP calculation for the Italian phylogroup indicated an even earlier demographic expansion (approximately 5.5 KYA) (Fig. 4B).

DISCUSSION

Quaternary refugia represent the geographical regions that species inhabit during periods of glacial or interglacial cycles when there is the maximum contraction in geographical range (Stewart *et al.*, 2009). There is support for both southern (Taberlet *et al.*, 1998; Hewitt, 2000) and northern glacial European refugia (Bilton *et al.*, 1998; Stewart & Lister, 2001; Kotlík *et al.*, 2006; Provan & Bennett 2008; Fløjgaard *et al.*, 2009; Vega *et al.*, 2010a, b). Rather than polarising the biogeographic patterns into southern and northern refugia (Tzedakis *et al.*, 2013), the paradigms of postglacial colonisation in Europe (Hewitt, 2000) can be improved with the acceptance of southern hotspots of diversification without northward colonisation (Bilton *et al.*, 1998) and the concept of refugia-within-refugia (Gómez & Lunt, 2007), as well as with the findings of northern glacial refugia (Stewart & Lister 2001; Provan & Bennett, 2008; Stewart *et al.*, 2009), to reflect the evolutionary processes across varied topographical areas that have shaped genetic diversity. The statistical phylogeographic results obtained here contribute to the understanding of the phylogeographic patterns and processes during the Quaternary glaciations that shaped the European biota, and provide further evidence to the emerging pattern of complex biogeographical histories in Europe (Pedreschi *et al.*, 2019).

Sorex minutus *phylogeography*

The significant genetic structure among phylogroups defined in this study illustrate the complex history of European colonisation, isolation and diversification of *S. minutus* during the Pleistocene and Holocene, and is not a simple case of isolation by distance and colonisation of Northern and Central Europe from expanding populations from the south. While the southern phylogroups, including the Iberian, Balkan, Italian and South Italian, were mostly restricted to the Southern European peninsulas (consistent with the traditional southern glacial refugia), the Northern and Western phylogroups were widespread geographically and were found north of the Mediterranean peninsulas, consistent with previous studies with fewer samples (Bilton *et al.*, 1998; Mascheretti *et al.*, 2003; Vega *et al.* 2010a, b) and with different molecular markers (McDevitt *et al.*, 2010).

The hypothesis of northern refugia is further supported by palaeontological and palynological evidence for other temperate and boreal species (Willis *et al.*, 2000; Willis & van Andel, 2004; Magri *et al.*, 2006; Sommer & Nadachowski, 2006), as well as many phylogeographic studies in small mammals, including the field vole *M. agrestis* (Jaarola & Searle, 2002; Herman *et al.*, 2019), bank vole *M. glareolus* (Deffontaine *et al.*, 2005; Kotlík *et al.*, 2006; Wójcik *et al.*, 2010), root vole *M. oeconomus* (Brunhoff *et al.*, 2003), common vole *M. arvalis* (Heckel *et al.*, 2005; Stojak *et al.*, 2016), common shrew *S. araneus* (Bilton *et al.*, 1998; Yannic *et al.*, 2008) and weasels *Mustela nivalis* (McDevitt *et al.*, 2012). For several small mammals, including *S. minutus*, suitable climatic conditions at the LGM could have been widespread across Central and Eastern Europe (Fløjgaard *et al.*, 2009; Vega *et al.*, 2010b; McDevitt *et al.* 2012; Stojak *et al.*, 2019).

Until recently, it was unclear which species of *Sorex* inhabit Crimea. According to Zagorodniuk (1996) it could be *S. (minutus) dahli* [mentioned in Hutterer (2005) as a synonym of *Sorex volnuchini* (*dahli*)], and Zaitsev *et al.* (2014) and Hutterer *et al.* (2016) indicated the presence of *S. minutus* in mainland Ukraine and in Crimea. Hutterer (2005) mentioned that *S. volnuchini* might be present in Crimea, but in Hutterer *et al.* (2016) *S.*

volnuchini is only found in southern Russia and Caucasus States, Turkey and northern Iran. Our research demonstrated that *S. volnuchini* may be present in the southern region of Crimea (based on one *MT-CYB* sequence), while *S. minutus* is present in mainland Ukraine and in the northern region of Crimea, but further sampling in this region is needed.

The finding of two phylogroups in the Iberian peninsula (i.e. Iberian and Western phylogroups) and two in the Italian peninsula (i.e. Italian and South Italian phylogroups), support the hypothesis of microevolutionary processes shaping the genetic diversity and structure within the Mediterranean peninsulas. In the Iberian Peninsula, the topography of the region with east-west mountain ranges and other high ground (over 1000 m a.s.l.), large rivers (which could act as barriers to dispersal), and the distinct seasonal precipitation and vegetation types (O'Regan, 2008), must have played an important role in the colonisation of the region and the genetic differentiation of populations. McDevitt *et al.* (2010) proposed that the Western phylogroup could have originated in the Dordogne region based on a limited number of samples from France, but the presence of this phylogroup in northern Iberia and the central position of Hap_61 (Pyrenees) could mean that an Iberian origin is possible instead. A similar process could explain the presence of the two phylogroups in the Italian peninsula (i.e. Italian and South Italian). The genetic differentiation of the South Italian phylogroup, further supported by morphological data (Vega *et al.*, 2010a, 2016), could be due to the unique geography of Southern Italy consisting of mountain massifs of Pollino, La Sila and Aspromonte separated by lowland areas, which from the Pliocene to the end of the Middle Pleistocene, at times of high sea level, were islands in a chain (Malatesta, 1985; Caloi *et al.*, 1989; Bonardi *et al.*, 2001; Bonfiglio *et al.*, 2002). The patterns of differentiation within refugial areas were concordant with the 'refugia-within-refugia' concept widely recognized for the Iberian Peninsula (Gómez & Lunt, 2007; Abellán & Svenning, 2019) and similar to microrefugia in the Balkans (Kryštufek *et al.*, 2007). For the Italian peninsula, a comparable 'refugia-within-refugia' pattern was found in several species (Amori *et al.*, 2008; Canestrelli *et al.*, 2008; Castiglia *et al.*, 2008; Vega *et al.*, 2010a, 2016; Senczuk *et al.*, 2017; Bisconti *et al.*, 2018).

The genetic similarity between the Western and South Italian phylogroups indicates a common history and it can be hypothesised that their common ancestor was more widespread throughout the Italian peninsula, probably displaced later by the Italian lineage in the Apennines and Western Alps. A similar scenario has been proposed for the water shrew *Neomys fodiens* (Castiglia *et al.*, 2007), Alpine salamander *Salamandra salamandra* (Steinfartz *et al.*, 2000), black pine *Pinus nigra* (Afzal-Rafii & Dodd, 2007) and green lizard *Lacerta bilineata bilineata* (Böhme *et al.*, 2007), which showed closely related South Italian and Western phylogroups most closely related to each other than to a North-Central Italian lineage.

The phylogeographic patterns found here were further supported by the determination of barriers that coincided with mountain ranges located on the north of the Iberian, Italian and Balkan peninsulas. Contact zones among phylogroups (i.e. localities where at least two *MT-CYB* phylogroups were present) were detected at the northern extremes of the southern peninsulas. During the LGM, glaciers covered most of the Alpine (Buoncristiani & Campy, 2004) and Pyrenean mountain ranges (Calvet, 2004), while glaciers in the Carpathians (Reuther *et al.*, 2007) and in the Balkan Peninsula (Hughes *et al.*, 2006) were found > 1,000 m a.s.l. When climate ameliorated and suitable habitat became available, pygmy shrew populations belonging to different phylogroups on different sides of the mountain ranges could have expanded and colonised previously glaciated areas thus forming the observed contact zones. Moreover, the widespread distribution and absence of phylogeographic structure of the Northern phylogroup could be explained by the apparent absence of major geographical barriers across Central and Northern Europe, and recolonization from northern refugia. Similarly, pygmy shrews belonging to the Western and Northern phylogroups could have quickly colonised mainland Britain across a land connection to continental Europe (i.e. Doggerland; Gaffney *et al.*, 2007), resulting in the genetic similarities observed between the British Isles and continental Europe.

Sorex minutus *demography*

The oldest fossils assigned to *S. minutus* were found in Podlesice and Mała Cave, Poland dated to the Early Pliocene between 4 and 5.3 MYA (Rzebik-Kowalska, 1998). An early widespread colonisation of Europe by *S. minutus* might have been possible because it was probably one of the first species of the genus *Sorex* in the continent (Rzebik-Kowalska, 1998, 2008). The Bayesian analysis revealed, however, more recent diversification events, with TMRCAs for the ingroup and the phylogroups in continental Europe between the Upper Pleistocene and Lower Holocene. This is consistent with recent studies on field vole (*Microtus agrestis*) phylogeography in Europe (Herman & Searle, 2011; Herman *et al.*, 2014) which demonstrated the importance of the Younger Dryas (11.7-12.9 KYA) glacial re-advance for the diversification within this species. Similar colonisation scenarios and divergence before the LGM from Eastern to Western Europe have been proposed for other species, including the common vole *Microtus arvalis* (Heckel *et al.*, 2005; Stojak *et al.*, 2016), the bank vole *Clethrionomys glareolus* (Deffontaine *et al.*, 2005; Kotlík *et al.*, 2006; Wójcik *et al.*, 2010), and the root vole *M. oeconomus* (Brunhoff *et al.*, 2003).

The population expansion signatures for the Northern and Western phylogroups, star-like patterns in phylogenetic networks and population expansion times support recent and quick colonisation events of central and northern Europe, and appear to reflect responses to postglacial climate warming. The Western lineage was restricted to Central, Western and South-Eastern France and North-Western Spain in continental Europe, but it was the only lineage found in Ireland and several islands off the west and north coasts of Britain. The region of the Dordogne in South-Western France was situated outside the LGM permafrost area and has temperate mammal fossil records dated to the end of the LGM; therefore, it has been suggested as another likely northern refugium (Sommer & Nadachowski, 2006; McDevitt *et al.*, 2010) where the Western lineage could have persisted and recolonised Western and Central France after the LGM. But as stated above, an Iberian origin for this phylogroup is also possible. However, SDM studies showed that suitable climatic conditions during the LGM for *S. minutus* and other temperate small mammal species could have been more continuous and present further north (Fløjgaard *et al.*, 2009; Vega *et al.*, 2010b), which could explain its widespread distribution in Western Europe and its presence in Britain. According to BSP results, it is plausible that Northern and Western phylogroups spread across Europe after the Younger Dryas. The British (island) group, belonging to the Northern phylogroup, showed a significant signature of population expansion. This expansion could have selectively displaced pygmy shrew populations of the Western lineage, which still remain in uplands and islands in the periphery to the north, west and south of Britain forming a 'Celtic fringe' (Searle *et al.*, 2009).

The widespread Italian lineage may be presumed to derive from a glacial refugium located somewhere within the vicinity of the Apennine mountain chain. A significant population expansion signature demonstrates that the Italian phylogroup went through a recent expansion phase, calculated in BSP for about 5.5 KYA. Contrastingly, the lack of a population expansion signature, the high nucleotide and haplotype diversities, and the highly divergent sequences showing a weak north/south subdivision of the Balkan phylogroup warrants further attention. The Balkans is a European hotspot for biodiversity given its environmental stability, topographic and climatic diversity and occasional connectedness with Asia Minor (Kryštufek & Reed, 2004; Kryštufek *et al.*, 2007, 2009; Bužan *et al.*, 2010), and it could be expected that some of these factors shaped the genetic diversity of the Balkan lineage there. Similarly, the lack of significant population expansion values for the Iberian lineage may relate to historical stable population sizes; however, the sample size was low and this result should be taken with caution.

Further considerations and implications

The comparison of the results obtained here with those elsewhere shows an emerging pattern of glacial refugia in Mediterranean peninsulas and further north in Central Europe for several species.

Although *S. minutus* is considered as a least concern species by the IUCN (Hutterer *et al.*, 2016), the distinct phylogroups deserve more attention than this implies. Genetic diversity is considered an important aspect of global biodiversity (McNeely *et al.*, 1990), and local and/or country-based conservation efforts are highly valued (for example, in Britain and Ireland the pygmy shrew is protected by law). The refugial areas in Southern Europe are often found in mountain ranges at the low-latitude margins of the present-day distribution ranges of species and are most likely to contain rear-edge populations where selection for local adaptations could have resulted in the evolution of distinct ecotypes (Cook, 1961; Hampe & Petit, 2005). Rear-edge populations, including the southern lineages of *S. minutus*, deserve further investigation and should be regarded for conservation because they are important to determine the responses of species to modern climate change (Petit *et al.*, 2003; Hampe & Petit, 2005).

In conclusion, the Eurasian pygmy shrew *Sorex minutus* is a good model for understanding biological diversity, colonisation patterns and the effects of past climate change on biological diversity. There is a mosaic of genetic lineages across continental Europe, characterised by different demographic histories and natural colonisation patterns, while island populations are characterised by recent natural and human-mediated colonisations. This study has notably expanded previous findings on *S. minutus*, with a more precise statistical phylogeographic analysis of the genetic variability and structure, colonisation routes, geographical barriers and historical demography across Europe. Specifically, we provided new data from the Iberian and Balkan peninsulas, and from Central and Eastern Europe (Poland, Ukraine and Russia), important for understanding postglacial events. *Sorex minutus* is not an easy species to obtain in large numbers, and the sampling described here represents a very substantial effort. However, it is a species that is unusually widespread and genetically subdivided and therefore can inform better than almost any other about the relative importance of southern and northern glacial refugia.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website.

Table S1. *Sorex minutus* dataset and sample information

Table S2. Pairwise geographic distances (in Km, below diagonal) and genetic differentiation (Slatkin's F_{ST}, above diagonal) among *Sorex minutus* phylogroups and other geographic groups

Figure S1. Correlogram of pairwise geographic and genetic distances among *Sorex minutus* phylogroups and other geographic groups.

Figure S2. Mismatch distributions of *Sorex minutus* phylogroups and other geographic groups.

TABLES

Table 1. DNA sequence polymorphism in *Sorex minutus* phylogroups and other geographic groups

Phylogroups	*N*	*S*	*P*	*H*	*Hd*	*Hd* (SD)	*π*	*π* (SD)	*k*
Ingroup	671	390	277	424	0.9899	0.0015	0.0143	0.0000	15.8670
Italian	26	51	19	18	0.9600	0.0230	0.0061	0.0004	6.7720
South Italian	4	16	0	4	1.0000	0.1770	0.0072	0.0020	8.0000
Balkan	22	55	28	17	0.9610	0.0290	0.0097	0.0009	10.7970
Iberian	6	15	6	5	0.9330	0.1220	0.0058	0.0013	6.4000
Western	283	147	83	102	0.9458	0.0067	0.0049	0.0002	5.4400
Irish	94	53	21	42	0.8920	0.0270	0.0020	0.0002	2.2180
Northern	330	311	197	278	0.9984	0.0005	0.0065	0.0002	7.1840
Continental groups									
Western (Continental)	15	28	11	13	0.9810	0.0310	0.0050	0.0006	5.5430
Northern (Continental)	226	241	142	188	0.9978	0.0007	0.0062	0.0002	6.9300
Other island groups									
Orkney Islands (All)	119	17	13	11	0.7720	0.0210	0.0027	0.0001	3.0140
Orkney Mainland	44	9	7	8	0.7550	0.0550	0.0013	0.0002	1.4790
Orkney South Ronaldsay	40	1	1	2	0.1420	0.0710	0.0001	0.0001	0.1420
Orkney Westray	33	0	0	1	0.0000	0.0000	0.0000	0.0000	0.0000
Orkney Hoy	2	2	0	2	1.0000	0.5000	0.0018	0.0009	2.0000
Belle Île	5	9	3	5	1.0000	0.1260	0.0038	0.0010	4.2000
British	91	146	61	80	0.9960	0.0030	0.0055	0.0003	6.1210

N = Sample size; *S* = Number of polymorphic (segregating) sites; *P* = Parsimony informative sites; *H* = Number of haplotypes; *Hd* = Haplotype diversity; SD = Standard Deviation; *π* = Nucleotide diversity; *k* = Average number of nucleotide differences.

