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Asynchronous ecological upheavals on the Western Mediterranean islands: New insights on the extinction of their autochthonous small mammals

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Abstract

Comparative studies on extinction scenarios are an invaluable contribution to enhance our understanding of their patterns and mechanisms underpinning them. This paper presents new radiocarbon dates based on specimens of five extinct mammal species from Mallorca and Sardinia. The new evidence permits to reanalyse the extinction dynamics on both islands. Radiocarbon ages directly obtained on bone collagen from these species show evidence of different extinction patterns on Mallorca and Sardinia. For Mallorca the most reliable scenario is a mass extinction of all non-volant mammal species as an immediate consequence of the first human irruption on the island. However, for Sardinia, the extinction of autochthonous mammals lasted over several millennia. The new radiocarbon dates of the last occurrence of endemic mammals suggest a sequence of punctuated extinction events throughout the late Sardinian Holocene. These events are here tentatively related to successive human colonisation waves. The current lack of chronological dates for some Sardinian fossil mammals impedes to outline a more accurate pattern of extinction events. The present paper points that Mallorca have been more vulnerable than Sardinia to the external disturbances introduced by humans. We suggest that the capacity of each island to absorb external perturbations could be related to the island area, the duration of the isolated evolution and the degree of faunal complexity.

Keywords

direct ^{14}C dating, extinction, late-Holocene, Mallorca, Sardinia, Small mammals

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Introduction

Extinction is a phenomenon currently affecting an increasing proportion of biodiversity (e.g. Barnosky et al., 2011; Ceballos et al., 2017). Nevertheless, the present extinction mass episode has deep roots, starting at least 40,000 years ago (MacPhee and Marx, 1997). Understanding extinction causes is thus as a key topic for the knowledge of the ecosystems function, as well as of their resilience and evolution.

Since prehistoric times and along the last few millennia, humans have discovered all the islands of the world, settling and colonising most of them. As a consequence of direct and indirect human actions, insular faunas were severely affected with most being extinguished. The loss of species has been accounted for, at least, 27% the endemic insular species of mammals (Alcover et al., 1998) and 60% of the birds (Steadman, 1991) that were present on the islands before the arrival of humans. On the Mediterranean islands, the extinction of mammals, after and as a consequence of the human arrival affected >90% of the autochthonous species of the pristine pre-human settlement faunas (Alcover et al., 1998; van der Geer et al., 2021).

All the Mediterranean insular mammalian megafauna (i.e. all species weighing more than 40–44 kg; Martin, 1984; Stuart, 1991) present at the beginning of the Holocene has disappeared. This extinction event also affected the small-sized (<5 kg; Bourlière, 1975) and the medium-sized (5–45 kg) mammals, with currently only three species of the insular Mediterranean autochthonous non-volant mammals surviving, *Crocidura zimmermanni* Wettstein 1953 on Crete, *Crocidura sicula* Miller 1901 on Sicily, Malta and surrounding islets, and *Mus cypriacus* Cucchi et al. (2006) on Cyprus (Masseti, 2012). The ancestors of these three species are present in the Pleistocene record of these islands (Cucchi et al., 2006; Hutterer, 1990; Reumer, 1986).

This paper explores the chronologies of the extinction of the autochthonous small mammals from two western Mediterranean islands, Mallorca, and Sardinia, documenting the last occurrence dates of different species. Both islands were settled by humans in

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prehistoric times (Mallorca: middle of the 3rd millennium BC, Alcover, 2008; Sardinia, 9–8th millennium BC, Lugliè, 2018) and in both cases, the ultimate impact was the total disappearance of their autochthonous endemic small mammals, although the precise chronology remains unsolved. (e.g. van der Geer et al., 2021; Vigne and Alcover, 1985). Conversely, based on the zooarchaeological record, in each island the time range between the prehistoric human colonisation and the small mammal extinction event seems to have followed a completely different pattern on each island. On Mallorca, the period of coexistence between humans and the small mammals was short (i.e. less than 100 years), whereas it was very long on Sardinia (i.e. more than 7000 years).

To approach the chronological framework of the small mammal extinction on Mallorca and Sardinia, we will consider the earliest occurrence dates of humans on both islands, the last occurrence dates for five autochthonous small mammals species, as well as some dates of the arrival of invasive species. In relation to the latter, we emend here a previous inference made by one of the authors (JAA) 40 years ago on the arrival chronology of an introduced species (Sanges and Alcover, 1980).

Material and methods

Species and specimen selection

The pool of prospective taxa considered in this paper consists of seven extinct species, two from Mallorca (an eulipotyphlan, *Nesiotites hidalgo* Bate 1944, and a rodent, *Hypnomys morpheus* Bate 1918), and five from Sardinia (two eulipotyphlans, *Asoriculus similis* [Hensel 1855] and *Talpa tyrrhenica* Bate 1945, two rodents, *Rhagamys orthodon* [Hensel 1856] and *Microtus* (*Tyrrhenicola*) *henseli* [Forsyth-Major 1905], and a lagomorph, *Prolagus sardus* [Wagner 1829]). Regarding the alien species, the only taxon considered here is the rodent *Rattus rattus* (Linnaeus 1758) that have been related to the decline and extinction of the endemic small mammals of the Thyrrenian islands (Vigne and Valladas, 1996; Wilkens, 2012).

