

Complete mitogenomes reveal limited genetic variability in the garden dormouse *Eliomys quercinus* of the Iberian Peninsula

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Abstract

Complete mitogenomes reveal limited genetic variability in the garden dormouse Eliomys quercinus of the Iberian Peninsula. The garden dormouse *Eliomys quercinus* is a poorly known Western Palearctic species experiencing a global decline. Even though the availability of genetic information is key to assess the drivers underlying demographic changes in wild populations and plan adequate management, data on *E. quercinus* are still scant. In this study, we reconstructed the complete mitogenomes of four *E. quercinus* individuals from southern Spain using in–solution enriched libraries, and found evidence of limited genetic variability. We then compared their cytochrome *b* sequences to those of conspecifics from other countries and supported the divergent but genetically depauperate position of this evolutionarily significant unit (ESU). The information produced will assist future conservation studies on this little–studied rodent.

Key words: Mammalia, Rodentia, Gliridae, Spain, Evolutionary significant unit, Rodent

Resumen

Los mitogenomas completos desvelan una limitada variabilidad genética del lirón careto Eliomys quercinus en la península ibérica. El lirón careto *Eliomys quercinus* es una especie paleártica occidental poco conocida cuyas poblaciones están experimentando un descenso a escala mundial. Aunque la información genética sea fundamental para determinar las causas de los cambios demográficos que se producen en las poblaciones salvajes y planificar adecuadamente su gestión, los datos sobre *E. quercinus* siguen siendo escasos. En este estudio reconstruimos el mitogenoma completo de cuatro individuos de *E. quercinus* del sur de España a través de librerías enriquecidas en solución y encontramos una variabilidad genética limitada. También comparamos las secuencias del citocromo *b* con las de conespecíficos de otros países y pudimos confirmar la divergencia, así como la baja diversidad genética de esta unidad evolutivamente significativa (ESU) en cuestión. Esta información será de ayuda para los futuros estudios de conservación de este roedor escasamente estudiado.

Palabras clave: Mammalia, Rodentia, Gliridae, España, Unidad evolutivamente significativa, Roedor

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Introduction

Small mammals are a taxonomically diverse group that includes species of major ecological importance in terrestrial ecosystems. A variety of life history traits and their responsiveness to environmental variation make them ideal bioindicators (Talmage and Walton, 1991). Changes in morphology and genetic diversity in small mammal populations over time reflect alterations in their environment (Hadly et al., 1998; Larsen and Matoq, 2019; Forcina and Leonard, 2020; Parker et al., 2020), making them valuable for understanding ongoing local and global changes. For these reasons, attention has recently been devoted to developing a suite of increasingly informative molecular markers for monitoring small mammal communities (Maroja et al., 2003; Meyer et al., 2006; Loiseau et al., 2007; Kanitz et al., 2009; Barbosa et al., 2013; Forcina et al., 2021). While some species like the 'lab rat' *Rattus norvegicus* and the black rat *R. rattus* have been the object of intense study (Aplin et al., 2011; Song et al., 2014) and benefit from well-developed genomic resources, many others, even in the same genus, are still scarcely known (Robins et al., 2010; Camacho-Sanchez et al., 2017, 2018; Liu et al., 2018; Thomson et al., 2018; Camacho-Sanchez and Leonard, 2020). This applies also to the house mouse *Mus musculus*, with some of its congeners largely understudied (Tong and Hoekstra, 2012). In the case of non-model species, the generation of basic genetic tools to be applied in a variety of systems would allow comparison and facilitate repeatability of the studies being, thus enabling important methodological improvements.

As a case in point, the garden dormouse (*Eliomys quercinus* Linnaeus, 1766) is a secretive representative of the family Gliridae (Rodentia) patchily distributed across Europe from the Urals to the Iberian Peninsula as well as on major western Mediterranean islands (Storch, 1978; Filippucci, 1999; Bertolino et al., 2008; fig. 1A). Other European members of this family are the forest dormouse (*Dryomys nitedula*), the edible dormouse (*Glis glis*), the hazel dormouse (*Muscardinus avellanarius*), and Roach's mouse-tailed dormouse (*Myomimus roachi*), with pairs of species often living in sympatry (Juškaitis and Šiožinytė, 2008). Even though a global demographic assessment has not been made, the garden dormouse is considered to be declining sharply in parts of its range over the last three decades (Bertolino, 2017), resulting in its inclusion among the species protected by Appendix III of the Bern Convention (The European Community, decision 82/72/EEC, Official Journal L of 10.02.1982), Annex IV, and 'Near Threatened' status by the International Union for the Conservation of Nature (IUCN, 2011). The most severe declines have been those observed in eastern Europe (Bertolino, 2017), but the local disappearance of this species, which occurs in a range of forested habitats, scrublands and cultivated land (Storch, 1978; Bertolino et al., 2008), has also been recorded in Italy (Amori, 1993; Sarà, 2008) and Spain (Ruiz and Roman, 1999), where its reduction occurred even within protected areas (Moreno, 2002; Santoro et al., 2017). The progressive reduction of suitable

habitats was suggested as the leading likely cause for its decline in central Europe, where vast portions of forested areas have been cleared and replaced by bush-dominated vegetation (Anděra, 1986, 1994), a less suitable habitat for dormice as a whole (Fedyń et al., 2021). However, the same cause cannot be invoked for western Europe, where the extent of forested areas is increasing (Martín-Forés et al., 2020). A long-term study carried out in Doñana National Park (DNP), a UNESCO Heritage Site in Andalucía (southern Spain), at the southernmost edge of the species range, registered a dramatic drop of the garden dormouse over almost four decades. Once referred to as an abundant species in the local small mammal community inhabiting the core of the protected area (Camacho and Moreno, 1989), Doñana Biological Reserve (DBR), it is now virtually locally absent (Santoro et al., 2017). The shift in habits by local predators triggered by hemorrhagic diseases decimating the local European rabbit (*Oryctolagus cuniculus*) population and climate change are still being debated as plausible causes underlying the decline of the garden dormouse in southern Spain. The increased predation rate of the garden dormouse – the second largest of the small mammals in the DBR community after lagomorphs – by means of a top-down control (Palomares et al., 1995) is a possibility. While this scenario looks plausible when considering the persistence of hemorrhagic diseases across Iberia (Abrantes et al., 2013) and a suite of new infections affecting the Iberian hare (*Lepus granatensis*) (Lopes et al., 2014; García-Bocanegra et al., 2019, 2021), the widespread use of pesticides along with changes in agroecosystem structure and function (Kuipers et al., 2012) – pressures that are also present in southern Spain (Santoro et al., 2017) – are generally invoked to explain the decreasing trend of garden dormouse observed at the global level (Bertolino, 2017). The spread of monoculture agriculture, in particular, has been suggested to be associated with a reduction of trophic resources causing their displacement by *Rattus* spp. (Cristaldi and Canipari, 1976; Macdonald and Barrett, 1993). DBR and DNP are largely bordered by agricultural land, but *Rattus* populations have also been observed to decline in the last decades in the reserve (Santoro et al., 2017), reducing the probability that they are an important factor.