1

Table 2. Population expansion tests for *Sorex minutus* phylogroups and other geographic groups

Phylogroups	R_2	*P*-value	*Fs*	*P*-value	τ	*t* (in years)	TMRCA (in KYA)	95% HPD (in KYA)
Ingroup	0.0198	**0.0004**	-741.2620	***	7.8590	6425	31.8	22.0-43.1
Italian	0.0521	**0.0000**	-5.8766	**0.0152**	6.7720	5536	7.2	4.8-10.2
South Italian	0.1822	0.1658	0.0687	0.2975	5.6340	-	7.7	4.2-12.1
Balkan	0.0830	0.0542	-3.6701	0.0768	7.1500	-	15.5	9.7-22.7
Iberian	0.1462	0.0888	0.0731	0.4290	4.0100	-	6.2	3.9-10.0
Western	0.0175	**0.0004**	-114.6990	***	3.6660	2997	9.3	6.7-12.6
Irish	0.0187	**0.0000**	-52.5664	***	1.3040	1066	5.9	4.9-6.9
Northern	0.0105	**0.0000**	-663.4730	***	6.5390	5346	11.8	7.7-16.8
Continental groups								
Western (Continental)	0.0793	**0.0045**	-6.0342	**0.0035**	5.5430	4532	-	-
Northern (Continental)	0.0128	**0.0000**	-386.4520	***	5.8010	4742	-	-
Other island groups								
Orkney Islands (All)	0.0880	0.5209	0.6044	0.6437	1.1740	-	-	-
Orkney Mainland	0.0839	0.2301	-1.6879	0.1892	1.4790	-	-	-
Orkney Hoy	0.5000	1.0000	NC	NC	2.0000	-	-	-
Orkney South Ronaldsay	0.0712	0.1770	-0.2182	0.4420	0.1420	-	-	-
Orkney Westray	NC	NC	NC	NC	NC	-	-	-
Belle Île	0.1915	0.2467	-1.6330	0.0732	3.5500	-	-	-
British	0.0161	**0.0000**	-122.8550	***	6.1210	5004	-	-

R_2 = Ramos-Onsins and Rozas (2002) test of neutrality; *P*-value = *P*-values of expansion tests expected under neutrality (*** = $P < 0.001$); *Fs* = Demographic population expansion test (Fu 1997); τ = ($2ut$) The mode of a mismatch distribution; *t* = Time of population expansion (for phylogroups with bi- or unimodal mismatch distributions); TMRCA = Time of divergence from the Most Recent Common Ancestor; 95% HPD = 95% Highest Posterior Density; KYA = Thousand Years Ago; NC = Not computable (not enough variation or samples)

2

3

1

FIGURE LEGENDS

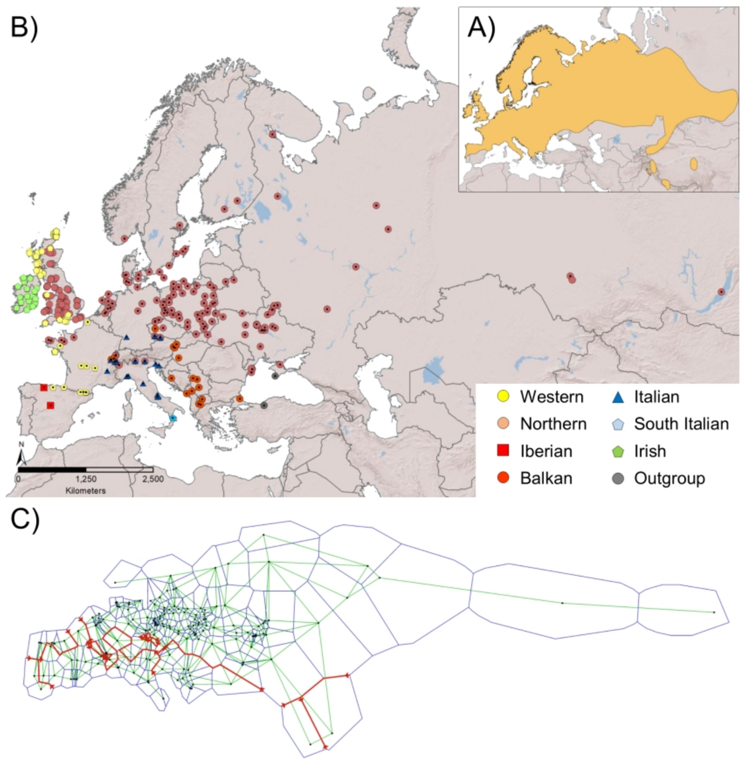
Figure 1. A) Map of Eurasia showing the geographical distribution of the Eurasian pygmy shrew *Sorex minutus* (Hutterer *et al.*, 2016). B) Sample localities of *S. minutus* used for this study and divided into mitochondrially encoded cytochrome b (*MT-CYB*) phylogroups (symbols with a dot represent samples used for inferring geographic barriers). C) Geographic barriers (red lines) for *S. minutus*; the barriers (up to a maximum of 10) were inferred using Monmonier's maximum difference algorithm which finds edges (boundaries) on the Voronoi tessellation (blue polygons) associated with the highest rate of change in genetic distances among a subset of continental samples (dots) interconnected with a Delaunay triangulation (green lines).

Figure 2. Phylogenetic reconstructions of the Eurasian pygmy shrew *Sorex minutus* using *MT-CYB* sequences. A) Bayesian phylogenetic tree (with posterior probabilities on branches) showing the phylogroups. B) Haplotype phylogenetic network with haplotypes represented as nodes and their evolutionary relationships represented by edges; relevant haplotypes named at the centre of star-like patterns.

Figure 3. Maximum Clade Credibility tree for 671 sequences of *Sorex minutus* from Europe and Siberia, annotated from 10,000 Bayesian genealogy sampling. Posterior probabilities of basal nodes indicate support for each lineage. Horizontal bars represent 95% HPD intervals for Time to Most Recent Common Ancestor (TMRCA) of each lineage (in thousand years ago, KYA).

Figure 4. Historical demography of the Eurasian pygmy shrew *Sorex minutus*. A) Mismatch distributions of groups with significant signatures of population expansion. B) Bayesian Skyline Plots (BSP) of phylogroups with significant signatures of population expansion. The

solid lines in BSP are median estimates and the shaded areas represent 95% Highest Probability Densities (confidence intervals).



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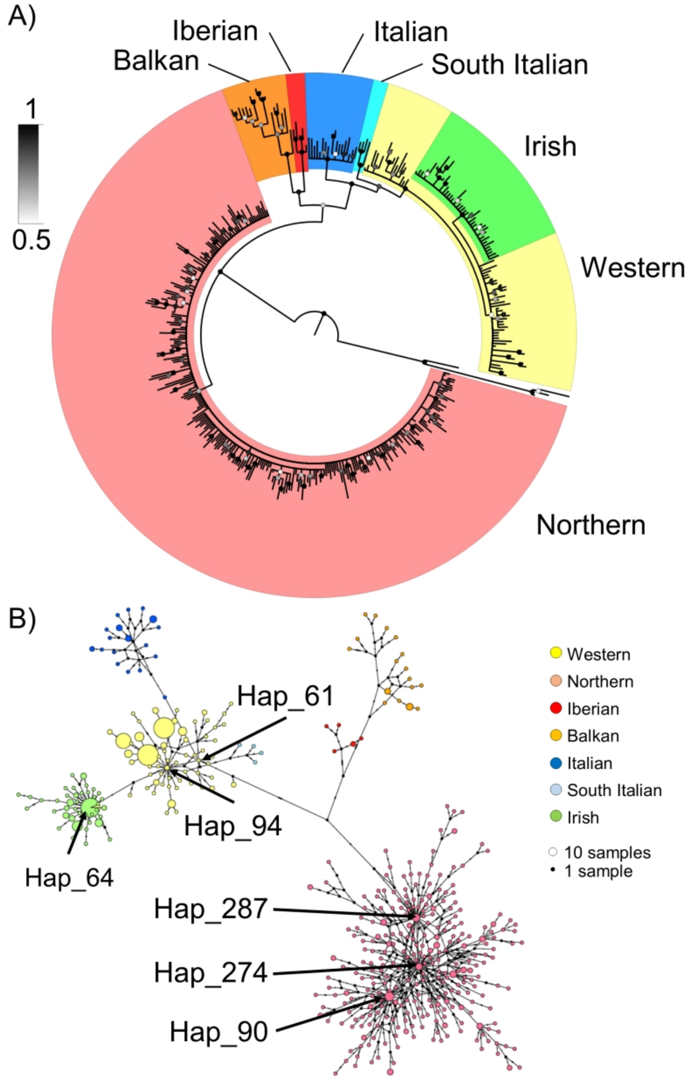

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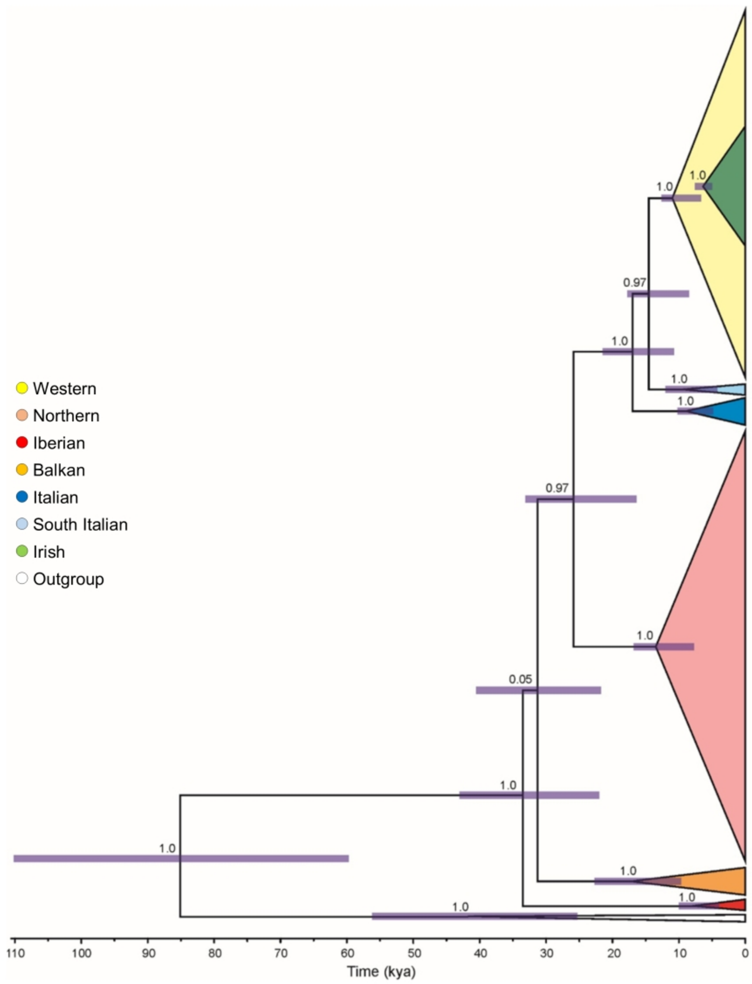

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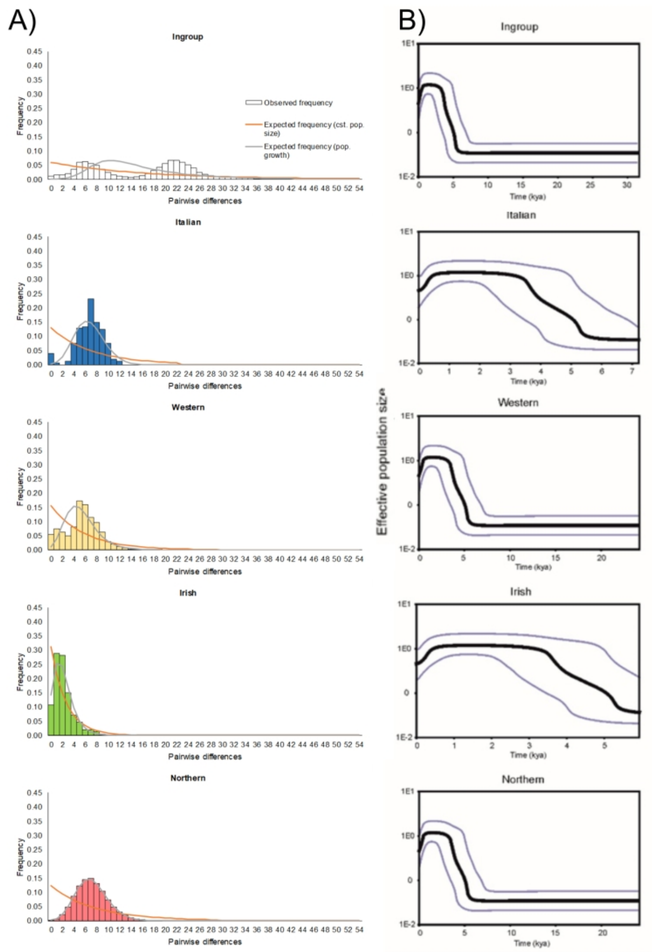

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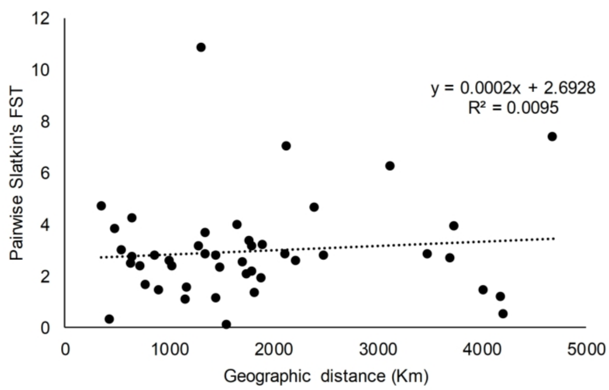

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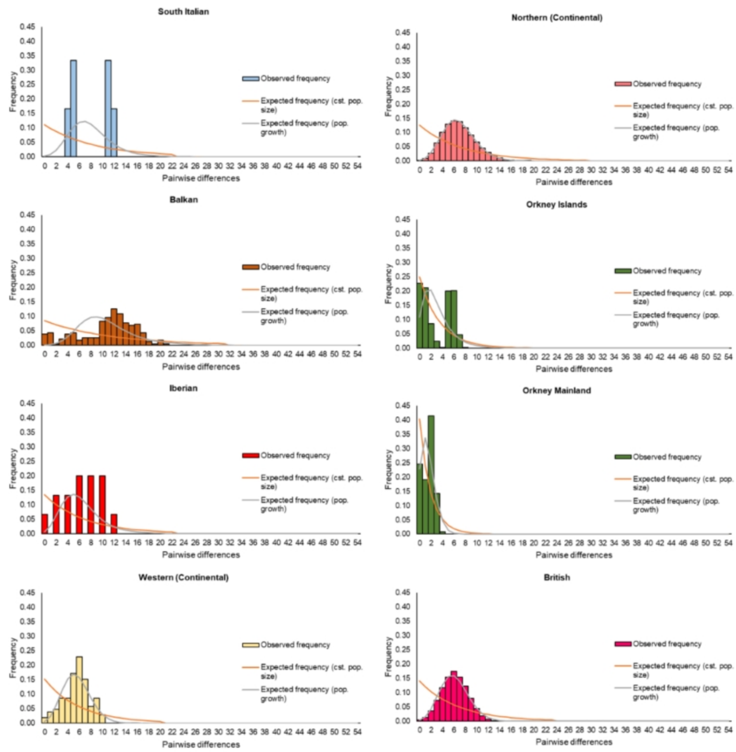