Specimens for dating were based on three main criteria: (1) unquestionable diagnostic bone characters, (2) stratigraphic position (when it was available) and (3) overall quality of preservation (indicated by lack of mineralisation, and similar appearance to the most ancient known bones of human-introduced small mammals). The dated material was housed at IMEDEA, mainly from old collections and an unreliable stratigraphic control due to irregularities and disturbances that hinder any stratigraphic interpretation. Thus, although upper-level specimens (i.e. surface or near-surface material) were prioritised for dating, other specimens coming from assumed more recent packages based on the highest presence of alien species were also retrieved. In any case, we privileged the apparent overall quality of preservation of the specimens even though the appearance is not a definitive criterion entailing chronology (well-preserved material can be of any age). The assumption is that the most recent specimens should be included in the set of materials with good quality of preservation. The combination of these criteria has been useful for the improvement of extinction/introduction chronologies (e.g. Alcover et al., 2009; Bover and Alcover, 2003; Bover et al., 2016; Bover and Alcover, 2008; Rando et al., 2014).

Potentially good samples for radiocarbon dating were obtained from five extinct species (i.e. all, except *T. tyrrhenica* and *A. similis*) and one invasive species (*R. rattus*). The material from Mallorca was from four sites (three caves: Cova des Garrover, Alcúdia; Cova de sa Tossa Alta, Escorca; Cova Estreta, Pollença; and a rockshelter: Balma de Son Matge, Valldemossa; see Figure 1), while the material from Sardinia included new dates from specimens collected in 1978 at Grotta Su Guanu (Oliena). All the new dated material was photographed (Canon EOS 400D, Canon EF 35 mm lens; Figure 2).

Sites description

Cova des Garrover (Alcúdia). A small cavity situated close to the Torrent de ses Fontanelles, at the peninsula of cap des Pinar, located between the bays of Alcúdia and Pollença (39º52′6.75″N; 3º10′19.92″E; 135 m a.s.l.). It has a small entrance hall and two branches, one on the left leads to a destroyed archaeological burial site, and the other on the right part of the hall is a descending small, narrow and short gallery. The *Nesiotites* bones here dated were found at the surface of this gallery. A description of the cave can be consulted in Encinas (2014: 111–112).

Cova Estreta (Pollença). This cave is situated upon the plain of Rafal d'Ariant, a remote place situated between Mortitx and Ariant (39º53′47.74″N; 2º55′31.14″E; 350 m a.s.l). It is clearly a run-off water conduction system that used the tectonic crevices that are basically oriented following two axes: one in the N-S direction, and the other, basically perpendicular to the first, in the E-W direction. The water has transported a large volume of sediments and fossils. The material dated (*N. hidalgo*, see Table 1, Figure 2f) was from the upper level of the grid square O7/N7, the boundary with N8. The description, topographical survey, and reference of the excavation grid of the cave are available at Encinas and Alcover (1997).

Cova de sa Tossa Alta (Escorca). A remote cave situated at the north of Puig Caragoler de Femenia, a mountain close to the Lluc Monastery (39º52′20.10″N; 2º52′38.57″E; 440 m a.s.l.). It presents an entrance 12 m wide with a rounded plant 30 m in diameter. At the inferior level of the cave there is a flattened area of about 170 m^2. The dated bones of *H. morpheus* (Table 1) were obtained from the surface, at the limit of this area, at a point close to the wall. A description and topographical survey of the cave can be consulted in Alcover et al. (2001).

Balma de Son Matge (Valldemossa). The rock shelter of Balma de Son Matge is located at the edge of the mountain passage of Estret de Valldemossa, one of the geographical passages between the Mallorcan central plain and the Northern range of mountains (39°41′30.4″N 2°37′48.5″E; 360 m a.s.l.). It is a wide rock shelter formed by one of the great rocks of the Lower Lias detached from the mountain of Son Pacs, opened at the north, with undefined limits. A further description and topographical survey of the rock shelter are presented in Alcover et al. (2001). A mandible of *H. morpheus* from the archaeological section of the sector 42–44 (Waldren 1982, Fig. 23a) was dated (Table 1, Figure 2a) but its exact stratigraphic position and date of collection are unknown.

Grotta Su Guanu (Oliena). Grotta Su Guanu (or Gonagosula) is situated at the eastern part of the Jurassic mountains of Oliena (Punta Sa Turgusa), in front of the basaltic plateau of Gollei (40°17′16.2″N; 9°30′25.5′E; 92 m a.s.l.). The cavity has a quasi-horizontal route, with three superposed galleries that communicate with each other in the anterior part, and opens through five entrances on an almost vertical wall on the Cedrino river. The bone deposit was situated at the Sala das Palombas and is derived, mainly or totally, from owl pellets. In 1978, it was somewhat disturbed, containing a few small remnants of prehistoric pottery, and totally covered by pigeon faeces. Seven sedimentary packages were obtained, coming from different parts of the deposit, and their relative age was approached according to the proportion of the endemic taxa present in each of them. The two packages that delivered a smaller proportion of endemic species were considered representative of the most recent deposition. The material here dated comes from these two packages (Sanges and Alcover, 1980), consisting of three right hemimandibles of *R. orthodon*

Table 1. New and current last radiocarbon dates of the endemic small mammals of Mallorca and Sardinia.