Like the related edible dormouse, which is still consumed in Europe (Peršič, 1998; Werner, 2007), the garden dormouse was considered a pest by orchard owners and was eaten. This practice has a long history, as documented in the archeological record, such as the Bronze Age site of Cerro de la Encina (province of Granada) (Friesch, 1987). An extended network of typical warrens (*gliraria*) and numerous jars (*dolia*) used to keep and fatten dormice (Carpaneto and Cristaldi, 1995) were found in the Roman settlement (1st century B.C.E.) of Arucci (province of Huelva) (Bermejo et al., 2015). The Romans' great appreciation of dormice meat would explain the occurrence of garden dormice in archeological sites scattered across the Roman Empire, even where the species is not native like Great Britain (O'Connor, 1986), perhaps resulting in naturalized populations on some islands.

Over the last two decades, scientific attention to this species has been spurred by its stunningly high karyotypic diversity, with the number of chromosomes ranging from $2N \frac{1}{4} 48$ to $2N \frac{1}{4} 54$ (Perez et al., 2013 and references therein). Likewise, garden dormice display remarkable range-wide morphological variation (Filippucci et al., 1988; Kryštufek and Kraft, 1997) which is unrelated to chromosomal variation, raising doubts about the taxonomic identity of several populations (Cristaldi and Canipari, 1976; Filippucci et al., 1988) and even leading to the proposal of new species within the genus (Miller, 1912). A specific investigation has been carried out to explore possible congruence between chromosomal information and population-level cytochrome *b* (*cyt b*) diversity (Perez et al., 2013). The study unveiled the existence of four distinct evolutionary significant units (ESUs: Moritz, 1994; Fraser and Bernatchez, 2001) –referred to as Iberian, Italian (including Corsica and Dalmatia), Western European (excluding Iberia) and Alpine– some of which host multiple chromosomal races and their hybrids. These data could suggest the persistence of gene flow between chromosomal races in spite of their different karyotype, in a similar way to what has been observed in the common shrew, *Sorex araneus* (Narain and Fredga, 1996).

The timing of divergence between the garden dormouse and its Middle Eastern relative, the Asian or large-eared dormouse (*E. melanurus*), and garden dormouse intraspecific divergence was estimated, respectively, at 7.0 ± 0.9 mya (Montgelard et al., 2003) and 4.2 ± 1 mya (Perez et al., 2013), well before Quaternary glaciations. Interestingly, Perez et al. (2013) found that the garden dormouse did not exhibit the typical pattern of northward postglacial recolonization from southern European refugia as observed in several other species (Hewitt, 1996, 1999; Weiss and Ferrand, 2007; Gentili et al., 2015; but see also Deffontaine et al., 2005; Kotlik et al., 2006; Feliner, 2011; Queirós et al., 2019), namely a decreasing trend of genetic diversity from the Iberian, Italian and Balkan peninsulas to the rest of the continent. However, the few genetic sequence based studies on the garden dormouse rely on a single mitochondrial DNA (mtDNA) locus, *cyt b*, and genetic data available for Spain are very limited, with only two genotyped individuals from the Balearics (Perez et al., 2013) and the Pyrenees (Barbosa et al., 2013). This knowledge gap is remarkable, especially considering previous evidence for multiple refugia within the Iberian Peninsula (i.e., Portugal: Perez et al., 2013) and the likely origin of the species there (Perez et al., 2013, Mansino et al., 2015), suggesting that it is a key region to unravel the evolutionary history of the species.

In order to provide new, useful molecular resources for this and related species, here we report complete mitochondrial genomes for four garden dormice from Andalucía (southern Spain, fig. 1). We also extracted and compared their *cyt b* sequences to those publicly available from conspecifics from across most of the species' range. The genetic information produced in this study paves the way for further studies addressing the conservation genetics of this declining rodent.

Material and methods

Sample collection and library preparation

We retrieved tissue (muscle and liver) from four garden dormouse specimens preserved at the biological collection of Doñana Biological Station (EBD-CSIC) in Seville, Spain. The specimens were collected in 2003–2013 from three sites in Andalucía (tables 1, 1s in supplementary material). DNA extraction, Illumina shotgun library preparation and sequencing were performed as in Forcina et al. (2021).