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Table S1. *Sorex minutus* dataset and sample information

ID	Country	County/Region	LongDEC	LatDEC	Phylogroup	Phylogroup 2	Source	Haplotype
ADAd0001	Andorra	Andorra	1.583333	42.583333	Western	ContinentalWestern	Mascheretti et al., 2003	Hap_1
ADAd0002	Andorra	Andorra	1.583333	42.583334	Western	ContinentalWestern	Mascheretti et al., 2003	Hap_2
ATDo1611	Austria	Donnerskirchen, Neusiedlersee	16.641250	47.895703	Balkan		This article	Hap_3
ATDo1612	Austria	Donnerskirchen, Neusiedlersee	16.641250	47.895704	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_4
ATIl0001	Austria	Illmitz	16.845403	47.764706	Balkan		This article	Hap_5
ATIl0003	Austria	Illmitz	16.845403	47.764707	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_6
ATIl0004	Austria	Illmitz	16.845403	47.764708	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_7
ATIl0005	Austria	Illmitz	16.845403	47.764709	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_8
BAOs5670	Bosnia Herzegovina	Osjecenica	16.288743	44.239741	Balkan		This article	Hap_9
BYLE0026	Belorusia	Lesnojeozero	26.691825	54.830219	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_10
CHBa0001	Switzerland	Bassins, Vaud	6.650000	46.533333	Northern	ContinentalNorthern	Mascheretti et al., 2003	Hap_11
CHBa5698	Switzerland	Bassins, Vaud	6.231061	46.462789	Northern	ContinentalNorthern	This article	Hap_12
CHBa5712	Switzerland	Bassins, Vaud	6.231061	46.462790	Balkan		This article	Hap_13
CHBa5756	Switzerland	Bassins, Vaud	6.231061	46.462791	Northern	ContinentalNorthern	Vega et al., 2010a	Hap_14
CHBr5421	Switzerland	Bretolet, Valais	6.865181	46.168864	Italian		Vega et al., 2010a	Hap_15
CHCE0889	Switzerland	Chalet des Enfants, Vaud	6.664442	46.574206	Balkan		Vega et al., 2010a	Hap_16
CHCG5272	Switzerland	Chalet a Gobet, Vaud	6.692656	46.564611	Northern	ContinentalNorthern	Vega et al., 2010a	Hap_17
CHCh7622	Switzerland	Champmartin, Vaud	6.997358	46.932742	Northern	ContinentalNorthern	Vega et al., 2010a	Hap_18
CHCu7581	Switzerland	Chablais Cudrefin, Vaud	7.026558	46.959283	Northern	ContinentalNorthern	Vega et al., 2010a	Hap_19
CHGl7628	Switzerland	Gletterens, Fribourg	6.936106	46.892650	Northern	ContinentalNorthern	Vega et al., 2010a	Hap_20
CHOC7576	Switzerland	Ostende Chevroux, Vaud	6.917847	46.894258	Northern	ContinentalNorthern	This article	Hap_20
CHOC7583	Switzerland	Ostende Chevroux, Vaud	6.917847	46.894259	Northern	ContinentalNorthern	Vega et al., 2010a	Hap_21
CHPN5442	Switzerland	Pont de Nant, Vaud	7.094307	46.249087	Italian		Vega et al., 2010a	Hap_22
CHVl4747	Switzerland	Val d'Illiez, Valais	6.892742	46.204300	Northern	ContinentalNorthern	Vega et al., 2010a	Hap_23
CHVl4748	Switzerland	Val d'Illiez, Valais	6.892742	46.204301	Italian		Vega et al., 2010a	Hap_24
CZBo0153	Czech Republic	Bohemia	13.569494	49.864183	Balkan		This article	Hap_25
CZBo0154	Czech Republic	Bohemia	13.569494	49.864184	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_26
CZBo0155	Czech Republic	Bohemia	13.569494	49.864185	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_27
CZBo0156	Czech Republic	Bohemia	13.569494	49.864186	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_28
CZCJ0001	Czech Republic	Ceske Jiretin	13.566667	50.683333	Northern	ContinentalNorthern	Mascheretti et al., 2003	Hap_29
CZDe0009	Czech Republic	Decin City, bern Bohemia	14.198800	50.805900	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_30
CZDe0010	Czech Republic	Decin City, bern Bohemia	14.198800	50.805901	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_31
CZMo0794	Czech Republic	Flaje, Most district, bern Bohemia, Krusne Hoy Mountains	13.537700	50.600300	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_32
CZOl0039	Czech Republic	Oleska	14.909572	49.948594	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_33
CZSS0237	Czech Republic	Srnin Sumava Mountains	13.475481	49.065617	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_34
CZSS0238	Czech Republic	Srnin Sumava Mountains	13.475481	49.065618	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_35
CZSS4767	Czech Republic	Srnin Sumava Mountains	13.475481	49.065619	Italian		Vega et al., 2010a	Hap_36
CZSS4838	Czech Republic	Srnin Sumava Mountains	13.475481	49.065620	Italian		Vega et al., 2010a	Hap_36
CZVl0001	Czech Republic	Vltava River West Side, Ceske Budejovice, Southern Bohemia	14.412928	48.911359	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_37
CZVl0002	Czech Republic	Vltava River West Side, Ceske Budejovice, Southern Bohemia	14.412928	48.911360	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_37
CZVl0003	Czech Republic	Vltava River West Side, Ceske Budejovice, Southern Bohemia	14.412928	48.911361	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_38
CZVl0004	Czech Republic	Vltava River West Side, Ceske Budejovice, Southern Bohemia	14.412928	48.911362	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_39
CZVl0005	Czech Republic	Vltava River East Side, Ceske Budejovice, Southern Bohemia	14.419040	48.911533	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_40
CZVl0006	Czech Republic	Vltava River East Side, Ceske Budejovice, Southern Bohemia	14.419040	48.911534	Italian		Vega et al., 2010a	Hap_41
CZVl0007	Czech Republic	Vltava River East Side, Ceske Budejovice, Southern Bohemia	14.419040	48.911535	Italian		Vega et al., 2010a	Hap_41
CZVl0008	Czech Republic	Vltava River East Side, Ceske Budejovice, Southern Bohemia	14.419040	48.911536	Italian		Vega et al., 2010a	Hap_41
DEBK0001	Germany	Beltringserharder Koog/Nordfriesland (BKN)	8.784617	54.675639	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_42

DEBK0020	Germany	Beltringserharder Koog/Nordfriesland (BKN)	8.784617	54.675640	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_43
DEBK0021	Germany	Beltringserharder Koog/Nordfriesland (BKN)	8.784617	54.675641	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_42
DEEb3996	Germany	Eberswalde	13.810889	52.833108	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_44
DEEn0005	Germany	Entin	10.603836	54.135908	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_45
DEHM0001	Germany	Hartz Mountains	10.666667	51.750000	Northern	ContinentalNorthern	Mascheretti et al., 2003	Hap_46
DENN0002	Germany	Norderoor Nördl Haselund/Nordfriesland	9.175908	54.589636	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_47
DENN0003	Germany	Norderoor Nördl Haselund/Nordfriesland	9.175908	54.589637	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_48
DEOe0001	Germany	Oetisheim	8.791475	48.970792	Italian		Vega et al., 2010a	Hap_49
DESa0003	Germany	Saxony Anholt Gardelegen	11.395539	52.477892	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_50
DESa0005	Germany	Saxony Anholt Gardelegen	11.395539	52.477893	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_51
DKAm0001	Denmark	Amager	12.583333	55.583333	Northern	ContinentalNorthern	Mascheretti et al., 2003	Hap_52
DKBo0001	Denmark	Bornholm	15.000000	55.033333	Northern	ContinentalNorthern	Mascheretti et al., 2003	Hap_53
DKBo0002	Denmark	Bornholm	15.000000	55.033334	Northern	ContinentalNorthern	Mascheretti et al., 2003	Hap_54
DKFy0001	Denmark	Fyn	10.800000	55.316667	Northern	ContinentalNorthern	Mascheretti et al., 2003	Hap_55
DKLa0001	Denmark	Langeland	10.716667	54.950000	Northern	ContinentalNorthern	Mascheretti et al., 2003	Hap_56
DKMa0005	Denmark	Mandø	8.552122	55.277164	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_57
DKMa0006	Denmark	Mandø	8.552122	55.277165	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_58
DKMa0007	Denmark	Mandø	8.552122	55.277166	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_59
DKRi0003	Denmark	Viking centre - Ribe	8.762797	55.327044	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_60
ESBa9709	Spain	Pyrenees	1.113629	42.564995	Western	ContinentalWestern	McDevitt et al., 2011	Hap_61
ESEM0069	Spain	Espinosa de los Monteros, Cantabria	-3.450258	43.142322	Western	ContinentalWestern	McDevitt et al., 2011	Hap_62
ESNa0047	Spain	Navarra	-1.645500	43.175708	Western	ContinentalWestern	McDevitt et al., 2011	Hap_63
ESNa0861	Spain	Navarra	-1.645500	43.175709	Western	ContinentalWestern	McDevitt et al., 2011	Hap_64
ESNa1131	Spain	Navarra	-1.645500	43.175710	Western	ContinentalWestern	McDevitt et al., 2011	Hap_64
ESNa1286	Spain	Navarra	-1.645500	43.175711	Western	ContinentalWestern	McDevitt et al., 2011	Hap_63
ESPE0047	Spain	Picos de Europa, Castilla-Leon	-4.999678	43.104939	Iberian		This article	Hap_65
ESPE0057	Spain	Picos de Europa, Castilla-Leon	-4.999678	43.104940	Iberian		This article	Hap_66
ESRa0002	Spain	Rascafria	-3.883333	40.900000	Iberian		Mascheretti et al., 2003	Hap_67
ESRa0003	Spain	Rascafria	-3.883333	40.900001	Iberian		Mascheretti et al., 2003	Hap_68
ESRa0640	Spain	Rascafria	-3.879364	40.903628	Iberian		This article	Hap_69
ESRa5939	Spain	Rascafria	-3.879364	40.903629	Iberian		This article	Hap_67
FILa0001	Finland	Lammi	25.116667	61.066667	Northern	ContinentalNorthern	Mascheretti et al., 2003	Hap_70
FISa0001	Finland	Saortu	27.250000	61.733333	Northern	ContinentalNorthern	Mascheretti et al., 2003	Hap_71
FRBI0001	France	Brittany	-3.195833	47.337500	Western	Bellelle	McDevitt et al., 2011	Hap_72
FRBI0002	France	Brittany	-3.195833	47.337501	Western	Bellelle	McDevitt et al., 2011	Hap_73
FRBI0005	France	Brittany	-3.200000	47.370833	Western	Bellelle	McDevitt et al., 2011	Hap_74
FRBI0011	France	Brittany	-3.122222	47.308333	Western	Bellelle	McDevitt et al., 2011	Hap_75
FRBI00LP	France	Brittany	-3.150000	47.350000	Western	Bellelle	McDevitt et al., 2011	Hap_76
FRBr2McD	France	Brittany	-1.625000	48.466667	Northern	ContinentalNorthern	McDevitt et al., 2011	Hap_77
FRCi0003	France	Cistriere Auvergne, Loire	3.540781	45.445856	Western	ContinentalWestern	McDevitt et al., 2011	Hap_78
FRDi3003	France	Divonne Les Bains, Ain	6.143175	46.356817	Italian		Vega et al., 2010a	Hap_36
FREB0001	France	Etang des Balceres, Des Angles, Pyrenees	2.080242	42.552475	Western	ContinentalWestern	McDevitt et al., 2011	Hap_79
FRFr0139	France	Fressenville, Abbeville, Normandie	0.001231	48.931408	Northern	ContinentalNorthern	McDevitt et al., 2011	Hap_80
FRLB0066	France	Lac des Bouillouses, Font-Romeu, Pyrenees	1.992267	42.561417	Western	ContinentalWestern	McDevitt et al., 2011	Hap_81
FRLi3McD	France	Limousin	2.133333	45.700000	Western	ContinentalWestern	McDevitt et al., 2011	Hap_82
FRLV0002	France	Lans en Vercors	5.589069	45.127964	Italian		Vega et al., 2010a	Hap_83
FRMo0001	France	Morlaix	-3.833333	48.583333	Northern	ContinentalNorthern	Mascheretti et al., 2003	Hap_84
FRNe0004	France	Nexon	1.250000	45.750000	Western	ContinentalWestern	McDevitt et al., 2011	Hap_76
FRPa0001	France	Paimpont, Broceliande forest, SW Renns, etang du pas du haux	-2.279472	48.001333	Western	ContinentalWestern	McDevitt et al., 2011	Hap_85