Island	Species	Lab. code	Site	14C age (year BP)	Age (2σ range, cal BC/AD)	C/N	δ 13C (‰)	δ 15N (‰)	References
Mallorca	*Nesiotites hidalgo*	Beta-163133	Cova des Garrover	4280 ± 50	3078–2697 cal BC	na	−18.1	na	Bover and Alcover (2008)
	Nesiotites hidalgo	KIA-39434	Cova Estreta	5160 ± 35	4047–3810 cal BC	na	−16.5	na	This study
	Hypnomys morpheus	KIA-30353	Cova de sa Tossa Alta	5890 ± 35	4844–4687 cal BC	2.8	−15.74	2.07	Bover and Alcover (2008)
	Hypnomys morpheus	RICH-27415	Balma de Son Matge	7505 ± 30	6441–6260 cal BC	3.6	na	na	This study
Sardinia	*Prolagus sardus*	UtC-300	Grotta Corbeddu	8750 ± 140	8235–7584 cal BC	na	na	na	Klein Hofmeijer et al. (1987)
	Prolagus sardus	RICH-27078	Grotta Su Guanu	2577 ± 28	810–590 cal BC	3.6	−23.3	+3.7	This study
	Rhagamys orthodon	RICH-27077	Grotta Su Guanu	2624 ± 27	822–776 cal BC	3.5	−19.2	+6.0	This study
	Microtus (Tyrrhenicola) henseli	RICH-27487	Grotta Su Guanu	2996 ± 25	1376–1125 cal BC	3.5	−22.8	na	This study
	Rattus rattus	RICH-27080.2.1	Grotta Su Guanu	935 ± 25	1032–1166 calAD	3.4	−19.8	+8.5	This study

na: not available.

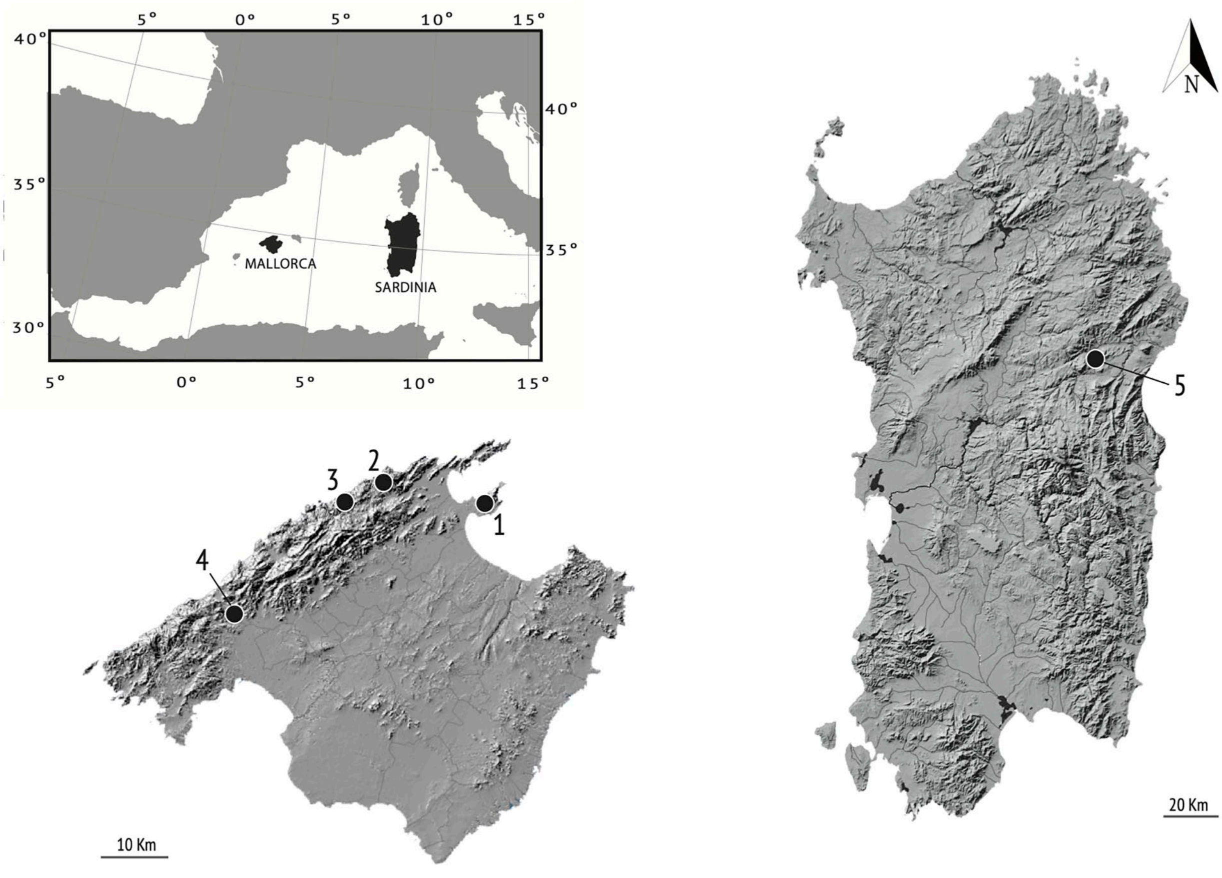

Figure 1. Map of Mallorca and Sardinia showing the 14C sampled localities. (1) Cova des Garrover, (2) Cova Estreta, (3) Cova de sa Tossa Alta, (4) Balma de Son Matge, (5) Grotta Su Guanu.

(Table 1, Figure 2b), two left and three right hemimandibles of *M. (T.) henseli* (Table 1, Figure 2c), a left humerus of *Rattus rattus* (Table 1, Figure 2d) and two right hemimandibles of *P. sardus* (Table 1, Figure 2e). The description of the cave and topographical survey are presented in Pappacoda and Occhipinti (1985).