Mitogenome assembly and phylogenetic inferences

Adapter trimming and minimal quality filtering on the 3'-end were performed with cutadapt 2.10 (Martin, 2011). A reference mitogenome was assembled de-novo with NOVOPlasty3.7 (Dierckxsens et al., 2017) by pooling the four samples and using the GenBank sequence of *E. quercinus cyt b* GQ453669 as a seed. Sequences from each individual were mapped to this reference mitogenome using BWA mem 0.7.12–r1039 (Li, 2013). SAMtools 1.3 (Li et al., 2009), was used to discard reads with quality mapping below 40 and remove PCR duplicates. Mitogenomes were annotated in MITOS webserver (Bernt et al., 2013). The annotations were manually edited after comparing them in Geneious 8.1.5 (<http://www.geneious.com>; Kearsley et al., 2012) with the NCBI staff-curated mitochondrial genomes of two closely related species: *M. avellanarius* NC_050264 and *G. glis* NC_001892. We used mafft v7.453 (Katoh et al., 2013) to produce an alignment including the newly sequenced individuals, *E. quercinus* GenBank reference MN935777, the above mentioned mitogenome GenBank references of other European dormice and GenBank reference HE978360 belonging to Kellen's dormouse (*Graphiurus kelleni*) (Fabre et al., 2013). Codon positions 1 and 2 from protein coding genes were retained. Third codon positions were removed as they are mostly saturated at the subfamily level (Breinholt and Kawahara, 2013; Hinckley et al., 2021). The best partition scheme was determined using PartitionFinder 2.1.1 (Lanfear et al., 2012), and grouped into 6 partitions. Gblocks (Castresana, 2000) was used to remove positions in the alignment with little homology or gaps. The final alignment consisted of 6,432 positions. We produced a maximum likelihood (ML) tree in RAxML 8.0.0 (Stamatakis, 2014). The tree was rooted with the edible dormouse based on a mammal phylogeny recently built with genome-wide data (Upham et al., 2019). AMAS (Borowiec, 2016) was used to handle the multiple sequence alignments.

Indices of diversity and biogeographic reconstructions

All garden dormouse *cyt b* sequences available in GenBank were retrieved with the *rentrez* package (Winter, 2017) in R 4.0 (R Core Team, 2020). They were aligned together with assembled *cyt b* sequences from the four new individuals using mafft. The resulting multiple sequence alignment was trimmed using trimAl v1.4.rev15 (Capella-Gutiérrez et al., 2009).

We computed the number of polymorphic sites (S), number of haplotypes (h), haplotype diversity (Θ), and nucleotide diversity (π) of the four mitogenomes with DnaSP 5.10.1 (Librado and Rozas, 2009). A nexus *cyt b* alignment (partial sequence: 573 bp; nt. positions 386–959) including the newly generated sequences ($n = 4$) and all the *E. quercinus* references available in GenBank ($n = 50$: table 1s in supplementary material) was produced in Geneious and imported in DnaSP for computing the same indexes as above on a country basis as well as for each of the four ESUs identified by Perez et al. (2013), assigning sequences retrieved in this and other studies on the basis of their genetic affiliation in the median-joining haplotype network (Bandelt et al., 1999) built by importing the *cyt b* alignment in PopART 1.7 (Leigh and Bryant, 2015).

DNA sequences from complete mitochondrial genomes are deposited in GenBank with accession numbers MZ130252–MZ130255, associated with the BioProject PRJNA727082. The data and code for data analysis are available at <https://github.com/csmiguel/eliomys> and permanent repository in Zenodo (Doi: [10.5281/zenodo.6337428](https://doi.org/10.5281/zenodo.6337428)).

Results

Mitogenome structure and genetic diversity

The new garden dormouse mitogenomes (GenBank accession number MZ130252–MZ130255) were 16,617 bp in length (10 bp shorter than GenBank reference MN935777 from Germany, the only *E. quercinus* entire mitogenome available at the time of manuscript writing), with a base composition of 33.6% A, 28.8% T, 24.3% C, and 13.3% G. They comprised 13 protein-coding genes, 2 ribosomal RNA (rRNA) genes, 22 transfer RNA (tRNA) genes, and the control region (D-loop). Coordinates for each feature are reported in table 2. We found three different mitogenome haplotypes, each one private to one sampling site (tables 1, 1s in supplementary material), but characterized by a limited variability (table 3) exemplified by the identification of only 19 segregating sites (S) in Spain, as opposed to 767 when they were compared with the homologous sequence from Germany (MN935777). The phylogenetic reconstructions of European garden dormice (fig. 3) confirmed –despite a moderate bootstrap support – the same topology inferred on the basis of single mtDNA and nuclear loci, with *Eliomys* and *Muscardinus* being sister taxa (Montgelard et al., 2003) and *Graphiurus* 'in turn' sister to them, and with *Glis* being the most basal taxon, as confirmed by genome-wide data (Upham et al., 2019). Levels of genetic diversity within countries and ESUs were variable (table 3).

Biogeographic reconstructions

Four distinct, previously described haplogroups emerged in the network (fig. 1B). One haplogroup consisted of individuals from the Iberian Peninsula and southern France, including the new haplotype

identified in this study. A second haplogroup included samples from the French and Italian Alps, and a third was distributed in central and western Europe (excluding Iberia), namely central and northern France, Belgium, Germany and Austria. The last haplogroup included individuals from the insular populations of Corsica, Sardinia and Sicily along with two continental representatives from Abruzzo (central Italy) and Croatia. Finally, individuals from Umbria (central Italy), just a few hundred kilometers north along the Italian Peninsula compared to the latter, were scattered in the middle of the four haplogroups.

Discussion

Small mammals are key components of many terrestrial ecosystems. However, some species –even widespread species– are still under-investigated. In this study, we contribute to the scanty genetic resources available for the widespread garden dormouse, *E. quercinus*, by generating four entire mitochondrial genomes and examining the biogeographic affiliation of three populations from a region for which no mitochondrial sequence data have been available to date.

A look at the sampling effort of this and previous studies (Perez et al., 2013; Barbosa et al., 2013) in a spatial perspective (fig. 1A) shows that our knowledge of eastern populations of this species – which are highly fragmented and scattered over a large and remote area– is incomplete. Paradoxically, this gap might inhibit the understanding of the reason(s) underlying the fast-paced decline of the garden dormouse in this portion of its range, and should be tackled with the prompt adoption of a range-wide monitoring program (Bertolino, 2017).