FRPC0001	France	Pas de Calais	2.302110	50.566000	Western	ContinentalWestern	McDevitt et al., 2011	Hap_86
FRPP5540	France	Pont Plancoet, Bretagne	-4.198681	48.651008	Northern	ContinentalNorthern	McDevitt et al., 2011	Hap_84
FRSM0001	France	nord, pont saint Marco	-2.040306	48.614361	Northern	ContinentalNorthern	McDevitt et al., 2011	Hap_87
GBAn0001	Wales	Anglesey	-4.340278	53.199167	Northern	Britain	McDevitt et al., 2011	Hap_88
GBAn0038	Wales	Anglesey	-4.666667	53.302778	Northern	Britain	McDevitt et al., 2011	Hap_89
GBAn0042	Wales	Anglesey	-4.382222	53.192778	Northern	Britain	McDevitt et al., 2011	Hap_90
GBAn0044	Wales	Anglesey	-4.330000	53.188889	Northern	Britain	McDevitt et al., 2011	Hap_91
GBAn0046	Wales	Anglesey	-4.435278	53.361667	Western	CelticFringeUKmain	McDevitt et al., 2011	Hap_92
GBAr0001	Scotland	Arran	-5.285556	55.556389	Western	CelticFringeUKIslands	McDevitt et al., 2011	Hap_93
GBAr0002	Scotland	Arran	-5.285556	55.556390	Western	CelticFringeUKIslands	McDevitt et al., 2011	Hap_94
GBAr0003	Scotland	Arran	-5.099167	55.485833	Western	CelticFringeUKIslands	McDevitt et al., 2011	Hap_95
GBAr0004	Scotland	Arran	-5.128056	55.450000	Western	CelticFringeUKIslands	McDevitt et al., 2011	Hap_96
GBAr0006	Scotland	Arran	-5.128056	55.450001	Western	CelticFringeUKIslands	McDevitt et al., 2011	Hap_97
GBAr0007	Scotland	Arran	-5.128056	55.450002	Western	CelticFringeUKIslands	McDevitt et al., 2011	Hap_98
GBAr0008	Scotland	Arran	-5.128056	55.450003	Western	CelticFringeUKIslands	McDevitt et al., 2011	Hap_97
GBBe0740	Scotland	Benbecula	-7.332778	57.427778	Western	CelticFringeUKIslands	McDevitt et al., 2011	Hap_99
GBBF0035	England	Bracknell Forest	-0.743611	51.450278	Northern	Britain	McDevitt et al., 2011	Hap_100
GBBF0036	England	Bracknell Forest	-0.743611	51.450279	Northern	Britain	McDevitt et al., 2011	Hap_101
GBCa0001	Wales	Carmarthenshire	-4.155278	51.760280	Northern	Britain	McDevitt et al., 2011	Hap_102
GBCa0002	Wales	Carmarthenshire	-4.147778	51.752500	Northern	Britain	McDevitt et al., 2011	Hap_103
GBCa0003	Wales	Carmarthenshire	-4.147778	51.752501	Northern	Islands	McDevitt et al., 2011	Hap_104
GBCa0004	Wales	Carmarthenshire	-4.581667	51.792222	Northern	Islands	McDevitt et al., 2011	Hap_105
GBCn0901	Scotland	Canna	-6.511667	57.059444	Western	CelticFringeUKIslands	McDevitt et al., 2011	Hap_106
GBCn0905	Scotland	Canna	-6.511667	57.059445	Western	CelticFringeUKIslands	McDevitt et al., 2011	Hap_106
GBCn0906	Scotland	Canna	-6.511667	57.059446	Western	CelticFringeUKIslands	McDevitt et al., 2011	Hap_106
GBCo00C1	England	Cornwall	-4.728333	50.475278	Northern	Islands	McDevitt et al., 2011	Hap_107
GBCo00C2	England	Cornwall	-4.728333	50.475279	Western	CelticFringeUKmain	McDevitt et al., 2011	Hap_108
GBCo0139	Wales	Conwy	-3.833333	53.283333	Northern	Britain	McDevitt et al., 2011	Hap_109
GBCr1100	Wales	Cardiganshire	-4.061111	52.438056	Northern	Britain	McDevitt et al., 2011	Hap_110
GBCu00B1	England	Cumbria	-3.234722	54.867778	Northern	Britain	McDevitt et al., 2011	Hap_111
GBCu00B2	England	Cumbria	-3.234722	54.867779	Northern	Britain	McDevitt et al., 2011	Hap_112
GBCu00D1	England	Cumbria	-3.234722	54.867780	Northern	Britain	McDevitt et al., 2011	Hap_112
GBCu0642	England	Cumbria	-3.152222	54.066111	Northern	Britain	McDevitt et al., 2011	Hap_113
GBCu0677	England	Cumbria	-2.968611	55.013889	Northern	Britain	McDevitt et al., 2011	Hap_114
GBDe0001	England	Derbyshire	-1.636944	52.944167	Northern	Britain	McDevitt et al., 2011	Hap_115
GBDe0002	England	Derbyshire	-1.636944	52.944168	Northern	Britain	McDevitt et al., 2011	Hap_116
GBDe0953	England	Derbyshire	-1.488889	53.061944	Northern	Britain	McDevitt et al., 2011	Hap_117
GBDo0458	England	Dorset	-2.363333	50.830556	Northern	Britain	McDevitt et al., 2011	Hap_118
GBDo0459	England	Dorset	-2.363333	50.830557	Northern	Britain	McDevitt et al., 2011	Hap_90
GBDo0460	England	Dorset	-2.363333	50.830558	Northern	Britain	McDevitt et al., 2011	Hap_119
GBDo0461	England	Dorset	-2.363333	50.830559	Western	CelticFringeUKmain	McDevitt et al., 2011	Hap_120
GBDo0462	England	Dorset	-2.363333	50.830560	Northern	Britain	McDevitt et al., 2011	Hap_118
GBEC0001	England	East Cottingwith	-0.916667	53.866667	Northern	Britain	Mascheretti et al., 2003	Hap_121
GBEH0001	England	East Hendred	-1.333333	51.566667	Northern	Islands	Mascheretti et al., 2003	Hap_122
GBER0177	Scotland	Easter Ross	-3.917500	57.753056	Western	CelticFringeUKmain	McDevitt et al., 2011	Hap_123
GBER0408	Scotland	Easter Ross	-3.917500	57.753057	Western	CelticFringeUKmain	McDevitt et al., 2011	Hap_123
GBER0410	Scotland	Easter Ross	-3.917500	57.753058	Northern	Britain	McDevitt et al., 2011	Hap_124
GBGa0001	Scotland	Gask	-3.666667	56.350000	Northern	Britain	Mascheretti et al., 2003	Hap_125
GBGa0002	Scotland	Gask	-3.666667	56.350001	Northern	Britain	Mascheretti et al., 2003	Hap_126

GBGi0001	Scotland	Gigha	-5.741033	55.683333	Western	CelticFringeUKIslands	McDevitt et al., 2011	Hap_127
GBGi0002	Scotland	Gigha	-5.741033	55.683334	Western	CelticFringeUKIslands	McDevitt et al., 2011	Hap_127
GBGi0003	Scotland	Gigha	-5.741033	55.683335	Western	CelticFringeUKIslands	McDevitt et al., 2011	Hap_127
GBGi0004	Scotland	Gigha	-5.741033	55.683336	Western	CelticFringeUKIslands	McDevitt et al., 2011	Hap_127
GBGi0005	Scotland	Gigha	-5.741033	55.683337	Western	CelticFringeUKIslands	McDevitt et al., 2011	Hap_127
GBGi0006	Scotland	Gigha	-5.741033	55.683338	Western	CelticFringeUKIslands	McDevitt et al., 2011	Hap_127
GBGl0001	England	Gloucestershire	-2.645000	51.788333	Northern	Islands	McDevitt et al., 2011	Hap_33
GBGl0043	England	Gloucestershire	-2.109722	51.651111	Northern	Britain	McDevitt et al., 2011	Hap_128
GBGl0047	England	Gloucestershire	-2.103056	51.809167	Northern	Britain	McDevitt et al., 2011	Hap_129
GBGr0001	England	Grittenham	-1.966667	51.550000	Northern	Britain	Mascheretti et al., 2003	Hap_130
GBHa0039	England	Hampshire	-1.080000	51.187222	Western	CelticFringeUKmain	McDevitt et al., 2011	Hap_131
GBHa0040	England	Hampshire	-1.225833	51.358889	Northern	Britain	McDevitt et al., 2011	Hap_132
GBHa0041	England	Hampshire	-1.225833	51.358890	Northern	Britain	McDevitt et al., 2011	Hap_133
GBHo0001	Scotland	Hoy	-3.333333	58.916667	Western	Orkney	McDevitt et al., 2011	Hap_134
GBHo0868	Scotland	Hoy	-3.382778	58.880278	Western	Orkney	McDevitt et al., 2011	Hap_135
GBIM0001	Isle of Man	Isle of Man	-4.483333	54.150000	Northern	Britain	Mascheretti et al., 2003	Hap_136
GBIM0002	Isle of Man	Isle of Man	-4.483333	54.150001	Northern	Britain	Mascheretti et al., 2003	Hap_137
GBIM0600	Isle of Man	Isle of Man	-4.483333	54.150002	Northern	Britain	McDevitt et al., 2011	Hap_138
GBIM0601	Isle of Man	Isle of Man	-4.351111	54.291389	Northern	Britain	McDevitt et al., 2011	Hap_139
GBIM0602	Isle of Man	Isle of Man	-4.451667	54.172500	Northern	Britain	McDevitt et al., 2011	Hap_138
GBIn0180	Scotland	Inverness	-3.485556	57.341111	Northern	Britain	McDevitt et al., 2011	Hap_140
GBIn0181	Scotland	Inverness	-4.416944	57.454444	Northern	Britain	McDevitt et al., 2011	Hap_141
GBIn0182	Scotland	Inverness	-4.416944	57.454445	Northern	Britain	McDevitt et al., 2011	Hap_142
GBIn0407	Scotland	Inverness	-3.960556	57.336389	Northern	Britain	McDevitt et al., 2011	Hap_143
GBIs0001	Scotland	Islay	-6.233333	55.750000	Western	CelticFringeUKIslands	McDevitt et al., 2011	Hap_144
GBIs0002	Scotland	Islay	-6.233333	55.750001	Western	CelticFringeUKIslands	McDevitt et al., 2011	Hap_145
GBIs0003	Scotland	Islay	-6.233333	55.750002	Western	CelticFringeUKIslands	McDevitt et al., 2011	Hap_146
GBIs0004	Scotland	Islay	-6.233333	55.750003	Western	CelticFringeUKIslands	McDevitt et al., 2011	Hap_147
GBIW0001	England	Isle of Wight	-1.252778	50.668889	Western	CelticFringeUKIslands	McDevitt et al., 2011	Hap_148
GBIW0002	England	Isle of Wight	-1.252778	50.668890	Western	CelticFringeUKIslands	McDevitt et al., 2011	Hap_148
GBIW0003	England	Isle of Wight	-1.471944	50.688889	Western	CelticFringeUKIslands	McDevitt et al., 2011	Hap_149
GBJu0815	Scotland	Jura	-5.943511	55.852778	Northern	Britain	McDevitt et al., 2011	Hap_150
GBJu0816	Scotland	Jura	-5.943511	55.852779	Northern	Britain	McDevitt et al., 2011	Hap_150
GBKe0009	England	Kent	1.257778	51.126944	Northern	Britain	McDevitt et al., 2011	Hap_151
GBKe0010	England	Kent	0.933889	51.067222	Northern	Britain	McDevitt et al., 2011	Hap_152
GBKe0972	England	Kent	0.960278	50.995278	Northern	Britain	McDevitt et al., 2011	Hap_153
GBKi0795	Scotland	Kintyre	-5.582778	55.281944	Western	CelticFringeUKIslands	McDevitt et al., 2011	Hap_154
GBKk0099	Scotland	Kirkcudbright	-3.823333	54.866944	Northern	Islands	McDevitt et al., 2011	Hap_114
GBKk0100	Scotland	Kirkcudbrightshire	-3.823333	54.866945	Northern	Britain	McDevitt et al., 2011	Hap_90
GBKk0589	Scotland	Kirkcudbrightshire	-3.781389	54.975556	Northern	Britain	McDevitt et al., 2011	Hap_155
GBLa1071	England	Lancashire	-2.432778	53.812222	Northern	Britain	McDevitt et al., 2011	Hap_156
GBLC0001	Wales	Lyn Conwy	-3.833333	53.283334	Northern	Islands	Mascheretti et al., 2003	Hap_157
GBLC0002	Wales	Lyn Conwy	-3.833333	53.283335	Northern	Britain	Mascheretti et al., 2003	Hap_158
GBLe0497	England	Leicestershire	-1.133333	52.633333	Northern	Britain	McDevitt et al., 2011	Hap_159
GBLo0001	England	Longnor	-1.883333	53.166667	Northern	Britain	Mascheretti et al., 2003	Hap_160
GBMa0001	England	Macclesfield	-2.033333	53.250000	Northern	Islands	Mascheretti et al., 2003	Hap_161
GBMu0858	Scotland	Mull	-5.837778	56.510000	Western	CelticFringeUKIslands	McDevitt et al., 2011	Hap_94
GBMu0859	Scotland	Mull	-5.837778	56.510001	Western	CelticFringeUKIslands	McDevitt et al., 2011	Hap_162
GBMu0860	Scotland	Mull	-5.861111	56.404722	Western	CelticFringeUKIslands	McDevitt et al., 2011	Hap_163

GBMu0861	Scotland	Mull	-6.200556	56.333611	Western	CelticFringeUKIslands	McDevitt et al., 2011	Hap_164
GBNo0001	England	Norfolk	0.591944	52.748056	Northern	Britain	McDevitt et al., 2011	Hap_165
GBNo0002	England	Norfolk	0.591944	52.748057	Northern	Britain	McDevitt et al., 2011	Hap_90
GBNo0003	England	Norfolk	0.556111	52.765000	Northern	Britain	McDevitt et al., 2011	Hap_166
GBNo0004	England	Norfolk	0.570556	52.762778	Northern	Britain	McDevitt et al., 2011	Hap_167
GBNU0319	Scotland	N. Uist	-7.322500	57.518056	Western	CelticFringeUKIslands	McDevitt et al., 2011	Hap_99
GBNU0325	Scotland	N. Uist	-7.322500	57.518057	Western	CelticFringeUKIslands	McDevitt et al., 2011	Hap_168
GBNY00F2	England	North Yorkshire	-1.073611	53.936389	Northern	Britain	McDevitt et al., 2011	Hap_169
GBNY00F3	England	North Yorkshire	-1.073611	53.936390	Northern	Britain	McDevitt et al., 2011	Hap_170
GBNY00Y1	England	North Yorkshire	-1.073611	53.936391	Northern	Britain	McDevitt et al., 2011	Hap_171
GBOM0001	Scotland	Orkney Mainland	-2.913056	58.906667	Western	Orkney	McDevitt et al., 2011	Hap_172
GBOM0002	Scotland	Orkney Mainland	-2.913056	58.906668	Western	Orkney	McDevitt et al., 2011	Hap_172
GBOM0003	Scotland	Orkney Mainland	-2.913056	58.906669	Western	Orkney	McDevitt et al., 2011	Hap_172
GBOM0004	Scotland	Orkney Mainland	-2.913056	58.906670	Western	Orkney	McDevitt et al., 2011	Hap_172
GBOM0260	Scotland	Orkney Mainland	-2.925556	58.918611	Western	Orkney	McDevitt et al., 2011	Hap_173
GBOM0261	Scotland	Orkney Mainland	-3.293056	59.128333	Western	Orkney	McDevitt et al., 2011	Hap_174
GBOM0262	Scotland	Orkney Mainland	-2.878333	58.904444	Western	Orkney	McDevitt et al., 2011	Hap_173
GBOM0418	Scotland	Orkney Mainland	-3.051389	58.944444	Western	Orkney	McDevitt et al., 2011	Hap_175
GBOM0419	Scotland	Orkney Mainland	-3.224444	58.970000	Western	Orkney	McDevitt et al., 2011	Hap_134
GBPe0005	Wales	Pembrokeshire	-4.657500	51.772500	Northern	Islands	McDevitt et al., 2011	Hap_176
GBPe0006	Wales	Pembrokeshire	-4.657500	51.772501	Northern	Islands	McDevitt et al., 2011	Hap_177
GBPe0026	Wales	Pembrokeshire	-4.953889	51.650833	Northern	Islands	McDevitt et al., 2011	Hap_178
GBPe0042	Wales	Pembrokeshire	-4.953889	51.650834	Northern	Islands	McDevitt et al., 2011	Hap_179
GBPr0132	Scotland	Perthshire	-4.003333	56.346389	Northern	Britain	McDevitt et al., 2011	Hap_180
GBRa0001	Scotland	Raasay	-6.033333	57.400000	Western	CelticFringeUKIslands	McDevitt et al., 2011	Hap_181
GBRa0002	Scotland	Raasay	-6.033333	57.400001	Western	CelticFringeUKIslands	McDevitt et al., 2011	Hap_182
GBRa0003	Scotland	Raasay	-6.033333	57.400002	Western	CelticFringeUKIslands	McDevitt et al., 2011	Hap_181
GBRa0004	Scotland	Raasay	-6.033333	57.400003	Western	CelticFringeUKIslands	McDevitt et al., 2011	Hap_181
GBRu0104	Scotland	Rum	-6.269167	56.987778	Western	CelticFringeUKIslands	McDevitt et al., 2011	Hap_106
GBRu0105	Scotland	Rum	-6.330000	57.029722	Western	CelticFringeUKIslands	McDevitt et al., 2011	Hap_106
GBRu0127	Scotland	Rum	-6.280278	57.012500	Western	CelticFringeUKIslands	McDevitt et al., 2011	Hap_183
GBSG0044	England	South Gloucestershire	-2.331667	51.561667	Northern	Britain	McDevitt et al., 2011	Hap_184
GBSh0006	England	Shropshire	-2.259722	52.574167	Northern	Islands	McDevitt et al., 2011	Hap_185
GBSh0007	England	Shropshire	-2.259722	52.574168	Northern	Britain	McDevitt et al., 2011	Hap_186
GBSo0002	England	Somerset	-2.659722	51.285556	Northern	Islands	McDevitt et al., 2011	Hap_187
GBSR0273	Scotland	S. Ronaldsay	-2.974722	58.780833	Western	Orkney	McDevitt et al., 2011	Hap_188
GBSR0274	Scotland	S. Ronaldsay	-2.921389	58.758611	Western	Orkney	McDevitt et al., 2011	Hap_188
GBSR0612	Scotland	S. Ronaldsay	-3.021667	58.820833	Western	Orkney	McDevitt et al., 2011	Hap_188
GBSR0613	Scotland	S. Ronaldsay	-3.021667	58.820834	Western	Orkney	McDevitt et al., 2011	Hap_189
GBSt0005	England	Staffordshire	-2.290278	52.723333	Northern	Britain	McDevitt et al., 2011	Hap_190
GBSt0030	England	Staffordshire	-2.092500	53.098333	Northern	Britain	McDevitt et al., 2011	Hap_191
GBSu0005	England	Suffolk	0.518889	52.247778	Northern	Britain	McDevitt et al., 2011	Hap_192
GBSu0006	England	Suffolk	0.541111	52.276944	Northern	Britain	McDevitt et al., 2011	Hap_193
GBSu0007	England	Suffolk	0.541111	52.276945	Northern	Islands	McDevitt et al., 2011	Hap_194
GBSu0008	England	Suffolk	0.541111	52.276946	Northern	Britain	McDevitt et al., 2011	Hap_195
GBSU0227	Scotland	S. Uist	-7.370833	57.323611	Western	CelticFringeUKIslands	McDevitt et al., 2011	Hap_99
GBSU0310	Scotland	S. Uist	-7.370833	57.323333	Western	CelticFringeUKIslands	McDevitt et al., 2011	Hap_196
GBWa0050	England	Warwickshire	-1.243056	52.127222	Northern	Britain	McDevitt et al., 2011	Hap_197
GBWa0051	England	Warwickshire	-1.243056	52.127223	Northern	Britain	McDevitt et al., 2011	Hap_197