Human arrival chronology

The chronology of human arrival to the different islands is usually controversial, so 'chronological hygiene' criteria (Anderson, 1991; Fitzpatrick, 2006; Spriggs, 1989; Spriggs and Anderson, 1993) were applied excluding, among others, the radiocarbon dates of charcoal and on wood samples to avoid the 'old wood effect' of these usually long-lived samples.

According to the available evidence, the first human occurrence on Mallorca was previous to 2282 cal BC (with a probability >90%) (Aramburu-Zabala and Martínez-Sánchez, 2015), bringing the most probable temporal range between ca. 2468 and 2282 cal BC (Bover et al., 2016; Table 1, RICH-21853, 3844 ± 36, 2468–2282 [90%], 2251–2231 [3.6%], 2221–2209 [1.8%] cal BC). Although more recently some authors have claimed an earlier human arrival (at the beginning of the third millennium BC) based on indirect paleoenvironmental approaches (e.g. Servera-Vives et al., 2018), the presented evidence is still inconclusive.

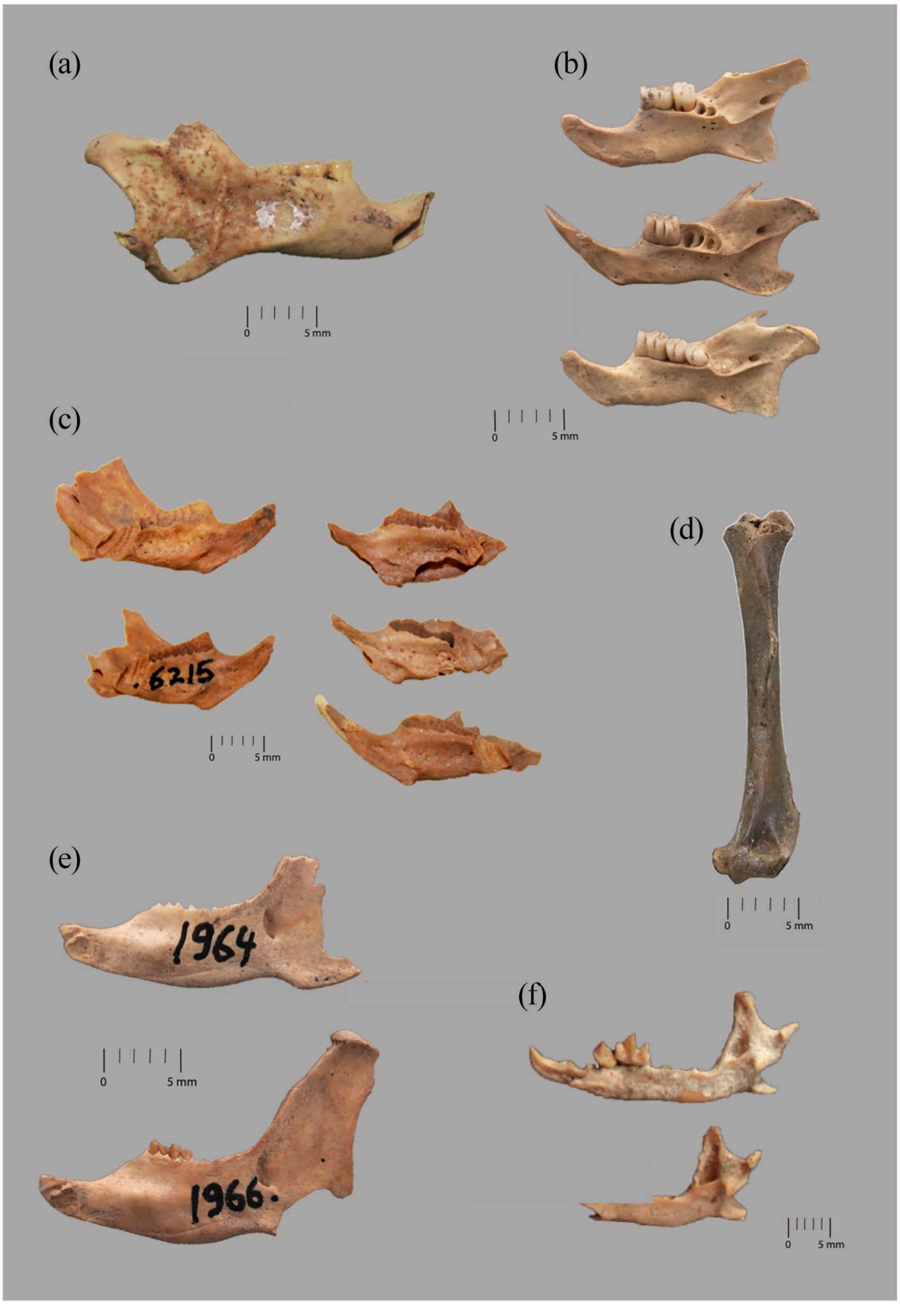

Figure 2. Radiocarbon dated specimens: (a) labial view of right mandible of *H. morpheus* (RICH-27415); (b) lingual view of three left mandibles of *R. orthodon* (RICH-27077); (c) lingual view of two left and three right mandibles of *M. henseli* (RICH-27487); (d) cranial view of left humerus of R. rattus (RICH-27080); (e) lingual view of two right mandibles of *P. sardus* (RICH-27078); (f) lingual view of two right mandibles of *N. hidalgo* (KIA-39434).