Around the Mediterranean region, whole mitochondrial genome sequences will enable elucidation of the origin of the insular populations inhabiting Sardinia, Sicily, and the neighboring Lipari (where no records have been reported for the last three decades: Sarà, 2008). Both morphology and partial *cyt b* sequences have been used to evaluate the relationship of insular populations to mainland populations. Some studies have proposed each island being granted a distinct subspecific status, while others have suggested a human-mediated introduction (Vigne, 1992; Masseti, 2005; Ientile and Massa 2008; Angelici et al., 2009). If garden dormice did arrive in the Balearics with the help of humans, based on fossil evidence, this introduction would have to date back to at least 2300–2200 B.C.E. (Traveset et al., 2009). This introduction may be supported by the genetic data, since the same *cyt b* haplotype was found in individuals from both Formentera (Balearics) and Andorra (fig. 1). Dating recent events using only *cyt b* can be very misleading, so the availability of whole mitogenome data is necessary to provide the resolution needed to reconstruct the routes and to date both recent human-mediated introductions and ancient natural dispersals. Mitochondrial genomes are particularly useful for molecular clock analyses due to the absence of recombination, the high mutation rate, and large numbers of previous studies providing

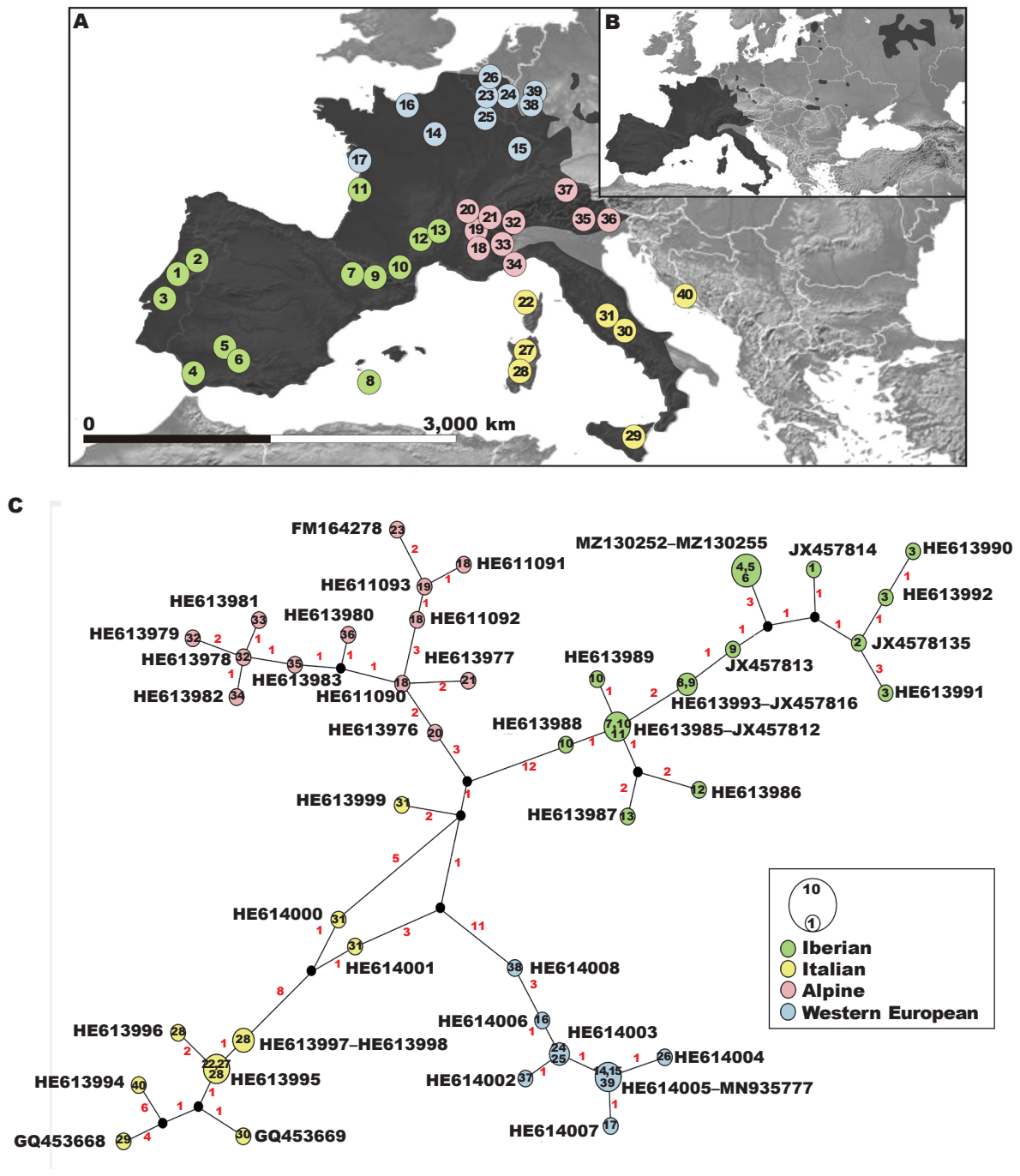


Fig. 1. A, sampling localities used in this study (see table 1s in supplementary material for bibliographic references); B, distribution range (dark shading) of the garden dormouse *E. quercinus* based on Bertolino (2017); C, median-joining network based on partial mitochondrial cytochrome *b* sequences (573 bp): black numbers embedded in circles (haplotypes) refer to sampling localities of figure 1A; red numbers refer to mutational steps. The diameter of each haplotype is proportional to its frequency in the dataset.

Fig. 1. A, localidades de muestreo de este estudio (véase la tabla 1s en material suplementario para consultar las referencias bibliográficas); B, área de distribución (gris oscuro) del lirón careto *E. quercinus* según Bertolino (2017); C, red de haplotipos utilizando el método de unión por la mediana (Median-Joining) basada en secuencias parciales del citocromo *b* (573 pares de bases): los números en negro dentro de los círculos (esto es, los haplotipos) se refieren a las localidades de muestreo mostradas en la figura 1A; los números en rojo indican los saltos mutacionales. El diámetro de cada haplotipo es proporcional a su frecuencia en la base de datos.