GBWi0042	England	Wiltshire	-2.149444	51.397500	Northern	Britain	McDevitt et al., 2011	Hap_198
GBWk0037	England	Wokingham	-0.903889	51.366389	Western	CelticFringeUKmain	McDevitt et al., 2011	Hap_199
GBWk0038	England	Wokingham	-0.903889	51.366390	Western	CelticFringeUKmain	McDevitt et al., 2011	Hap_200
GBWl0669	England	Walney	-3.227500	54.077222	Northern	Britain	McDevitt et al., 2011	Hap_201
GBWl0670	England	Walney	-3.227500	54.077223	Northern	Britain	McDevitt et al., 2011	Hap_201
GBWl0671	England	Walney	-3.227500	54.077224	Northern	Britain	McDevitt et al., 2011	Hap_201
GBWo0009	England	Worcestershire	-2.124722	52.310000	Northern	Britain	McDevitt et al., 2011	Hap_202
GBWo0011	England	Worcestershire	-2.029444	52.412500	Northern	Islands	McDevitt et al., 2011	Hap_203
GBWo0012	England	Worcestershire	-2.413333	52.266667	Northern	Britain	McDevitt et al., 2011	Hap_204
GBWR0176	Scotland	Wester Ross	-5.331667	57.481944	Western	CelticFringeUKmain	McDevitt et al., 2011	Hap_205
GBWR0178	Scotland	Wester Ross	-5.331667	57.481945	Western	CelticFringeUKmain	McDevitt et al., 2011	Hap_206
GBWS0011	England	West Sussex	0.307500	50.844722	Northern	Islands	McDevitt et al., 2011	Hap_207
HUTa3711	Hungary	Táska village, Fehérvíz moorland	17.500000	46.616667	Balkan		This article	Hap_208
IEAI0001	Ireland	Aran Island	-8.528647	54.993439	Western	Irish	McDevitt et al., 2011	Hap_64
IECa0001	Ireland	Camolin	-6.416667	52.583333	Western	Irish	Mascheretti et al., 2003	Hap_209
IECl0001	Ireland	Cloghan	-7.750000	53.250000	Western	Irish	Mascheretti et al., 2003	Hap_210
IECo0095	Ireland	Cork	-7.828344	51.949406	Western	Irish	McDevitt et al., 2011	Hap_211
IECo0098	Ireland	Cork	-7.828344	51.949407	Western	Irish	McDevitt et al., 2011	Hap_211
IECo0099	Ireland	Cork	-7.828344	51.949408	Western	Irish	McDevitt et al., 2011	Hap_211
IECo0100	Ireland	Cork	-7.828344	51.949409	Western	Irish	McDevitt et al., 2011	Hap_212
IECo0101	Ireland	Cork	-7.828344	51.949410	Western	Irish	McDevitt et al., 2011	Hap_211
IECo0102	Ireland	Cork	-7.828344	51.949411	Western	Irish	McDevitt et al., 2011	Hap_213
IECo0103	Ireland	Cork	-7.828344	51.949412	Western	Irish	McDevitt et al., 2011	Hap_214
IECo0104	Ireland	Cork	-7.828344	51.949413	Western	Irish	McDevitt et al., 2011	Hap_215
IECo0105	Ireland	Cork	-7.828344	51.949414	Western	Irish	McDevitt et al., 2011	Hap_216
IECo0108	Ireland	Cork	-7.828344	51.949415	Western	Irish	McDevitt et al., 2011	Hap_217
IECt0001	Ireland	Castlebridge	-6.500000	52.416667	Western	Irish	Mascheretti et al., 2003	Hap_218
IEDN0001	Ireland	Donegal	-8.300000	54.650000	Western	Irish	McDevitt et al., 2011	Hap_219
IEDN0009	Ireland	Donegal	-8.300000	54.650001	Western	Irish	McDevitt et al., 2011	Hap_220
IEDy0001	Ireland	Derry	-7.250000	55.000000	Western	Irish	McDevitt et al., 2011	Hap_64
IEDy0003	Ireland	Derry	-7.250000	55.000001	Western	Irish	McDevitt et al., 2011	Hap_221
IEDy0004	Ireland	Derry	-7.250000	55.000002	Western	Irish	McDevitt et al., 2011	Hap_64
IEDy0005	Ireland	Derry	-7.250000	55.000003	Western	Irish	McDevitt et al., 2011	Hap_221
IEDy0006	Ireland	Derry	-7.250000	55.000004	Western	Irish	McDevitt et al., 2011	Hap_221
IEDy0007	Ireland	Derry	-7.250000	55.000005	Western	Irish	McDevitt et al., 2011	Hap_221
IEDy0008	Ireland	Derry	-7.250000	55.000006	Western	Irish	McDevitt et al., 2011	Hap_221
IEDy0009	Ireland	Derry	-7.250000	55.000007	Western	Irish	McDevitt et al., 2011	Hap_221
IEDy0010	Ireland	Derry	-7.250000	55.000008	Western	Irish	McDevitt et al., 2011	Hap_221
IEDy0011	Ireland	Derry	-7.250000	55.000009	Western	Irish	McDevitt et al., 2011	Hap_221
IEDy0012	Ireland	Derry	-7.250000	55.000010	Western	Irish	McDevitt et al., 2011	Hap_221
IEGa0039	Ireland	Galway	-8.866667	53.150000	Western	Irish	McDevitt et al., 2011	Hap_222
IEGa0046	Ireland	Galway	-8.866667	53.150001	Western	Irish	McDevitt et al., 2011	Hap_223
IEGa0047	Ireland	Galway	-8.966667	53.133333	Western	Irish	McDevitt et al., 2011	Hap_64
IEGa0050	Ireland	Galway	-8.966667	53.133334	Western	Irish	McDevitt et al., 2011	Hap_224
IEGa0057	Ireland	Galway	-8.966667	53.133335	Western	Irish	McDevitt et al., 2011	Hap_225
IEGW0001	Ireland	Donegal	-8.383333	55.050000	Western	Irish	McDevitt et al., 2011	Hap_226
IEGW0026	Ireland	Donegal	-8.383333	55.050001	Western	Irish	McDevitt et al., 2011	Hap_226
IEGW005a	Ireland	Donegal	-8.383333	55.050002	Western	Irish	McDevitt et al., 2011	Hap_226
IEGW005b	Ireland	Donegal	-8.383333	55.050003	Western	Irish	McDevitt et al., 2011	Hap_226

IEKe0001	Ireland	Kerry	-9.533333	52.055556	Western	Irish	McDevitt et al., 2011	Hap_64
IEKe0002	Ireland	Kerry	-9.533333	52.055557	Western	Irish	McDevitt et al., 2011	Hap_227
IEKe0004	Ireland	Kerry	-9.533333	52.055558	Western	Irish	McDevitt et al., 2011	Hap_64
IEKe0005	Ireland	Kerry	-9.533333	52.055559	Western	Irish	McDevitt et al., 2011	Hap_64
IEKeP3kY	Ireland	Kerry	-9.533333	52.055560	Western	Irish	McDevitt et al., 2011	Hap_228
IEKi0084	Ireland	Kildare	-6.977778	53.279722	Western	Irish	McDevitt et al., 2011	Hap_64
IEKi0085	Ireland	Kildare	-6.977778	53.279723	Western	Irish	McDevitt et al., 2011	Hap_64
IEKi0086	Ireland	Kildare	-6.977778	53.279724	Western	Irish	McDevitt et al., 2011	Hap_229
IEKi0087	Ireland	Kildare	-6.977778	53.279725	Western	Irish	McDevitt et al., 2011	Hap_64
IEKi0089	Ireland	Kildare	-6.977778	53.279726	Western	Irish	McDevitt et al., 2011	Hap_230
IELa0LSa	Ireland	Laois	-7.500000	52.783333	Western	Irish	McDevitt et al., 2011	Hap_231
IELa0LSb	Ireland	Laois	-7.500000	52.783334	Western	Irish	McDevitt et al., 2011	Hap_232
IELa0LSc	Ireland	Laois	-7.500000	52.783335	Western	Irish	McDevitt et al., 2011	Hap_64
IELe0001	Ireland	Leitrim	-7.786111	53.958333	Western	Irish	McDevitt et al., 2011	Hap_233
IELe0007	Ireland	Leitrim	-7.786111	53.958334	Western	Irish	McDevitt et al., 2011	Hap_64
IELe0008	Ireland	Leitrim	-7.768889	53.991111	Western	Irish	McDevitt et al., 2011	Hap_64
IELe0018	Ireland	Leitrim	-7.773333	53.986667	Western	Irish	McDevitt et al., 2011	Hap_64
IELe0019	Ireland	Leitrim	-7.773333	53.986668	Western	Irish	McDevitt et al., 2011	Hap_64
IELi0058	Ireland	Limerick	-8.834167	52.584167	Western	Irish	McDevitt et al., 2011	Hap_234
IELi0059	Ireland	Limerick	-8.834167	52.584168	Western	Irish	McDevitt et al., 2011	Hap_235
IELi0060	Ireland	Limerick	-8.834167	52.584169	Western	Irish	McDevitt et al., 2011	Hap_236
IELi0068	Ireland	Limerick	-8.834167	52.584170	Western	Irish	McDevitt et al., 2011	Hap_64
IELi0069	Ireland	Limerick	-8.769167	52.617500	Western	Irish	McDevitt et al., 2011	Hap_64
IELi0080	Ireland	Limerick	-8.769167	52.617501	Western	Irish	McDevitt et al., 2011	Hap_64
IELi0082	Ireland	Limerick	-8.769167	52.617502	Western	Irish	McDevitt et al., 2011	Hap_237
IELo011a	Ireland	Louth	-6.183333	54.033333	Western	Irish	McDevitt et al., 2011	Hap_238
IELo011b	Ireland	Louth	-6.183333	54.033334	Western	Irish	McDevitt et al., 2011	Hap_238
IELo011c	Ireland	Louth	-6.183333	54.033335	Western	Irish	McDevitt et al., 2011	Hap_238
IEMa0020	Ireland	Mayo	-9.250000	54.166667	Western	Irish	McDevitt et al., 2011	Hap_239
IEMa0025	Ireland	Mayo	-9.250000	54.166668	Western	Irish	McDevitt et al., 2011	Hap_239
IEMa0032	Ireland	Mayo	-9.316667	54.233333	Western	Irish	McDevitt et al., 2011	Hap_240
IEMa0037	Ireland	Mayo	-9.316667	54.233334	Western	Irish	McDevitt et al., 2011	Hap_241
IEOf0019	Ireland	Offaly	-7.750000	53.250001	Western	Irish	McDevitt et al., 2011	Hap_242
IEOf0026	Ireland	Offaly	-7.750000	53.250002	Western	Irish	McDevitt et al., 2011	Hap_64
IEOf0048	Ireland	Offaly	-7.750000	53.250003	Western	Irish	McDevitt et al., 2011	Hap_242
IESl0001	Ireland	Slane	-6.500000	53.750000	Western	Irish	Mascheretti et al., 2003	Hap_64
IEWa0001	Ireland	Waterford	-7.333333	52.175000	Western	Irish	McDevitt et al., 2011	Hap_243
IEWa0002	Ireland	Waterford	-7.333333	52.175001	Western	Irish	McDevitt et al., 2011	Hap_64
IEWa0003	Ireland	Waterford	-7.333333	52.175002	Western	Irish	McDevitt et al., 2011	Hap_229
IEWa0004	Ireland	Waterford	-7.333333	52.175003	Western	Irish	McDevitt et al., 2011	Hap_243
IEWa0005	Ireland	Waterford	-7.333333	52.175004	Western	Irish	McDevitt et al., 2011	Hap_229
IEWB0001	Ireland	Whiting Bay	-7.833333	51.833333	Western	Irish	Mascheretti et al., 2003	Hap_244
IEWB0002	Ireland	Whiting Bay	-7.833333	51.833334	Western	Irish	Mascheretti et al., 2003	Hap_245
IEWB0003	Ireland	Whiting Bay	-7.833333	51.833335	Western	Irish	Mascheretti et al., 2003	Hap_211
IEWe0005	Ireland	Wexford	-6.841667	52.233333	Western	Irish	McDevitt et al., 2011	Hap_246
IEWe0008	Ireland	Wexford	-6.841667	52.233334	Western	Irish	McDevitt et al., 2011	Hap_64
IEWe0018	Ireland	Wexford	-6.841667	52.233335	Western	Irish	McDevitt et al., 2011	Hap_246
IEWe0031	Ireland	Wexford	-6.841667	52.233336	Western	Irish	McDevitt et al., 2011	Hap_64
IEWe0033	Ireland	Wexford	-6.841667	52.233338	Western	Irish	McDevitt et al., 2011	Hap_246