The first human presence on Sardinia roughly dates back about ten thousand years ago (Luglìè, 2014, 2018). The current most ancient ^{14}C age available for the presence of humans on this island documents that it is previous to 7873 cal BC, with a probability >95.4% (Su Carroppu, AA80545: 9200 ± 180 BP, 9125–7873 cal BC; Luglìè, 2018).

Radiocarbon analysis

All the new dates herein were obtained by the ^{14}C Laboratory of the Koninklijk Instituut voor het Kunstpatrimonium (KIK-IRPA), Brussels. Collagen extraction was performed following Longin's (1971) method. Briefly, 1% HCl was added to neutralise the sample, which was then washed with MilliQ-water. The extract was gelatinised in a solution of pH = 3, at 90°C for 12 h, filtered through a Millipore 7 µm-glass filter and subsequently freeze-dried before analysis of ^{14}C, stable isotopes (δ ^{13}C and δ^{15}N), %C, %N and the atomic C:N ratio.

All samples were transformed into graphite using an automatic graphitisation device AGE (Němec et al., 2010; Wacker et al., 2010; Wojcieszak et al., 2020), and ^{14}C concentrations were measured by accelerated mass spectrometry (AMS) at the Royal Institute for Cultural Heritage (Brussels) (Boudin et al., 2015). ^{14}C results are expressed in BP (Before Present) according to Stuiver and Polach (1977) Calibration and Bayesian analysis were executed with the Oxcal 4.3.2 programme (Bronk Ramsey, 2009) using the new atmospheric data from Reimer et al. (2020).

Results

Table 1 presents the new obtained radiocarbon dates of the extinct small mammal species of Mallorca and Sardinia as well as one

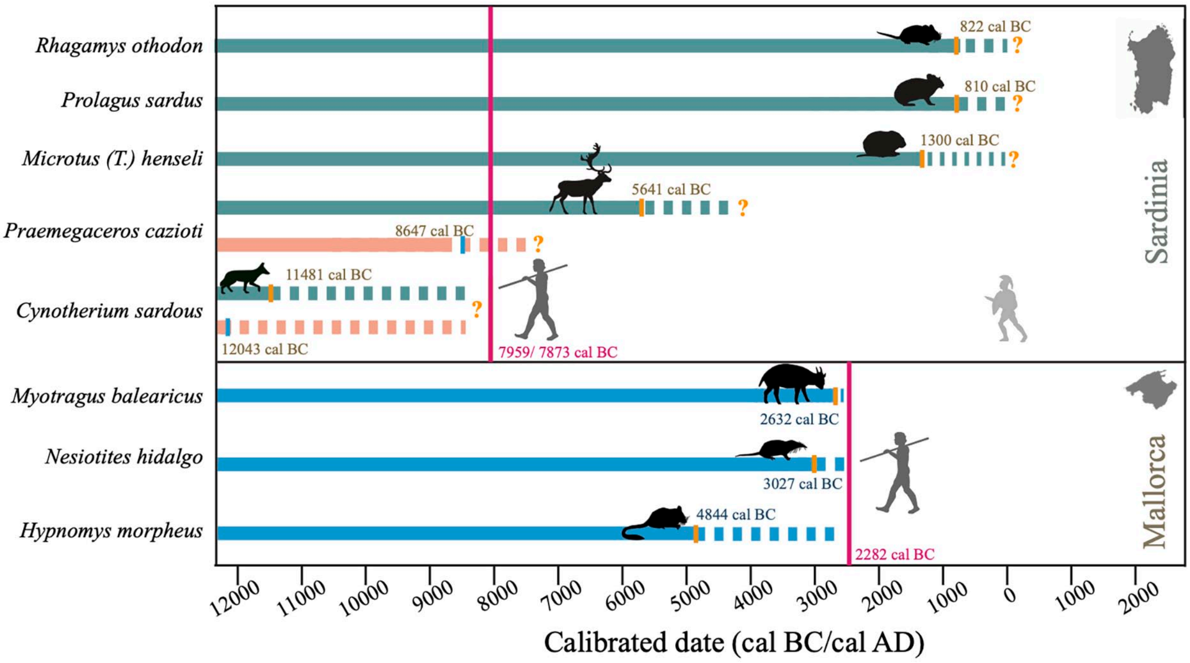

Figure 3. Timeline of extinct animals from Mallorca and Sardinia. Continuous horizontal line: documented presence. Discontinuous horizontal line: assumed presence, still without radiocarbon support. Red vertical line: earliest documented human presence. Pink horizontal line indicates selected cases of Corsica as comparison.

introduced small mammal from Sardinia. Both quality indicators (atomic C:N ratio and collagen weight %C and %N) indicate that the quality of all the samples was good and their collagen was uncontaminated.

The new ^{14}C ages obtained of bones include two species of small Mallorcan mammals (*N. hidalgo* and *H. morpheus*) and three small Sardinian mammals (*P. sardus*, *R. orthodon*, and *M. henseli*). Two of the Sardinian ages represents the sole and, consequently, the most recent available dates for *M. henseli* and *R. orthodon*, while the other one represents the most recent available date for the Sardinian pika *P. sardus*.