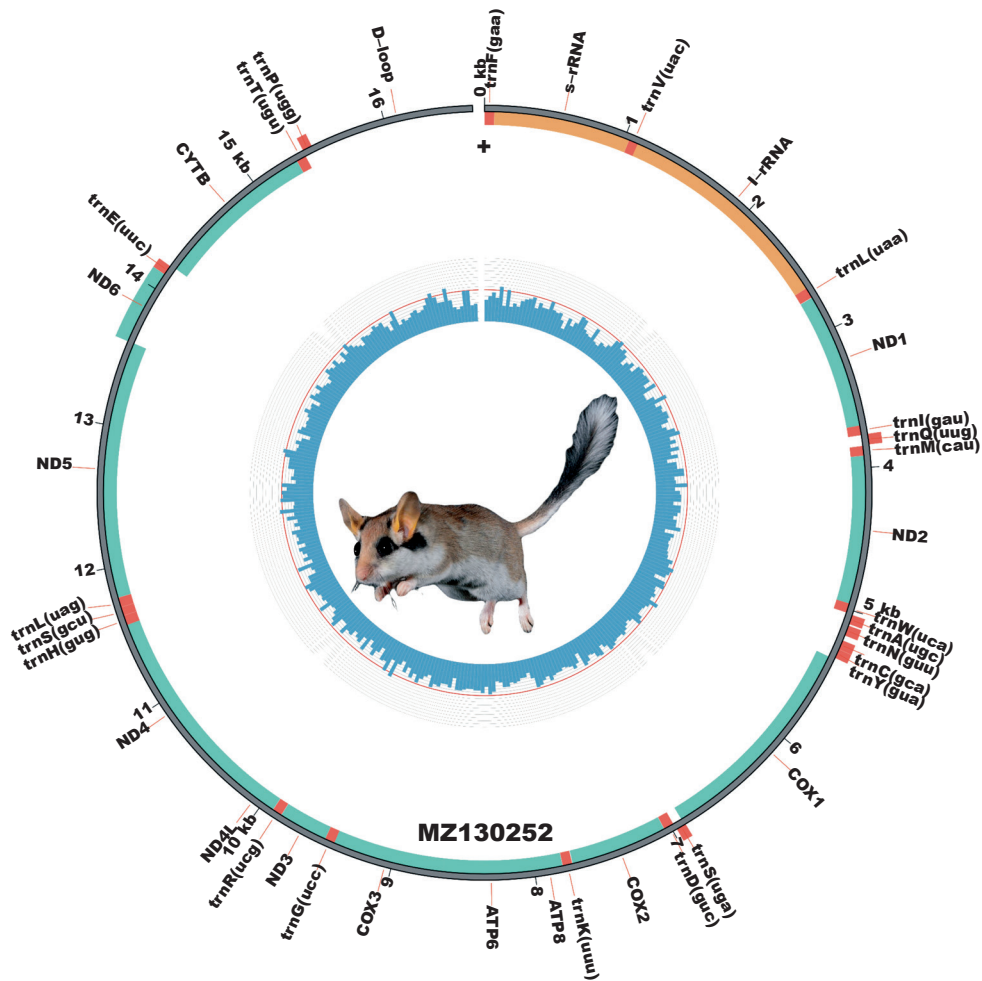


Fig. 2. Graphical representation of garden dormouse *E. quercinus* mitogenome. Protein-coding genes, ribosomal RNA (rRNA) genes and transfer RNA (tRNA) genes are indicated in blue, orange and red, respectively, along the light (external part of the grey circle) and heavy (internal part of the circle) strand of the mitogenome. The blue vertical bars inside the circle are indicative of the sequence depth across the entire assembly.

Fig. 2. Representación gráfica del mitogenoma de lirón careto, *E. quercinus*. Los genes que codifican las proteínas y los que codifican los ARN ribosomales (ARNr) y de transferencia (ARNt) están indicados en azul, naranja y rojo, respectivamente, a lo largo de la cadena ligera (parte exterior del círculo gris) y la pesada (parte interior del círculo gris). Las barras azules dentro del círculo indican la cobertura a lo largo de todo el ensamblaje genómico.

reference data and rates (Gilbert et al., 2008; Singh et al., 2009; Duminil and Besnard, 2021; Yu et al., 2021). The characterization of mitochondrial genomes can also be useful to look at relationships between lineages within species (McGowen et al., 2009; Morin et al., 2010; Fabre et al., 2017; He et al., 2021), where single mitochondrial genes do not have sufficient power to resolve them (Galewski et al., 2005; Zardoya and Meyer, 1996; Sasaki et al., 2005; Viricel and Rosel, 2011; He et al., 2015). This is even more important when recent and rapid speciation events are not paralleled by the accumulation of morphological disparity, as happened

with the genus *Rattus* (Rowe et al., 2011). In the case of the garden dormice, the availability of complete mitogenomes will lay the ground for testing hypotheses regarding the species history and will contribute to resolving the contentious relationships between populations from the Maghreb and the eastern Mediterranean, now recognized as belonging to *E. munbyanus* (Holden, 2005) and *E. melanurus* (Montgelard et al., 2003), respectively. Moreover, complete mitogenomes might assist in pinpointing the populations of highest conservation value, as has occurred in other taxa for which the use of single mitochondrial genes had failed

Table 1. List of garden dormice *E. quercinus* specimens used in this study: SV, specimen voucher; GenBank, GenBank accession number.

Tabla 1. Listado de ejemplares de lirón careto E. quercinus usados en este estudio: SV, código de la muestra; GenBank, número de acceso en GenBank.

SV	Collection site	Collection date	Lat./Long.	GenBank
EBD 32997M	Jerez de la Frontera (Zoological Garden)	21/11/2013	N 36.7; W -6.1	MZ130252
EBD 32795M	Jerez de la Frontera	28/03/2011	N 36.6, W -6.2	MZ130253
EBD 32745M	Córdoba	01/01/2003	N 38.0, W -4.8	MZ130254
EBD 29942M	Montilla (Córdoba)	03/05/2012	N 37.6, W -4.6	MZ130255

Table 2. Features (total length in bp, start and end codon: left to right) of mitochondrial protein-coding genes and the D-loop in *E. quercinus* as compared with other European dormice. No mitogenome is currently available for *D. nitedula* or *M. roachi*. Animal photos are not to scale, for credits see the Acknowledgements.

Tabla 2. Características (longitud total en pares de bases, codón de inicio y codón de terminación: desde la izquierda hacia la derecha) de los genes codificantes de proteínas en la mitocondria y de la región control en E. quercinus en comparación con otros lirones europeos. Actualmente, no hay ningún genoma mitocondrial secuenciado de D. nitedula ni de M. roachi. Las fotos de los animales no están a escala, se pueden ver los agradecimientos en el apartado "Acknowledgements".