IEWe0036	Ireland	Wexford	-6.416667	52.583334	Western	Irish	McDevitt et al., 2011	Hap_247
IEWe0054	Ireland	Wexford	-6.416667	52.583335	Western	Irish	McDevitt et al., 2011	Hap_64
IEWe0055	Ireland	Wexford	-6.416667	52.583336	Western	Irish	McDevitt et al., 2011	Hap_64
IEWe020a	Ireland	Wexford	-6.841667	52.233337	Western	Irish	McDevitt et al., 2011	Hap_64
IEWe023a	Ireland	Wexford	-6.841667	52.233339	Western	Irish	McDevitt et al., 2011	Hap_248
IEWe023b	Ireland	Wexford	-6.841667	52.233340	Western	Irish	McDevitt et al., 2011	Hap_64
IEWi00Qa	Ireland	Wicklow	-6.383333	53.000000	Western	Irish	McDevitt et al., 2011	Hap_64
IEWi00Qb	Ireland	Wicklow	-6.383333	53.000001	Western	Irish	McDevitt et al., 2011	Hap_249
IEWi00Qc	Ireland	Wicklow	-6.383333	53.000002	Western	Irish	McDevitt et al., 2011	Hap_64
ITAb0001	Italy	Abruzzo	14.000000	42.000000	Italian		Mascheretti et al., 2003	Hap_250
ITAb0002	Italy	Abruzzo	14.000000	42.000001	Italian		Mascheretti et al., 2003	Hap_251
ITCa5342	Italy	Camigliatello, Calabria	16.445953	39.338611	SouthItalian		Vega et al., 2010a	Hap_252
ITGe0001	Italy	San Carlo di Cese	8.832010	44.477300	Italian		Vega et al., 2010a	Hap_253
ITGe0003	Italy	Molino Vecchio, Valbrevenna	9.064750	44.555300	Italian		Vega et al., 2010a	Hap_254
ITMa00NT	Italy	Majella Mountains, Abruzzo	13.928433	42.285431	Italian		Vega et al., 2010a	Hap_251
ITMa0175	Italy	Majella Mountains, Abruzzo	14.115697	42.083411	Italian		Vega et al., 2010a	Hap_255
ITMa0176	Italy	Majella Mountains, Abruzzo	14.115697	42.083412	Italian		Vega et al., 2010a	Hap_251
ITMa0177	Italy	Majella Mountains, Abruzzo	14.115697	42.083413	Italian		Vega et al., 2010a	Hap_256
ITMa0178	Italy	Majella Mountains, Abruzzo	14.115697	42.083414	Italian		Vega et al., 2010a	Hap_251
ITMa0179	Italy	Majella Mountains, Abruzzo	14.115697	42.083415	Italian		Vega et al., 2010a	Hap_255
ITPr0001	Italy	Prasota, Mazzo di Valtellina, Sondrio	10.248014	46.286975	Italian		Vega et al., 2010a	Hap_257
ITPr0004	Italy	Prasota, Mazzo di Valtellina, Sondrio	10.248014	46.286976	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_258
ITSi0011	Italy	La Sila, Cosenza	16.491144	39.352214	SouthItalian		Vega et al., 2010a	Hap_259
ITSi0017	Italy	La Sila, Cosenza	16.491144	39.352215	SouthItalian		Vega et al., 2010a	Hap_260
ITSi0021	Italy	La Sila, Cosenza	16.491144	39.352216	SouthItalian		Vega et al., 2010a	Hap_261
ITTg0049	Italy	Torgnon, Valle d'Aosta, Piemonte	7.571240	45.807200	Northern	ContinentalNorthern	This article	Hap_262
ITTo1578	Italy	Toscana, Arezzo, Castelfranco di Sopra	11.550125	43.617606	Italian		Vega et al., 2010a	Hap_263
ITTr0001	Italy	Trento	11.833333	46.250000	Italian		Mascheretti et al., 2003	Hap_264
ITTr0002	Italy	Trento	11.833333	46.250001	Northern	ContinentalNorthern	Mascheretti et al., 2003	Hap_265
LTVi0001	Lithuania	Vilnius	25.316667	54.666667	Northern	ContinentalNorthern	Mascheretti et al., 2003	Hap_266
LTVi0002	Lithuania	Vilnius	25.316667	54.666668	Northern	ContinentalNorthern	Mascheretti et al., 2003	Hap_267
MELo6362	Montenegro	Lovćen	18.818774	42.405763	Balkan		This article	Hap_268
MEMK0001	Montenegro	Mount Komovi	19.658139	42.694703	Balkan		This article	Hap_269
MKJa12477	Macedonia	Jakupica Mountains	21.418861	41.689061	Balkan		This article	Hap_270
MKJa9222	Macedonia	Jakupica Mountains	21.418861	41.689062	Balkan		This article	Hap_271
MKMG0001	Macedonia	Mount Galicica	20.850800	41.101494	Balkan		This article	Hap_272
MKPe0001	Macedonia	Pelister Mountains	21.166667	41.000000	Balkan		Mascheretti et al., 2003	Hap_273
NLBo0001	Netherlands	Boxtel	5.333333	51.600000	Northern	ContinentalNorthern	Mascheretti et al., 2003	Hap_274
NLCa0002	Netherlands	Callantsoog, b Holland	4.693670	52.830300	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_275
NLDi0001	Netherlands	Dieren, Gelderland	6.081540	52.047900	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_90
NLDi0062	Netherlands	Diessen	5.175208	51.474775	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_50
NLFr0017	Netherlands	Freisland, Ameland, Buren	5.796036	53.445303	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_90
NLFr0040	Netherlands	Friesland, Ameland, Buren	5.796036	53.445304	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_90
NLOv0042	Netherlands	Overijssel, National Park de Hoge Velmx	6.456994	52.495319	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_276
NLWa0001	Netherlands	Wageningen	5.666667	51.966667	Northern	ContinentalNorthern	Mascheretti et al., 2003	Hap_277
NLZV0044	Netherlands	Zeeuws Vlaanderen	5.722117	52.718142	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_274
NOAs0301	Norway	near Arendal	8.450000	58.600000	Northern	ContinentalNorthern	McDevitt et al., 2011	Hap_278
OMHa0003	Scotland	Orkney Mainland, Harray	-3.190167	59.033728	Western	Orkney	McDevitt et al., 2011	Hap_134
OMHa0004	Scotland	Orkney Mainland, Harray	-3.190167	59.033729	Western	Orkney	McDevitt et al., 2011	Hap_134

OMHa0006	Scotland	Orkney Mainland, Harray	-3.190167	59.033730	Western	Orkney	McDevitt et al., 2011	Hap_279
OMHa0009	Scotland	Orkney Mainland, Harray	-3.190167	59.033731	Western	Orkney	McDevitt et al., 2011	Hap_279
OMHa0011	Scotland	Orkney Mainland, Harray	-3.190167	59.033732	Western	Orkney	McDevitt et al., 2011	Hap_279
OMHo0014	Scotland	Orkney Mainland, Hobbister	-3.067628	58.946361	Western	Orkney	McDevitt et al., 2011	Hap_175
OMHo0015	Scotland	Orkney Mainland, Hobbister	-3.067628	58.946362	Western	Orkney	McDevitt et al., 2011	Hap_175
OMKi0013	Scotland	Orkney Mainland, Kirbister	-3.110083	58.949994	Western	Orkney	McDevitt et al., 2011	Hap_175
OMSa0001	Scotland	Orkney Mainland, Sandwick	-3.297169	59.048261	Western	Orkney	McDevitt et al., 2011	Hap_172
OMSa0002	Scotland	Orkney Mainland, Sandwick	-3.297169	59.048262	Western	Orkney	McDevitt et al., 2011	Hap_134
OMSe0001	Scotland	Orkney Mainland, Settiscarth	-3.103428	59.050525	Western	Orkney	McDevitt et al., 2011	Hap_172
OMSe0002	Scotland	Orkney Mainland, Settiscarth	-3.103428	59.050526	Western	Orkney	McDevitt et al., 2011	Hap_172
OMSO0006	Scotland	Orkney Mainland, Saint Ola	-2.950003	58.950019	Western	Orkney	McDevitt et al., 2011	Hap_175
OMSO0007	Scotland	Orkney Mainland, Saint Ola	-2.950003	58.950020	Western	Orkney	McDevitt et al., 2011	Hap_173
OMSO0008	Scotland	Orkney Mainland, Saint Ola	-2.950003	58.950021	Western	Orkney	McDevitt et al., 2011	Hap_173
OMSO0009	Scotland	Orkney Mainland, Saint Ola	-2.950003	58.950022	Western	Orkney	McDevitt et al., 2011	Hap_173
OMSO0010	Scotland	Orkney Mainland, Saint Ola	-2.950003	58.950023	Western	Orkney	McDevitt et al., 2011	Hap_173
OMSO0011	Scotland	Orkney Mainland, Saint Ola	-2.950003	58.950024	Western	Orkney	McDevitt et al., 2011	Hap_280
OMSO0013	Scotland	Orkney Mainland, Saint Ola	-2.950003	58.950025	Western	Orkney	McDevitt et al., 2011	Hap_173
OMSO0014	Scotland	Orkney Mainland, Saint Ola	-2.950003	58.950026	Western	Orkney	McDevitt et al., 2011	Hap_173
OMSO0015	Scotland	Orkney Mainland, Saint Ola	-2.950003	58.950027	Western	Orkney	McDevitt et al., 2011	Hap_173
OMSO0017	Scotland	Orkney Mainland, Saint Ola	-2.950003	58.950028	Western	Orkney	McDevitt et al., 2011	Hap_280
OMSO0020	Scotland	Orkney Mainland, Saint Ola	-2.950003	58.950029	Western	Orkney	McDevitt et al., 2011	Hap_281
OMSO0026	Scotland	Orkney Mainland, Saint Ola	-2.950003	58.950030	Western	Orkney	McDevitt et al., 2011	Hap_173
OMSO0029	Scotland	Orkney Mainland, Saint Ola	-2.950003	58.950031	Western	Orkney	McDevitt et al., 2011	Hap_173
OMSO0036	Scotland	Orkney Mainland, Saint Ola	-2.950003	58.950032	Western	Orkney	McDevitt et al., 2011	Hap_173
OMTa0001	Scotland	Orkney Mainland, Tankerness	-2.850033	58.950033	Western	Orkney	McDevitt et al., 2011	Hap_173
OMTa0002	Scotland	Orkney Mainland, Tankerness	-2.850033	58.950034	Western	Orkney	McDevitt et al., 2011	Hap_173
OMTa0003	Scotland	Orkney Mainland, Tankerness	-2.850033	58.950035	Western	Orkney	McDevitt et al., 2011	Hap_173
OMTa0004	Scotland	Orkney Mainland, Tankerness	-2.850033	58.950036	Western	Orkney	McDevitt et al., 2011	Hap_173
OMTa0005	Scotland	Orkney Mainland, Tankerness	-2.850033	58.950037	Western	Orkney	McDevitt et al., 2011	Hap_173
OMTa0006	Scotland	Orkney Mainland, Tankerness	-2.850033	58.950038	Western	Orkney	McDevitt et al., 2011	Hap_173
OMTa0007	Scotland	Orkney Mainland, Tankerness	-2.850033	58.950039	Western	Orkney	McDevitt et al., 2011	Hap_173
OMTa0008	Scotland	Orkney Mainland, Tankerness	-2.850033	58.950040	Western	Orkney	McDevitt et al., 2011	Hap_281
OMTa0009	Scotland	Orkney Mainland, Tankerness	-2.850033	58.950041	Western	Orkney	McDevitt et al., 2011	Hap_173
OSGr0006	Scotland	Orkney South Ronaldsay, Grimness	-2.916700	58.816678	Western	Orkney	McDevitt et al., 2011	Hap_188
OSGr0007	Scotland	Orkney South Ronaldsay, Grimness	-2.916700	58.816679	Western	Orkney	McDevitt et al., 2011	Hap_188
OSGr0008	Scotland	Orkney South Ronaldsay, Grimness	-2.916700	58.816680	Western	Orkney	McDevitt et al., 2011	Hap_188
OSGr0009	Scotland	Orkney South Ronaldsay, Grimness	-2.916700	58.816681	Western	Orkney	McDevitt et al., 2011	Hap_188
OSGr0010	Scotland	Orkney South Ronaldsay, Grimness	-2.916700	58.816682	Western	Orkney	McDevitt et al., 2011	Hap_188
OSGr0011	Scotland	Orkney South Ronaldsay, Grimness	-2.916700	58.816683	Western	Orkney	McDevitt et al., 2011	Hap_188
OSGr0012	Scotland	Orkney South Ronaldsay, Grimness	-2.916700	58.816684	Western	Orkney	McDevitt et al., 2011	Hap_188
OSGr0013	Scotland	Orkney South Ronaldsay, Grimness	-2.916700	58.816685	Western	Orkney	McDevitt et al., 2011	Hap_188
OSGr0014	Scotland	Orkney South Ronaldsay, Grimness	-2.916700	58.816686	Western	Orkney	McDevitt et al., 2011	Hap_188
OSGr0015	Scotland	Orkney South Ronaldsay, Grimness	-2.916700	58.816687	Western	Orkney	McDevitt et al., 2011	Hap_188
OSGr0016	Scotland	Orkney South Ronaldsay, Grimness	-2.916700	58.816688	Western	Orkney	McDevitt et al., 2011	Hap_188
OSGr0018	Scotland	Orkney South Ronaldsay, Grimness	-2.916700	58.816689	Western	Orkney	McDevitt et al., 2011	Hap_188
OSGr0020	Scotland	Orkney South Ronaldsay, Grimness	-2.916700	58.816690	Western	Orkney	McDevitt et al., 2011	Hap_188
OSGr0023	Scotland	Orkney South Ronaldsay, Grimness	-2.916700	58.816691	Western	Orkney	McDevitt et al., 2011	Hap_188
OSGr0025	Scotland	Orkney South Ronaldsay, Grimness	-2.916700	58.816692	Western	Orkney	McDevitt et al., 2011	Hap_188
OSGr0027	Scotland	Orkney South Ronaldsay, Grimness	-2.916700	58.816693	Western	Orkney	McDevitt et al., 2011	Hap_188