Additionally, the ^{14}C age obtained of one humerus of *Rattus rattus* (Linnaeus 1758) coming from Grotta Su Guanu (RICH-27080: 937 ± 25 BP; 1032–1166 cal AD) excludes its prehistoric age, therefore the previous proposal for a very early arrival (Sanges and Alcover, 1980) should be discarded. This result does not provide new insights into the potential involvement of this species in the extinction of the endemic small mammals of the Thyrrenian islands. The attested temporal mismatch between the age of *R. rattus* and those obtained of extinct small mammals from the same sampled unit confirms the convenience of obtaining direct dates for each species.

Discussion

Th extinction dynamic in Mallorca

According to the previously available data and the new radiocarbon dates, the documented age of the last occurrence of the two autochthonous small mammals from Mallorca is before but close to the first human settlement (Figure 3). A biogeographic analysis, previously presented by Bover et al. (2008), pointed to an anthropogenic extinction of these species. This event is coeval with the *Myotragus balearicus* Bate 1909 extinction in Mallorca, for which the available last known occurrence radiocarbon date (2632 cal BC; Cova des Màrmol, RICH-21772, 4035 ± 32 BP, 2663–2651 [1.3%], 2632–2468 [94.1%] cal. BC, Bover et al., 2016) strongly points to its relationship with the first human presence on the island (previous to 2282 BC). The temporal length between these two events, that is, (1) the last occurrence date documented for *M. balearicus* and (2) the first occurrence date documented for human presence, was established in less than 1660 years by Bover and Alcover (2003) and improved to less than 350 years by Bover et al. (2016) based on the new ^{14}C dates. Concerning the ultimate causes, the available data suggest a ‘mass extinction’ event probably linked to diseases introduced by the first human settlers (Bover and Alcover, 2003, 2008).

The Eastern Balearic Islands or Gymnesic Islands (Mallorca, Menorca and surrounding islets) were the most isolated islands over all the Mediterranean, and their vertebrate fauna originated from a Messinian colonisation, followed by 5.3 Ma of isolated evolution that derived to highly modified organisms (e.g. Mas et al., 2018). Three mammal lineages (a caprine, a glirid and a soricid) from the initial stock that colonised Mallorca in the Messinian evolved until the Holocene.

Prior to the human arrival, the Gymnesics were encapsulated worlds without any direct contact with the surrounding mainland. This long-term isolated condition affected mainly terrestrial (i.e. non-flying) vertebrates and no examples of overseas immigration have been recorded among them in contrast to the Pityusic Islands of Eivissa and Formentera, closer to the mainland, where a single case of overseas immigration has been reported by Torres-Roig et al. (2021). As a result of this long-term evolution on a limited insular territory, the singular mammals were strongly modified, adapting to the peculiar and stable ecological conditions of the islands. The arrival of humans, tentatively established ca. 4350–4280 years ago (Alcover, 2008; Bover et al., 2016), should have destabilised the ecological equilibrium, changing, probably very quickly, the pre-human ecosystems due to catastrophic upheaval. Evidence of this shock appears not only through the removal of the autochthonous mammalian fauna that was replaced by the introduction of an initial stock of five domestic species (at least one of them, the goat, also living in a feral state) and two rodents, but also through the palynological record that documents a vegetational change on these islands coinciding with the disappearance of all the endemic terrestrial mammals (see a discussion in Alcover, 2008).

Although the currently available information on the chronology of the endemic Mallorcan mammals represents one of the best approaches of the chronologies of extinction throughout the Mediterranean region, the degree of resolution of the available ^{14}C ages does not allow to establish the relative timing of the extinction of different species. Under geological (or even archaeological) terms, the extinction of all the autochthonous mammals of the Eastern Balearics can be considered simultaneous to human arrival.

The extinction dynamic in Sardinia

The complex biogeographic history of Sardinia is interweaved with Corsica (e.g. van der Geer et al., 2021), and for practical reasons, herein we only emphasise the mammalian fauna that was probably present on the island at the first human arrival. It was a depauperated fauna entailing a mosaic of species with different timelines, some derived from Messinian colonists, while others derived from Middle Pleistocene immigrants (some other species, like otters, perhaps arrived through punctual and scattered episodes of overseas colonisation): a cervid (*Praemegaceros cazioti* [Depéret, 1897]), a canid (*Cynotherium sardous* Studiati 1857), an ochotonid (*Prolagus sardus* Wagner 1829), four mustelids (*Enhydrictis galictoides* Forsyth-Major 1902 and three otters, *Sardolutra ichnusae* Malatesta 1977, *Algarolutra majori* [Malatesta 1978] and *Megalenhydris barbaricina* Willemsen and Malatesta 1987), two rodents (*M.* (*T.*) *henseli* and *R. orthodon*) and two/three eulipotyphlans (*Asoriculus similis* [Hensel 1855]/A. corsicanus [Bate 1944] and *Talpa tyrrhenica* Bate 1945). All these species were endemic to the Sardinia-Corsica block. Excluding the carnivores, the remaining taxa are relatively common in several Late Pleistocene localities of Sardinia (Comaschi Caria, 1968; Palombo, 2006; Zoboli and Pillola, 2016; Zoboli et al., 2019; Zoboli and Pillola, 2017) and Corsica (Croitor et al., 2006; Salotti et al., 2000). The persistence of the dwarf proboscidean *Mammuthus lamarmorai* (Forsyth-Major 1883) in the Sardinian Late Pleistocene is still debated (Palombo and Zedda, 2020; Palombo et al., 2017; Pillola and Zoboli, 2017; Zoboli et al., 2018).