	<i>Eliomys quercinus</i> MZ130252	<i>Glis glis</i> NC_001892	<i>Muscardinus avellanarius</i> NC_050264	<i>Dryomys nitedula</i>	<i>Myomimus roachi</i>
					
ND1	957, ATG, TAA	955, ATG, T--	956, ATG, TA-	-	-
ND2	1,042, ATC, T--	1,041, ATC, TAA	1,042, ATT, T--	-	-
COI	1,554, ATG, AGG	1,542, ATG, AGG	1,548, ATG, AGA	-	-
COII	684, ATG, TAA	684, ATG, TAA	684, ATG, TAA	-	-
ATP8	192, ATG, TAA	204, ATG, TAA	192, ATG, TAA	-	-
ATP6	681, ATG, TAA	679, ATG, T--	681, ATG, TAA	-	-
COIII	784, ATG, T--	784, ATG, T--	784, ATG, T--	-	-
ND3	348, ATT, TAA	346, ATT, T--	348, ATA, TAA	-	-
ND4L	297, ATG, TAA	297, ATG, TAA	297, ATG, TAA	-	-
ND4	1,378, ATG, T--	1,378, ATG, T--	1,378, ATG, T--	-	-
ND5	1,812, ATA, TAA	1,812, ATA, TAA	1,809, ATA, TAA	-	-
ND6	525, ATG, TAG	525, ATG, TAG	525, ATG, TAG	-	-
Cyt b	1,140, ATG, AGA	1,140, ATG, AGA	1,140, ATG, TA-	-	-
D-loop	1,146	1,157	1,272	-	-

Table 3. Cyt *b* genetic diversity: N, number of sequences; S, number of polymorphic sites, h, number of haplotypes; Θ , haplotype diversity; and π , nucleotide diversity of the loci amplified across countries and ESUs as inferred by Perez et al. (2013) (n.d., not determined).

Tabla 3. Diversidad genética del citocromo b: N, número de secuencias; S, número de sitios polimórficos; h, número de haplotipos; Θ , diversidad haplotípica; y π , diversidad nucleotídica de los loci amplificados relativos a cada país y ESU según Pérez et al. (2013) (n.d., no determinado).

Locus	Country/ESU	N	S	h	Θ	π
Mitogenome	Spain	4	19	3	0.833	0.001
Cyt <i>b</i>	Portugal	5	7	5	1	0.005
	Spain	6	7	3	0.6	0.006
	Andorra	2	1	2	1	0.002
	France	17	56	16	0.985	0.033
	Belgium	4	27	3	0.83	0.024
	Italy	16	36	14	0.983	0.022
	Austria	1	n.d.	1	n.d	n.d
	Germany	2	5	2	1	0.009
	Croatia	1	n.d	1	n.d	n.d
	Iberian	19	21	13	0.942	0.009
	Italian	12	30	9	0.939	0.014
	Western European	10	8	7	0.911	0.004
	Alpine	13	16	13	1	0.008

to identify unique lineages (Knaus et al., 2011; Johri et al., 2020; Sun et al., 2021), an achievement which is particularly important in the case of endangered species for which new entire mitogenomes are being generated for this specific purpose (Ruiz et al., 2021; Wang et al., 2021; Skorupski, 2022).

The scarcity of genetic data for the garden dormouse from the Iberian Peninsula is a serious gap in our knowledge. Although southern Spain is the southernmost limit of the species' distribution, it appears to host a remarkable phenotypic diversity, and four subspecies have been proposed for this area: *E. q. lusitanicus* in the south-west, *E. q. quercinus* elsewhere on its mainland, *E. q. gymnesicus* in Mallorca and Menorca, and *E. q. ophiusae* in Formentera (Moreno, 2005). Iberia was an important boreal refugium for many species throughout Pleistocene climate fluctuations (Povoas et al., 1992; Kowalski, 2001; López Antoñanzas and Cuenca Bescós, 2002; Marks et al., 2002; Bicho et al., 2003; López-García et al., 2010; Horníková et al., 2021), but the population structure of the garden dormouse predates these environmental changes (Perez et al., 2013). A high level of morphological diversity is compatible with the fossil record that suggests that southern Spain is likely the center of origin for the species (Mansino et al., 2015), a hypothesis also supported by the molecular phylogeny (Perez et al., 2013). Our results, however, found limited genetic variability in the Iberian ESU in spite of its divergent

position, which is in line with the now consolidated view that the genetically most diverse populations are not those located at the southernmost latitude but at intermediate latitudes, as a consequence of the admixture of divergent lineages arose in separate refugia (Petit et al., 2003; Werner, 2007). In this respect, our results pointed to France, home to garden dormice falling into three different ESUs, as the country hosting the highest genetic diversity for this species (fig. 1; table 3). This outcome is in sharp contrast with that which emerged for the edible dormouse, with the entire continental lineage exhibiting a limited variability –presumably as the result of a recent expansion from a single refuge (Hürner et al., 2010). The garden dormouse pattern is more similar to that found in the hazel dormouse, which is characterized by a strong genetic structure of highly divergent lineages with low internal diversity (Mouton et al., 2012).