OSGr0028	Scotland	Orkney South Ronaldsay, Grimness	-2.916700	58.816694	Western	Orkney	McDevitt et al., 2011	Hap_188
OSGr0029	Scotland	Orkney South Ronaldsay, Grimness	-2.916700	58.816695	Western	Orkney	McDevitt et al., 2011	Hap_188
OSGr0039	Scotland	Orkney South Ronaldsay, Grimness	-2.916700	58.816696	Western	Orkney	McDevitt et al., 2011	Hap_188
OSWW0006	Scotland	Orkney South Ronaldsay, Wind Wick	-2.940694	58.766808	Western	Orkney	McDevitt et al., 2011	Hap_188
OSWW0007	Scotland	Orkney South Ronaldsay, Wind Wick	-2.940694	58.766809	Western	Orkney	McDevitt et al., 2011	Hap_188
OSWW0008	Scotland	Orkney South Ronaldsay, Wind Wick	-2.940694	58.766810	Western	Orkney	McDevitt et al., 2011	Hap_188
OSWW0009	Scotland	Orkney South Ronaldsay, Wind Wick	-2.940694	58.766811	Western	Orkney	McDevitt et al., 2011	Hap_188
OSWW0010	Scotland	Orkney South Ronaldsay, Wind Wick	-2.940694	58.766812	Western	Orkney	McDevitt et al., 2011	Hap_188
OSWW0011	Scotland	Orkney South Ronaldsay, Wind Wick	-2.940694	58.766813	Western	Orkney	McDevitt et al., 2011	Hap_188
OSWW0012	Scotland	Orkney South Ronaldsay, Wind Wick	-2.940694	58.766814	Western	Orkney	McDevitt et al., 2011	Hap_188
OSWW0013	Scotland	Orkney South Ronaldsay, Wind Wick	-2.940694	58.766815	Western	Orkney	McDevitt et al., 2011	Hap_188
OSWW0014	Scotland	Orkney South Ronaldsay, Wind Wick	-2.940694	58.766816	Western	Orkney	McDevitt et al., 2011	Hap_188
OSWW0015	Scotland	Orkney South Ronaldsay, Wind Wick	-2.940694	58.766817	Western	Orkney	McDevitt et al., 2011	Hap_188
OSWW0017	Scotland	Orkney South Ronaldsay, Wind Wick	-2.940694	58.766818	Western	Orkney	McDevitt et al., 2011	Hap_188
OSWW0018	Scotland	Orkney South Ronaldsay, Wind Wick	-2.940694	58.766819	Western	Orkney	McDevitt et al., 2011	Hap_189
OSWW0019	Scotland	Orkney South Ronaldsay, Wind Wick	-2.940694	58.766820	Western	Orkney	McDevitt et al., 2011	Hap_188
OSWW0020	Scotland	Orkney South Ronaldsay, Wind Wick	-2.940694	58.766821	Western	Orkney	McDevitt et al., 2011	Hap_188
OSWW0021	Scotland	Orkney South Ronaldsay, Wind Wick	-2.940694	58.766822	Western	Orkney	McDevitt et al., 2011	Hap_188
OSWW0024	Scotland	Orkney South Ronaldsay, Wind Wick	-2.940694	58.766823	Western	Orkney	McDevitt et al., 2011	Hap_188
OSWW0025	Scotland	Orkney South Ronaldsay, Wind Wick	-2.940694	58.766824	Western	Orkney	McDevitt et al., 2011	Hap_189
OWLS0001	Scotland	Orkney Westray, Loch of Swartmill	-2.933353	59.283347	Western	Orkney	McDevitt et al., 2011	Hap_134
OWLS0002	Scotland	Orkney Westray, Loch of Swartmill	-2.933353	59.283348	Western	Orkney	McDevitt et al., 2011	Hap_134
OWLS0003	Scotland	Orkney Westray, Loch of Swartmill	-2.933353	59.283349	Western	Orkney	McDevitt et al., 2011	Hap_134
OWLS0005	Scotland	Orkney Westray, Loch of Swartmill	-2.933353	59.283350	Western	Orkney	McDevitt et al., 2011	Hap_134
OWLS0024	Scotland	Orkney Westray, Loch of Swartmill	-2.933353	59.283351	Western	Orkney	McDevitt et al., 2011	Hap_134
OWLS0025	Scotland	Orkney Westray, Loch of Swartmill	-2.933353	59.283352	Western	Orkney	McDevitt et al., 2011	Hap_134
OWLS0036	Scotland	Orkney Westray, Loch of Swartmill	-2.933353	59.283353	Western	Orkney	McDevitt et al., 2011	Hap_134
OWLS0037	Scotland	Orkney Westray, Loch of Swartmill	-2.933353	59.283354	Western	Orkney	McDevitt et al., 2011	Hap_134
OWLS0038	Scotland	Orkney Westray, Loch of Swartmill	-2.933353	59.283355	Western	Orkney	McDevitt et al., 2011	Hap_134
OWLS0055	Scotland	Orkney Westray, Loch of Swartmill	-2.933353	59.283356	Western	Orkney	McDevitt et al., 2011	Hap_134
OWLS0059	Scotland	Orkney Westray, Loch of Swartmill	-2.933353	59.283357	Western	Orkney	McDevitt et al., 2011	Hap_134
OWLS0060	Scotland	Orkney Westray, Loch of Swartmill	-2.933353	59.283358	Western	Orkney	McDevitt et al., 2011	Hap_134
OWLS0061	Scotland	Orkney Westray, Loch of Swartmill	-2.933353	59.283359	Western	Orkney	McDevitt et al., 2011	Hap_134
OWLS0072	Scotland	Orkney Westray, Loch of Swartmill	-2.933353	59.283360	Western	Orkney	McDevitt et al., 2011	Hap_134
OWLS0073	Scotland	Orkney Westray, Loch of Swartmill	-2.933353	59.283361	Western	Orkney	McDevitt et al., 2011	Hap_134
OWLS0082	Scotland	Orkney Westray, Loch of Swartmill	-2.933353	59.283362	Western	Orkney	McDevitt et al., 2011	Hap_134
OWLS0083	Scotland	Orkney Westray, Loch of Swartmill	-2.933353	59.283363	Western	Orkney	McDevitt et al., 2011	Hap_134
OWLS0084	Scotland	Orkney Westray, Loch of Swartmill	-2.933353	59.283364	Western	Orkney	McDevitt et al., 2011	Hap_134
OWLS0085	Scotland	Orkney Westray, Loch of Swartmill	-2.933353	59.283365	Western	Orkney	McDevitt et al., 2011	Hap_134
OWNe0002	Scotland	Orkney Westray, Ness	-2.866747	59.233358	Western	Orkney	McDevitt et al., 2011	Hap_134
OWNe0003	Scotland	Orkney Westray, Ness	-2.866747	59.233359	Western	Orkney	McDevitt et al., 2011	Hap_134
OWNe0004	Scotland	Orkney Westray, Ness	-2.866747	59.233360	Western	Orkney	McDevitt et al., 2011	Hap_134
OWNe0005	Scotland	Orkney Westray, Ness	-2.866747	59.233361	Western	Orkney	McDevitt et al., 2011	Hap_134
OWNe0006	Scotland	Orkney Westray, Ness	-2.866747	59.233362	Western	Orkney	McDevitt et al., 2011	Hap_134
OWNe0007	Scotland	Orkney Westray, Ness	-2.866747	59.233363	Western	Orkney	McDevitt et al., 2011	Hap_134
OWNe0008	Scotland	Orkney Westray, Ness	-2.866747	59.233364	Western	Orkney	McDevitt et al., 2011	Hap_134
OWNe0009	Scotland	Orkney Westray, Ness	-2.866747	59.233365	Western	Orkney	McDevitt et al., 2011	Hap_134
OWNe0026	Scotland	Orkney Westray, Ness	-2.866747	59.233366	Western	Orkney	McDevitt et al., 2011	Hap_134
OWNe0028	Scotland	Orkney Westray, Ness	-2.866747	59.233367	Western	Orkney	McDevitt et al., 2011	Hap_134

OWNe0030	Scotland	Orkney Westray, Ness	-2.866747	59.233368	Western	Orkney	McDevitt et al., 2011	Hap_134
OWNe0041	Scotland	Orkney Westray, Ness	-2.866747	59.233369	Western	Orkney	McDevitt et al., 2011	Hap_134
OWNe0062	Scotland	Orkney Westray, Ness	-2.866747	59.233370	Western	Orkney	McDevitt et al., 2011	Hap_134
OWNe0103	Scotland	Orkney Westray, Ness	-2.866747	59.233371	Western	Orkney	McDevitt et al., 2011	Hap_134
PLBg_71469	Poland	Bogdaniec	15.067890	52.688519	Northern	ContinentalNorthern	This article	Hap_359
PLBl0001	Poland	Blizocin	22.266667	51.600000	Northern	ContinentalNorthern	Mascheretti et al., 2003	Hap_282
PLBo_60680	Poland	Bobolice	16.586622	53.955494	Northern	ContinentalNorthern	This article	Hap_351
PLBo_60757	Poland	Bobolice	16.586622	53.955494	Northern	ContinentalNorthern	This article	Hap_351
PLBo_60758	Poland	Bobolice	16.586622	53.955494	Northern	ContinentalNorthern	This article	Hap_351
PLBr_92123	Poland	Bratkowice	21.874701	50.114330	Northern	ContinentalNorthern	This article	Hap_382
PLBr_92181	Poland	Bratkowice	21.874701	50.114330	Northern	ContinentalNorthern	This article	Hap_383
PLBr_92195	Poland	Bratkowice	21.874701	50.114330	Northern	ContinentalNorthern	This article	Hap_383
PLCi_40797	Poland	Cisna	22.329300	49.210735	Northern	ContinentalNorthern	This article	Hap_335
PLCi_40985	Poland	Cisna	22.329300	49.210735	Northern	ContinentalNorthern	This article	Hap_336
PLCz_43736	Poland	Czarna Białostocka	23.281820	53.302898	Northern	ContinentalNorthern	This article	Hap_337
PLCz_43743	Poland	Czarna Białostocka	23.281820	53.302898	Northern	ContinentalNorthern	This article	Hap_338
PLCz_43822	Poland	Czarna Białostocka	23.281820	53.302898	Northern	ContinentalNorthern	This article	Hap_339
PLDa_59630	Poland	Darżlubie	18.323056	54.703333	Northern	ContinentalNorthern	This article	Hap_344
PLDa_59739	Poland	Darżlubie	18.323056	54.703333	Northern	ContinentalNorthern	This article	Hap_345
PLDa_59780	Poland	Darżlubie	18.323056	54.703333	Northern	ContinentalNorthern	This article	Hap_346
PLDe_89330	Poland	Dębno	16.523407	51.338131	Northern	ContinentalNorthern	This article	Hap_376
PLDe_89430	Poland	Dębno	16.523407	51.338131	Northern	ContinentalNorthern	This article	Hap_377
PLDe_89667	Poland	Dębno	16.523407	51.338131	Northern	ContinentalNorthern	This article	Hap_378
PLGl_70776	Poland	Głusko	15.944162	53.045467	Northern	ContinentalNorthern	This article	Hap_357
PLGl_70813	Poland	Głusko	15.944162	53.045467	Northern	ContinentalNorthern	This article	Hap_357
PLGl_70910	Poland	Głusko	15.944162	53.045467	Northern	ContinentalNorthern	This article	Hap_358
PLGo_47840	Poland	Górowo Iławeckie	20.483333	54.266667	Northern	ContinentalNorthern	This article	Hap_341
PLGo_48006	Poland	Górowo Iławeckie	20.483333	54.266667	Northern	ContinentalNorthern	This article	Hap_339
PLGo_48117	Poland	Górowo Iławeckie	20.483333	54.266667	Northern	ContinentalNorthern	This article	Hap_342
PLGo_89259	Poland	Goszcz	17.482466	51.395901	Northern	ContinentalNorthern	This article	Hap_375
PLKK_88317	Poland	Kobiór/Kobibór	18.939444	50.060278	Northern	ContinentalNorthern	This article	Hap_370
PLKK_88318	Poland	Kobiór/Kobibór	18.939444	50.060278	Northern	ContinentalNorthern	This article	Hap_371
PLKK_88392	Poland	Kobiór/Kobibór	18.939444	50.060278	Northern	ContinentalNorthern	This article	Hap_372
PLKo_102789	Poland	Kosobudy	23.074467	50.629036	Northern	ContinentalNorthern	This article	Hap_397
PLKo_102880	Poland	Kosobudy	23.074467	50.629036	Northern	ContinentalNorthern	This article	Hap_398
PLKo_102884	Poland	Kosobudy	23.074467	50.629036	Northern	ContinentalNorthern	This article	Hap_399
PLKO_79019	Poland	Krosno Odrzańskie	15.096315	52.057320	Northern	ContinentalNorthern	This article	Hap_363
PLKO_80960	Poland	Krosno Odrzańskie	15.536229	51.559242	Northern	ContinentalNorthern	This article	Hap_350
PLKr_101253	Poland	Kryńszczak	22.363787	51.990589	Northern	ContinentalNorthern	This article	Hap_392
PLKr_101488	Poland	Kryńszczak	22.363787	51.990589	Northern	ContinentalNorthern	This article	Hap_274
PLKr_101522	Poland	Kryńszczak	22.363787	51.990589	Northern	ContinentalNorthern	This article	Hap_393
PLKr_56668	Poland	Krzystkowice	15.235579	51.798953	Northern	ContinentalNorthern	This article	Hap_44
PLLo_100647	Poland	Łochów	21.710556	52.531667	Northern	ContinentalNorthern	This article	Hap_390
PLLo_100648	Poland	Łochów	21.710556	52.531667	Northern	ContinentalNorthern	This article	Hap_341
PLLo_100678	Poland	Łochów	21.710556	52.531667	Northern	ContinentalNorthern	This article	Hap_391
PLMi_69500	Poland	Międzychód	15.892540	52.598550	Northern	ContinentalNorthern	This article	Hap_355
PLMi_69843	Poland	Międzychód	15.892540	52.598550	Northern	ContinentalNorthern	This article	Hap_356
PLNo_47464	Poland	Nowogród	21.879444	53.226389	Northern	ContinentalNorthern	This article	Hap_335
PLNo_47591	Poland	Nowogród	21.879444	53.226389	Northern	ContinentalNorthern	This article	Hap_340

PLNu_100350	Poland	Nużec	23.173407	52.477722	Northern	ContinentalNorthern	This article	Hap_389
PLOs_115146	Poland	Ostróda	19.964795	53.696301	Northern	ContinentalNorthern	This article	Hap_339
PLOs_115150	Poland	Ostróda	19.964795	53.696301	Northern	ContinentalNorthern	This article	Hap_339
PLPo_26984	Poland	Pomorze	23.362616	54.046066	Northern	ContinentalNorthern	This article	Hap_325
PLPo_26985	Poland	Pomorze	23.362616	54.046066	Northern	ContinentalNorthern	This article	Hap_326
PLPo_27182	Poland	Pomorze	23.362616	54.046066	Northern	ContinentalNorthern	This article	Hap_327
PLPr_89890	Poland	Przysucha	20.631796	51.357877	Northern	ContinentalNorthern	This article	Hap_379
PLPr_89893	Poland	Przysucha	20.631796	51.357877	Northern	ContinentalNorthern	This article	Hap_380
PLPr_89902	Poland	Przysucha	20.631796	51.357877	Northern	ContinentalNorthern	This article	Hap_381
PLPu_48614	Poland	Pułkownikówka	18.982429	54.233230	Northern	ContinentalNorthern	This article	Hap_343
PLRo_88680	Poland	Rogalice	17.608795	50.961720	Northern	ContinentalNorthern	This article	Hap_373
PLRo_88712	Poland	Rogalice	17.608795	50.961720	Northern	ContinentalNorthern	This article	Hap_373
PLRo_88713	Poland	Rogalice	17.608795	50.961720	Northern	ContinentalNorthern	This article	Hap_374
PLRz_21223	Poland	Rzepin	14.832640	52.345688	Northern	ContinentalNorthern	This article	Hap_323
PLRz_21284	Poland	Rzepin	14.832640	52.345688	Northern	ContinentalNorthern	This article	Hap_324
PLSi_60205	Poland	Sierżno	17.471008	54.121005	Northern	ContinentalNorthern	This article	Hap_347
PLSi_60256	Poland	Sierżno	17.471008	54.121005	Northern	ContinentalNorthern	This article	Hap_348
PLSi_60304	Poland	Sierżno	17.471008	54.121005	Northern	ContinentalNorthern	This article	Hap_349
PLSo_103116	Poland	Sobibór	23.641667	51.475000	Northern	ContinentalNorthern	This article	Hap_400
PLSo_103118	Poland	Sobibór	23.641667	51.475000	Northern	ContinentalNorthern	This article	Hap_401
PLSo_103283	Poland	Sobibór	23.641667	51.475000	Northern	ContinentalNorthern	This article	Hap_323
PLSt_36121	Poland	Starzyna	23.531132	52.585400	Northern	ContinentalNorthern	This article	Hap_330
PLSt_60470	Poland	Stary Kraków	16.616111	54.438611	Northern	ContinentalNorthern	This article	Hap_350
PLSt_60531	Poland	Stary Kraków	16.616111	54.438611	Northern	ContinentalNorthern	This article	Hap_350
PLSw_36762	Poland	Świętokrzyski PN	20.962500	50.901944	Northern	ContinentalNorthern	This article	Hap_331
PLSw_36877	Poland	Świętokrzyski PN	20.962500	50.901944	Northern	ContinentalNorthern	This article	Hap_331
PLSw_37798	Poland	Świętokrzyski PN	20.962500	50.901944	Northern	ContinentalNorthern	This article	Hap_332
PLSz_79991	Poland	Szprotawa	15.536229	51.559242	Northern	ContinentalNorthern	This article	Hap_367
PLSz_80045	Poland	Szprotawa	15.536229	51.559242	Northern	ContinentalNorthern	This article	Hap_368
PLSz_80236	Poland	Szprotawa	15.536229	51.559242	Northern	ContinentalNorthern	This article	Hap_369
PLTr_60989	Poland	Trzebieszki	16.617777	53.361942	Northern	ContinentalNorthern	This article	Hap_352
PLTr_61166	Poland	Trzebieszki	16.617777	53.361942	Northern	ContinentalNorthern	This article	Hap_353
PLTr_61209	Poland	Trzebieszki	16.617777	53.361942	Northern	ContinentalNorthern	This article	Hap_354
PLWi_39015	Poland	Wierzchlas	18.107185	53.517961	Northern	ContinentalNorthern	This article	Hap_333
PLWi_39077	Poland	Wierzchlas	18.107185	53.517961	Northern	ContinentalNorthern	This article	Hap_334
PLWi_92325	Poland	Wiśniowa	21.660091	49.869003	Northern	ContinentalNorthern	This article	Hap_384
PLWi_92366	Poland	Wiśniowa	21.660091	49.869003	Northern	ContinentalNorthern	This article	Hap_385
PLWo_93527	Poland	Wojsław	21.516667	50.383333	Northern	ContinentalNorthern	This article	Hap_386
PLWo_93557	Poland	Wojsław	21.516667	50.383333	Northern	ContinentalNorthern	This article	Hap_387
PLWo_93558	Poland	Wojsław	21.516667	50.383333	Northern	ContinentalNorthern	This article	Hap_388
PLWs_77065	Poland	Wschowa	16.314138	51.805599	Northern	ContinentalNorthern	This article	Hap_360
PLWs_77067	Poland	Wschowa	16.314138	51.805599	Northern	ContinentalNorthern	This article	Hap_361
PLWs_77323	Poland	Wschowa	16.314138	51.805599	Northern	ContinentalNorthern	This article	Hap_362
PLWy_79694	Poland	Wymiarki	15.075700	51.508865	Northern	ContinentalNorthern	This article	Hap_364
PLWy_79697	Poland	Wymiarki	15.075700	51.508865	Northern	ContinentalNorthern	This article	Hap_365
PLWy_79774	Poland	Wymiarki	15.075700	51.508865	Northern	ContinentalNorthern	This article	Hap_366
PLZa_101886	Poland	Zagożdżon	21.450278	51.481667	Northern	ContinentalNorthern	This article	Hap_394
PLZa_101887	Poland	Zagożdżon	21.450278	51.481667	Northern	ContinentalNorthern	This article	Hap_395
PLZa_102061	Poland	Zagożdżon	21.450278	51.481667	Northern	ContinentalNorthern	This article	Hap_396