Conversely to Mallorca, the obtained data from Sardinia documents that, after the human arrival and during a long period exceeding 7000 years, at least three of the five autochthonous small mammals survived, sharing the island ecosystems with humans and their introduced fauna (Figure 3). This long-term survival contrasts with an apparently shorter-term survival of *P. cazioti*, whose fossil traces disappear at least 2300 years after the first human arrival on the island.

No radiocarbon dates exist for *T. tyrrhenica* and *A. similis*, which are also elusive in the recent fossil records, suggesting, but no proving, that the Sardinian mole and the Sardinian shrew could have been disappeared before the remaining small mammals of the island. *Asoriculus* seems to be present at least in two Mesolithic/early Neolithic archaeological contexts of SW Sardinia (unpublished data) and in the Neolithic layer of Grotta Corbeddu (van der Geer, 2008). Nevertheless, although the shrew was probably present on the island at the first human settlement, this cannot be currently documented through directly obtained radiocarbon dates. Likewise, there is no direct dating of mustelid bones and, consequently, their presence at the time of the first human settlement cannot be discarded either. The absence of evidence of *M. lamarmorai* during the latest glacial suggests, but does not prove, that probably it disappeared at the beginning of the Late Pleistocene. The recent discovery in the NW Sardinia of an external imprint of an elephant tusk, tentatively ascribed to *M.* cf. *M. lamarmorai*, seems to confirm the persistence of an elephant population until at least the Marine Isotope Stage 5c (MIS 5c) between ca. 96–87 ka (Palombo and Zedda, 2020).

The earliest known date for the human presence in Sardinia can be established ca. 10,000 years ago (Su Carroppu, AA80545: 9200 ± 180 BP, 9125–7873 cal BC; Luglié, 2018). Regarding Corsica, the scenario is similar to Sardinia, as the earliest date is previous to 7959 cal BC (Campo Stefanu, Corsica, Beta 318791, 8940 ± 40 BP, 8259–7959 cal BC; Poz 44201, 8970 ± 60 BP, 8289–7957 cal BC; Luglié, 2018). The human arrival on both islands triggered a series of modifications in the existing mammalian communities. Notwithstanding this, the scale and rate of disappearance of the mammalian fauna were not as complete and fast as it is outlined in the Balearics, since in Sardinia a few species survived to the first human in Sardinia. Among them, the endemic cervid (*P. cazioti*) survived in Sardinia at least ca. 2300 years after the first human arrival (last known occurrence date: BO472L, 6460 ± 130 BP, 5641–5075 cal BC, Grotta Juntu; Benzi et al., 2007), although only 318 years before to the earliest known occurrence of Neolithic people (based on human bones, Grotta Rifugio, Beta 334479, 6430 ± 40 BP, 5476–5323; Luglié, 2018), suggesting a possible link between the *P. cazioti* extinction and the arrival of the Neolithic colonisers. The last known occurrence date of *P. cazioti* in Corsica is currently 8718 cal BC (Teppa di U Lupinu, LY-2779, 9292 ± 58 BP, 8704–8324 cal BC; Salotti et al., 2008), and its extinction chronology is uncertain, possibly related to the first human settlers from Corsica or to its Neolithic occupation.

Only two ^{14}C ages of bone collagen of *C. sardous* are available, both from Sardinia and Corsica. Nevertheless, both falls >1000 years before the first documented dates for the human presence. This fact, together with the scarcity of *Cynotherium* fossil bones (as expected for a predatory mammal), *call* for an extremely *cautious* approach when establishing the chronology and causes of its extinction, as it has been insufficiently recorded and ^{14}C dated. The last known occurrence date of *C. sardous* in Sardinia is currently 11464 cal BC (Grotta Corbeddu, UtC-2583, 11350 ± 100 BP, 11481–11146 cal BC; Klein Hofmeijer, 1996), while its last known occurrence date in Corsica is currently 12043 cal BC in Corsica (Castiglione 3, UtC-2583, 11760 ± 110 BP, 12043–11407 cal BC; Pereira et al., 2006). The lineage of *Cynotherium* started its island evolution >800,000 years ago (Madurell-Malapeira et al., 2015), although its presence has been quite elusive in the fossil record. Its long survival on the island together with the current last occurrence dates available for Corsica and Sardinia makes it reasonable to suggest that the species was probably present at the time of the first human arrival.

With the ^{14}C dates reported here, we document the persisted coexistence with humans of at least three of the five autochthonous small mammals on Sardinia. In the absence of a good stratigraphic record in Grotta Su Guanu, we can only establish that the last occurrence of *P. sardus* on the island was after 810 cal BC, after 822 cal BC for *R. orthodon* and after 1376 cal BC for of *M.* (*T.*) *henseli*. On Corsica, the stratigraphic framework from Monte di Tuda cave (Vigne and Valladas, 1996; Vigne et al., 1997) points to the survival of the autochthonous small mammals at least until 393 BC. These authors suggest that the last occurrence of *A. corsicanus* occurred between 393 and 151 cal BC, while the last occurrence of *Rhagamys*, *Prolagus* and *Microtus* (*Tyrrhenicola*) should have taken place sometime between 393 BC and 1459 AD. According to the available dates from Castellu (Vigne and Valladas, 1996), this last range can be shortened to between 393 BC and the 6th century AD. Unfortunately, no information on the singularity or aggregative nature, as well as the specific taxonomic identity of the dated material, was provided. Dating strata without giving the exact information on what has been dated introduces some uncertainties, so the Monte di Tuda last occurrence dates should be accepted with some caution, waiting for the confirmation of the last occurrence dates of the individual species through the direct dating of their bones.