Structure within the Iberian Peninsula seems possible (Gómez and Lunt, 2007; Ferrero et al., 2011; Abellán and Svenning, 2014) and is suggested by these preliminary data (fig. 1), but only the genotyping of further individuals at multiple nuclear loci will clarify whether or not this is the case. Studies of other small mammals from this region have revealed a shallow mtDNA genetic structure despite high phenotypic variation (Lucas et al., 2015). In light of the high karyotypic diversity contained in this species (Perez et al., 2013), assessing the chromosomal races of

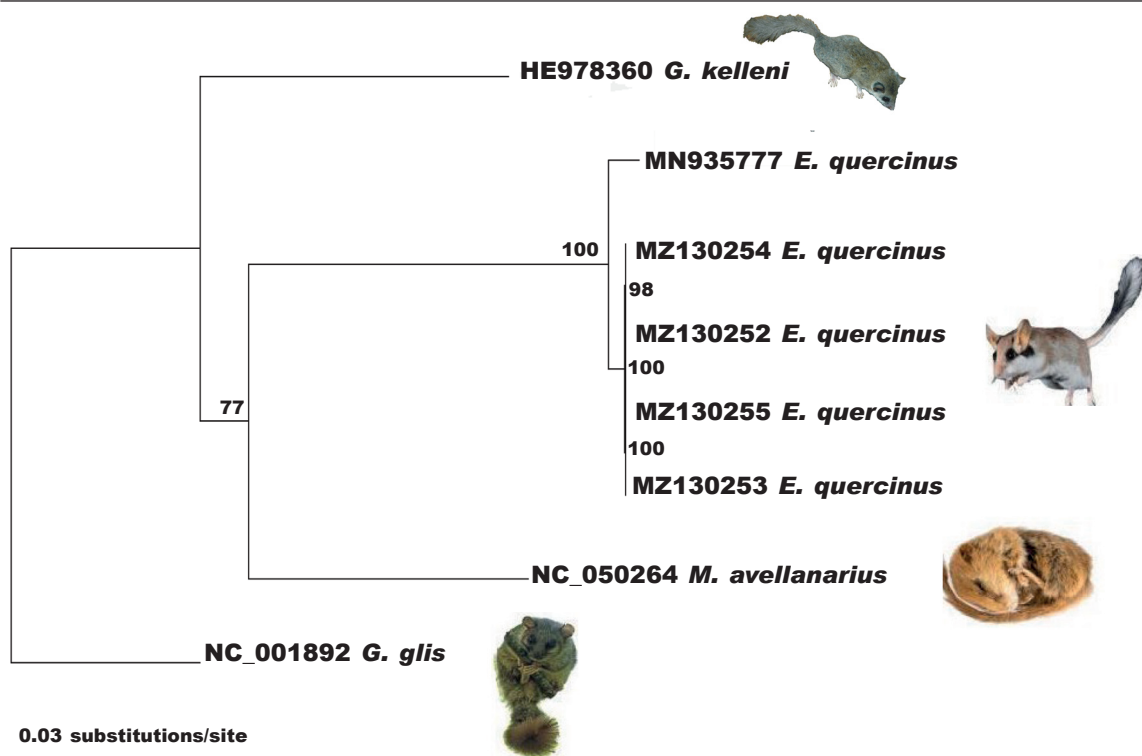


Fig. 3. Maximum likelihood (ML) dormice phylogeny based on the whole mitogenome (14,906 bp).

Fig. 3. Filogenia de máxima verosimilitud (ML) de los lirones europeos basada en el mitogenoma entero (14.906 pares de bases).

the garden dormouse from southern Spain and other largely unexplored regions of the Iberian Peninsula would add key information to our understanding of the evolutionary history of this charismatic species.

The garden dormouse was historically widely distributed across the entire region but appears to have declined substantially in southern Spain. This local demographic trend has been inferred based on a limited number of trapping sites, and a rebound has been suggested in recent times (<https://www.efe.com/efe/andalucia/huelva/constatan-aumento-de-lirones-careto-en-donana-indicador-mejora-forestal/50001127-4474704>). Thus, more systematic genetic and ecological surveys for this species are needed to understand its occurrence outside protected areas, such as in orange and olive orchards and vineyards, where it is still recorded relatively frequently (Rey Benayas et al., 2017) according to GBIF records from the last 14 years (GBIF, 2021; Villares Muyo and Ruiz Franco, 2020) and from a recent study from central Italy based on common barn-owl (*Tyto alba*) pellets (Paniccia et al., 2022). Nevertheless, a paucity of information for central and southern Portugal (Cabral et al., 2005) points to a likely decline in Portugal as well. There are many possible drivers of this decline, and they are not mutually exclusive. The garden dormouse is generally regarded as a cold-adapted

species (Lanni et al., 1990; Perez et al., 2013; Giroud et al., 2018), even if for some authors this would likely apply to the northern chromosomal race as opposed to that from Iberia (Libois et al., 2012). Indeed, southern Spain is hot and dry, at the limit of the species' tolerance to environmental factors. Should the increasing demographic trend suggested in Andalusia be confirmed, climate warming as a leading driver of global decline in this species would be called into question. The level and distribution of genetic diversity in Iberian garden dormice may be important for assessing the conservation priority of different populations in the context of the much advocated monitoring project for this species (Bertolino et al., 2014), and determine if they are able to survive these increasing challenges. For this purpose, the sequencing of unlinked nuclear loci, such as introns (Igea et al., 2010; Rodríguez-Prieto et al., 2014), tested in the garden dormouse (Forcina et al., 2021), or other exonic markers widely used across rodent phylogenies (Schenk et al., 2013), is recommended as well.

In conclusion, we hope that the genetic resources reported here will stimulate further research aimed at understanding and preserving the genetic and morphological diversity of the garden dormouse and that of its poorly studied European relatives.

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Supplementary material

Table 1s. Detailed information on the samples used in this study. NA: not available; * this accession number actually refers to the first *E. quercinus* mitogenome deposited in GenBank and from which we extracted the cyt *b*. Locality information was provided by Sarah Viola Emser (Genomics Core Facility, Vetmeduni Vienna) to Giovanni Forcina. For more details about karyotype information see Perez et al. (2013): GenBank, GenBank accession number; N. number in figure 1A.

Tabla 1s. Información detallada sobre las muestras utilizadas en este estudio. NA: no disponible. *Este número de accesión se refiere en realidad al primer mitogenoma de *E. quercinus* depositado en GenBank y del que se extrajo el citocromo *b*. La información sobre la localidad la aportó a Giovanni Forcina la Sra. Sarah Viola Emser (Genomics Core Facility, Vetmeduni Vienna). Para obtener información más detallada sobre el cariotipo, véase Pérez et al. (2013): GenBank, número de acceso en GenBank; N. número en la figura 1A.