PLZi_88044	Poland	Zielona	18.985233	50.547363	Northern	ContinentalNorthern	This article	Hap_341
PLZy_30037	Poland	Żytkiejmy	22.683333	54.347778	Northern	ContinentalNorthern	This article	Hap_328
PLZy_30465	Poland	Żytkiejmy	22.683333	54.347778	Northern	ContinentalNorthern	This article	Hap_329
PLZy_30720	Poland	Żytkiejmy	22.683333	54.347778	Northern	ContinentalNorthern	This article	Hap_40
RODa0161	Romania	Danube delta	29.603683	44.925383	Northern	ContinentalNorthern	This article	Hap_283
RSJa7390	Serbia	Jastrebac	20.587060	44.093560	Balkan		This article	Hap_284
RSMK1078	Serbia	Mount Kopaonik, Suvo Rudiste	20.893620	43.163242	Balkan		This article	Hap_271
RSMK7008	Serbia	Mount Kopaonik, Suvo Rudiste	20.893620	43.163243	Balkan		This article	Hap_271
RSVa7855	Serbia	Valjevo	19.882841	44.246277	Balkan		This article	Hap_271
RUBr0001	Russia	Brjansk	34.000000	52.333333	Northern	ContinentalNorthern	Mascheretti et al., 2003	Hap_285
RUBr0002	Russia	Brjansk	34.000000	52.333334	Northern	ContinentalNorthern	Mascheretti et al., 2003	Hap_286
RUCh0063	Russia	Cheboksary	47.015310	56.073350	Northern	ContinentalNorthern	This article	Hap_287
RUCh0064	Russia	Cheboksary	47.015310	56.073360	Northern	ContinentalNorthern	This article	Hap_287
RUKa1107	Russia	Karelia Republic	33.123778	66.551667	Northern	ContinentalNorthern	This article	Hap_288
RUKa1108	Russia	Karelia Republic	33.123778	66.551668	Northern	ContinentalNorthern	This article	Hap_288
RUKa1113	Russia	Karelia Republic	33.113111	66.558944	Northern	ContinentalNorthern	This article	Hap_289
RULB0001	Russia	Lake Baikal, Siberia	108.000000	53.666667	Northern	ContinentalNorthern	Mascheretti et al., 2003	Hap_290
RUNo0001	Russia	Novosibirsk, Siberia	82.779117	55.201433	Northern	ContinentalNorthern	Ohdachi et al., 2006	Hap_291
RUNo0002	Russia	Novosibirsk, Siberia	83.100000	54.816667	Northern	ContinentalNorthern	Mascheretti et al., 2003	Hap_292
RUNo0003	Russia	Novosibirsk, Siberia	83.100000	54.816668	Northern	ContinentalNorthern	Mascheretti et al., 2003	Hap_293
RUPe0001	Russia	Pertozero	34.000000	62.083333	Northern	ContinentalNorthern	Mascheretti et al., 2003	Hap_294
RUSv0058	Russia	Svetlopoliansk	52.413700	59.411660	Northern	ContinentalNorthern	This article	Hap_295
RUSy0037	Russia	Syktyvkar	50.428000	61.369500	Northern	ContinentalNorthern	This article	Hap_287
RUTa0001	Russia	Tambov	42.250000	51.916667	Northern	ContinentalNorthern	Mascheretti et al., 2003	Hap_296
RUTa0002	Russia	Tambov	42.250000	51.916668	Northern	ContinentalNorthern	Mascheretti et al., 2003	Hap_297
SEGo0001	Sweden	Gotland Vastergarn	18.166667	57.466667	Northern	Islands	Mascheretti et al., 2003	Hap_298
SEGo0002	Sweden	Gotland Vastergarn	18.166667	57.466668	Northern	Islands	Mascheretti et al., 2003	Hap_299
SEGo0003	Sweden	Gotland Tingstade	18.600000	57.700000	Northern	Islands	Mascheretti et al., 2003	Hap_300
SEJa0001	Sweden	Jamj	15.866667	56.166667	Northern	ContinentalNorthern	Mascheretti et al., 2003	Hap_301
SEJa0002	Sweden	Jamj	15.866667	56.166668	Northern	ContinentalNorthern	Mascheretti et al., 2003	Hap_302
SEOl0001	Sweden	Oland	17.083333	57.266667	Northern	Islands	Mascheretti et al., 2003	Hap_303
SEOl0002	Sweden	Oland	17.083333	57.266668	Northern	Islands	Mascheretti et al., 2003	Hap_304
SERe0001	Sweden	Revinge	14.333333	55.583333	Northern	ContinentalNorthern	Mascheretti et al., 2003	Hap_305
SERe0002	Sweden	Revinge	14.333333	55.583334	Northern	ContinentalNorthern	Mascheretti et al., 2003	Hap_306
SEUp0001	Sweden	Uppsala	17.666667	59.750000	Northern	ContinentalNorthern	Mascheretti et al., 2003	Hap_307
SING0001	Slovenia	Nova Gorica, Anhovo	13.657053	45.944656	Italian		Vega et al., 2010a	Hap_308
SIPo0001	Slovenia	Postjma	14.208181	45.781067	Italian		Vega et al., 2010a	Hap_309
SKBr5730	Slovakia	Bratislava	17.107736	48.147883	Balkan		This article	Hap_310
SKBr5733	Slovakia	Bratislava	17.107736	48.147884	Northern	ContinentalNorthern	This article	Hap_6
SKBr5734	Slovakia	Bratislava	17.107736	48.147885	Balkan		This article	Hap_310
SKBr5735	Slovakia	Bratislava	17.107736	48.147886	Balkan		This article	Hap_310
SKBr5736	Slovakia	Bratislava	17.107736	48.147887	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_311
SKBr5743	Slovakia	Bratislava	17.107736	48.147888	Northern	ContinentalNorthern	This article	Hap_6
SKKe0418	Slovakia	Kezmarok Jezersko, Magura Mountains	20.371147	49.288747	Northern	ContinentalNorthern	This article	Hap_33
SKKe0419	Slovakia	Kezmarok Jezersko, Magura Mountains	20.371147	49.288748	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_187
TRAr0001	Turkey	*Sorex volnuchini*	40.898814	31.723833	Outgroup	Outgroup	Mascheretti et al., 2003	Hap_425
TRAr6106	Turkey	*Sorex volnuchini*	40.898815	31.723833	Outgroup	Outgroup	This article	Hap_426
TRSA6079	Turkey	*Sorex volnuchini*	40.898816	31.723833	Outgroup	Outgroup	This article	Hap_427
TRSM0001	Turkey	Strandzha Mountains	27.683333	41.750000	Balkan		Mascheretti et al., 2003	Hap_312

TRSM0002	Turkey	Strandzha Mountains	27.683333	41.750001	Balkan		Mascheretti et al., 2003	Hap_313
UACh_Sm05UA	Ukraine	Cherkasy1	31.307463	49.699916	Northern	ContinentalNorthern	This article	Hap_406
UACh0001	Ukraine	Cherkassy	31.500000	49.716667	Northern	ContinentalNorthern	Mascheretti et al., 2003	Hap_314
UACk_Sm09UA	Ukraine	Cherkasy2	31.431766	49.876058	Northern	ContinentalNorthern	This article	Hap_410
UACn_Sm40UA	Ukraine	Chernigiv	33.080539	51.837271	Northern	ContinentalNorthern	This article	Hap_422
UACn_Sm41UA	Ukraine	Chernigiv	32.951634	51.613213	Northern	ContinentalNorthern	This article	Hap_423
UACn_Sm42UA	Ukraine	Chernigiv	32.978952	51.618128	Northern	ContinentalNorthern	This article	Hap_424
UACr_Sm16UA	Ukraine	Crimea	34.420714	45.867575	Northern	ContinentalNorthern	This article	Hap_274
UAIF_Sm33UA	Ukraine	Ivano-Frankovsk	24.572465	48.427207	Northern	ContinentalNorthern	This article	Hap_419
UAJa0043	Ukraine	Jaduty	32.316667	51.366667	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_315
UAKa0024	Ukraine	Kanev	31.834931	49.692781	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_316
UAKa0025	Ukraine	Kanev	31.834931	49.692782	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_317
UAKa0180	Ukraine	Kazanki	44.517990	33.571930	Outgroup	Outgroup	This article	Hap_428
UAKa0250	Ukraine	Kanev	31.834931	49.692783	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_317
UAKi_Sm01UA	Ukraine	Kiev	30.491315	50.338831	Northern	ContinentalNorthern	This article	Hap_402
UAKi_Sm10UA	Ukraine	Kiev2	31.858608	49.987798	Northern	ContinentalNorthern	This article	Hap_411
UAKi_Sm12UA	Ukraine	Kiev	30.503392	50.244776	Northern	ContinentalNorthern	This article	Hap_413
UAKi_Sm18UA	Ukraine	Kiev	30.496701	50.271562	Northern	ContinentalNorthern	This article	Hap_413
UAKi_Sm19UA	Ukraine	Kiev2	31.858608	49.987798	Northern	ContinentalNorthern	This article	Hap_414
UAKi_Sm24UA	Ukraine	Kiev	30.559818	50.260968	Northern	ContinentalNorthern	This article	Hap_415
UAKi_Sm25UA	Ukraine	Kiev	30.541810	50.278688	Northern	ContinentalNorthern	This article	Hap_416
UALV0255	Ukraine	L'Vov	31.083333	47.900000	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_318
UAOd_Sm06UA	Ukraine	Odessa1	29.748193	45.349009	Northern	ContinentalNorthern	This article	Hap_407
UAOd_Sm07UA	Ukraine	Odessa2	29.748193	45.349009	Northern	ContinentalNorthern	This article	Hap_408
UAOd_Sm38UA	Ukraine	Odessa	29.748193	45.349009	Northern	ContinentalNorthern	This article	Hap_407
UAPo_Sm08UA	Ukraine	Poltava	33.563931	49.937811	Northern	ContinentalNorthern	This article	Hap_409
UASu_Sm02UA	Ukraine	Sumy	33.394014	52.262812	Northern	ContinentalNorthern	This article	Hap_403
UASu_Sm03UA	Ukraine	Sumy	33.394014	52.262812	Northern	ContinentalNorthern	This article	Hap_404
UASu_Sm04UA	Ukraine	Sumy	33.394014	52.262812	Northern	ContinentalNorthern	This article	Hap_405
UASu_Sm36UA	Ukraine	Sumy	33.394014	52.262812	Northern	ContinentalNorthern	This article	Hap_420
UASu_Sm37UA	Ukraine	Sumy	33.394014	52.262812	Northern	ContinentalNorthern	This article	Hap_421
UATi0266	Ukraine	Tishki	33.110944	50.107567	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_287
UAVi0253	Ukraine	Vinnitsa	28.562333	49.230672	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_319
UAVi0254	Ukraine	Vinnitsa	28.562333	49.230673	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_320
UAVo_Sm11UA	Ukraine	Volyn	23.798755	51.478853	Northern	ContinentalNorthern	This article	Hap_412
UAVo0256	Ukraine	Volyn	24.856700	51.124033	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_321
UAZh_Sm30UA	Ukraine	Zhytomir	28.107131	51.495035	Northern	ContinentalNorthern	This article	Hap_287
UAZh0257	Ukraine	Zhitomer	28.614911	50.261669	Northern	ContinentalNorthern	Vega et al., 2010b	Hap_322
UKOd_Sm31UA	Ukraine	Odessa	29.756303	45.301814	Northern	ContinentalNorthern	This article	Hap_417
UKOd_Sm32UA	Ukraine	Odessa	29.578441	45.420647	Northern	ContinentalNorthern	This article	Hap_418

Table S2. Pairwise geographic distances (in Km, below diagonal) and genetic differentiation (Slatkin's F_{ST}, above diagonal) among *Sorex minutus* phylogroups and other geographic groups

	Italian	South Italian	Balkan	Iberian	Belle Île	Britain	Northern (Continental)	Western (Continental)	Orkney Islands	Irish
Italian	-	1.6558	3.0387	3.6919	1.594	2.8852	2.3798	1.4534	2.8673	4.009
South Italian	773.14	-	2.5113	3.3869	1.3569	2.8562	2.3204	1.1713	2.7079	4.682
Balkan	547.27	628.96	-	1.9234	2.5617	3.1494	2.8093	2.7975	6.2456	7.0533
Iberian	1349.26	1768.56	1880.98	-	4.265	3.185	2.6191	3.8498	7.3804	10.8797
Belle Ile	1162.82	1815.47	1701.44	640.58	-	2.7595	2.179	0.3345	1.2148	2.4003
Britain	1347.34	2108.66	1795.12	1286.79	647.11	-	0.1449	2.6083	3.9225	4.7265
Northern (Continental)	1022.36	1488.84	863.37	2218.78	1788.28	1554.91	-	2.0767	2.791	3.2035
Western (Continental)	903.9	1444.78	1448.34	476.18	434.81	1006.85	1742.75	-	0.5436	1.1193
Orkney Islands	3476.34	3693.42	3127.67	4679.14	4175.54	3739.02	2477.61	4206.5	-	1.4635
Irish	1652.35	2396.73	2124.06	1311.98	726.86	346.14	1897.29	1151.96	4016.56	-