	GenBank	Locality	Country	Karyotype	ESU	Reference	N
1	JX457814	Caramulo, Tondela, Viseu	Portugal	NA	Iberian	Barbosa et al. (2013)	1
2	JX457815	Lamas de Olo, Parque Natural do Alvão, Vila Real	Portugal	NA	Iberian	Barbosa et al. (2013)	2
3	HE613990	NA	Portugal	48 Iberian	Iberian	Perez et al. (2013)	3
4	HE613991	NA	Portugal	48 Iberian	Iberian	Perez et al. (2013)	3
5	HE613992	NA	Portugal	48 Iberian	Iberian	Perez et al. (2013)	3
6	MZ130252	Jerez de la Frontera (Zoobotánico), Cádiz	Spain	NA	Iberian	This study	4
7	MZ130253	Jerez de la Frontera, Cádiz	Spain	NA	Iberian	This study	4
8	MZ130254	Cordoba	Spain	NA	Iberian	This study	5
9	MZ130255	Montilla, Cordoba	Spain	NA	Iberian	This study	6
10	JX457812	Alins, Areu	Spain	NA	Iberian	Barbosa et al. (2013)	7
11	HE613993	Formentera, Balearic Islands	Spain	48 Iberian	Iberian	Perez et al. (2013)	8
12	JX457813	El Serrat, Ordino	Andorra	NA	Iberian	Barbosa et al. (2013)	9
13	JX457816	El Serrat, Ordino	Andorra	NA	Iberian	Barbosa et al. (2013)	9
14	HE613985	Bouillouses, Pyrenees–Orientales	France	NA	Iberian	Perez et al. (2013)	10
15	HE613988	Bouillouses, Pyrenees–Orientales	France	NA	Iberian	Perez et al. (2013)	10
16	HE613989	Bouillouses, Pyrenees–Orientales	France	NA	Iberian	Perez et al. (2013)	10
17	HE613985	Saint Dizant du Gua, Charente–Maritime	France	NA	Iberian	Perez et al. (2013)	11
18	HE613986	Mont–Lozère, Lozere	France	NA	Iberian	Perez et al. (2013)	12
19	HE613987	Le Fraisse, Lozère	France	NA	Iberian	Perez et al. (2013)	13
20	HE614005	Orleans, Loiret	France	NA	Western European	Perez et al. (2013)	14
21	HE614005	Hunawihr, Haut–Rhin	France	NA	Western European	Perez et al. (2013)	15
22	HE614006	Saint Philbert des Champs, Normandy	France	NA	Western European	Perez et al. (2013)	16
23	HE614007	Lairoux, Vendee	France	NA	Western European	Perez et al. (2013)	17
24	HE611090	Hautes–Alpes	France	NA	Alpine	Perez et al. (2013)	18
25	HE611091	Hautes–Alpes	France	NA	Alpine	Perez et al. (2013)	18
26	HE611092	Hautes–Alpes	France	NA	Alpine	Perez et al. (2013)	18
27	HE611093	Savoie	France	NA	Alpine	Perez et al. (2013)	19
28	HE613976	Saint–Ours, Savoie	France	NA	Alpine	Perez et al. (2013)	20
29	HE613977	Les Chapieux, Savoie	France	NA	Alpine	Perez et al. (2013)	21
30	HE613995	Algajola, Corsica	France	NA	Italian	Perez et al. (2013)	22
31	FM164278	Huy, Liege	Belgium	NA	Alpine	Perez et al. (2013)	23
32	HE614003	Xhoris, Liege	Belgium	NA	Western European	Perez et al. (2013)	24
33	HE614003	Villers en Fagne, Namur	Belgium	NA	Western European	Perez et al. (2013)	25
34	HE614004	Brussels	Belgium	NA	Western European	Perez et al. (2013)	26
35	HE613995	Monte Limbara, Olbia–Tempio, Sardinia	Italy	NA	Italian	Perez et al. (2013)	27
36	HE613995	Gavoi, Nuoro, Sardinia	Italy	NA	Italian	Perez et al. (2013)	28
37	HE613996	Gavoi, Nuoro, Sardinia	Italy	50 Sardinian	Italian	Perez et al. (2013)	28
38	HE613997	Gavoi, Nuoro, Sardinia	Italy	50 Sardinian	Italian	Perez et al. (2013)	28
39	HE613998	Gavoi, Nuoro, Sardinia	Italy	50 Sardinian	Italian	Perez et al. (2013)	28
40	GQ453668	Maletto, Catania, Sicilia	Italy	NA	Italian	Gornung et al. (2010)	29
41	GQ453669	Campo Felice, L'Aquila, Abruzzo	Italy	NA	Italian	Gornung et al. (2010)	30
42	HE613999	Polino, Terni, Umbria	Italy	48 Italian	Italian	Perez et al. (2013)	31
43	HE614000	Polino, Terni, Umbria	Italy	48 Italian	Italian	Perez et al. (2013)	31
44	HE614001	Polino, Terni, Umbria	Italy	48 Italian	Italian	Perez et al. (2013)	31
45	HE613978	Aosta, Valle d'Aosta	Italy	54 Alpine	Alpine	Perez et al. (2013)	32
46	HE613979	Aosta, Valle d'Aosta	Italy	NA	Alpine	Perez et al. (2013)	32
47	HE613981	Pietraporzio, Cuneo, Piemonte	Italy	54 Alpine	Alpine	Perez et al. (2013)	33
48	HE613982	Triora, Imperia, Liguria	Italy	54 Alpine	Alpine	Perez et al. (2013)	34
49	HE613983	Caoria, Trento, Trentino–Alto Adige	Italy	52 Alpine	Alpine	Perez et al. (2013)	35
50	HE613980	Pordenone, Friuli–Venezia Giulia	Italy	52 Alpine	Alpine	Perez et al. (2013)	36
51	HE614002	Bad Laterns, Vorarlberg	Austria	50 northern	Western European	Perez et al. (2013)	37
52	HE614008	Koblentz, Rhineland–Palatinate	Germany	50 northern	Western European	Perez et al. (2013)	38
53	MN935777*	Ebertseifen, Niederfischbach, Rhineland–Palatinate	Germany	NA	Western European	GenBank submission	39
54	HE613994	Živogošće, Dalmatia	Croatia	48 Italian	Italian	Perez et al. (2013)	40