Taken together, the results prevent the presentation of a complete overview of the extinction processes on this island. Nevertheless, some relevant points can be outlined, although emphasising that a noticeable part and some details of the Sardinian extinction processes will need further research:

1. The direct impact of the Mesolithic people on the autochthonous mammalian Sardinian fauna remains still unresolved. The first human settlers of Sardinia should have been hunter-gatherers (Lugliè, 2018). Among the mammals, their potential prey included *P. cazioti* and the small *P. sardus* (and even perhaps different carnivores), although there is only direct evidence for the latter (Vigne and Desse-Berset, 1995). It is unknown how human hunting affected the subsistence of these species, but at least these two of these species did not become extinct at that time. The remaining Pleistocene small mammals were apparently unaffected by Mesolithic settlers.
2. The arrival at the VI millennium BC (Lugliè, 2018) of a new wave with Neolithic colonisers and domesticates appears to be one of the factors that promoted the *P. cazioti* extinction. Its last occurrence date is so close to the first presence of Neolithic people that points to a causal relationship. This extinction could be related to hunting by Neolithic people (unproved) or to the introduction of new pathogens and diseases via the newly arrived domesticates (i.e. cattle, pig, sheep and goat; also, unproved), while the introduction of predators and the burning of the vegetation can be reasonably excluded as a cause of the deer extinction. The natural, and therefore sole potential predator of *P. cazioti* present at that time was the dog (Wilkens, 2012). However, no remains of dogs have been attested outside human settlements as should be expected if this species was a driver for the extinction of *P. cazioti*. No indirect marks of dog predation (i.e. tooth marks) have been recorded on any endemic mammal bone, so it is plausible to exclude the dog as a factor leading to the extinction. Furthermore, the burning of the vegetation can also be reasonably excluded as a cause of the extinction of *P. cazioti* due to the large size of the island and the high mobility of the deer to avoid the risk of wildfire, thus burned areas. Additionally, no evidence of a great burning episode is present in the archaeological record of the island (Beffa et al., 2016).
3. New mainland influences came into play with the development of the successive Chalcolithic, Bronze and Early Iron Age cultures and their respective new waves of settlers (Knapp and Van Dommelen, 2015). Despite the circulation of goods and people during this period, no extinctions were recorded. All the documented last occurrence dates for *Rhagamys*, *Microtus* (*Tyrrhenicola*) and *Prolagus* fall at the end of this period, suggesting that their timing of extinction and consequences are causatively related to the next invasive phase.
4. New human immigrations and cultural change occurred on Sardinia during the first millennium BC (Phoenicians, ca. 750–700 BC; Carthaginians, 510 BC; Romans, 238 BC; Brigaglia et al., 2006). All these different socio-political formations promoted the military and commercial development of the island; hence Sardinia was fully integrated into the exchange networks of the Mediterranean. This new interconnectedness condition is probably related to the documented new wave of alien mammal introductions (Wilkens, 2012; Wilkens and Carenti, 2006).

Contrasting trends and drivers

All the Holocene extinctions of autochthonous small mammals from Mallorca and Sardinia seems to have been human-related. The asynchrony of the extinction of small mammals and, by extension, of all the autochthonous mammals on Mallorca and Sardinia, allows us to approach their causes. Wood et al. (2017) consider three main drivers for the prehistoric extinction of mammals on islands, namely, (1) the introduction of predators, pathogens and diseases, (2) hunting by humans and (3) the burning and destruction of the ecosystem. On Mallorca where the classic triad of autochthonous mammalian species disappeared simultaneously and in a very early phase of the human settlement, the last two drivers have been excluded, as well as the introduction of predators, thus the introduction of pathogens/diseases is the most probable driver for the extinction of the small mammals (for discussion, see Bover and Alcover, 2008), and of *Myotragus* (Bover and Alcover, 2003; Bover et al., 2016).

On Sardinia, the extinction pattern is more complex, as mammalian extinctions did not occur immediately after the first settlement and besides they were not simultaneous, rather scattered along seven millennia. Additionally, uncertainties derived from the full absence of radiocarbon dates of bone collagen of proportions of the native fauna (mustelids, shrew and mole) and the introduced fauna (e.g. there is a lack of dates of the first occurrence for many introduced species) should be added to our analyses.

The palynological record from the Holocene of Sardinia is widely unknown, with only a few studies devoted to it (e.g. Beffa et al., 2016; Di Rita and Melis, 2013; Pittau et al., 2012, 2018; Ucchesu et al., 2015). Unfortunately, none of these papers cover the complete temporal interval discussed here. Besides, the analysed sites, scattered over different parts of the island, are distant, thereby hindering the direct comparison of them. To our knowledge, no data exists on the immediately pre-human vegetation on Sardinia, and there is only one site with some Mesolithic vegetation record (Sa Curcurica, Nuoro; Beffa et al., 2016). The vegetation of this site during the last Mesolithic and early Neolithic does not change and is considerably different to that of the western Neolithic sites in the last period. Nevertheless, no data exist of the vegetation in the eastern area before the Mesolithic. The few data attributed to the Neolithic age (Sa Punta and Santa Giusta, Oristano; Pittau et al., 2018) are inconclusive regarding the changes which occurred in the Oristano Gulf area in relation to previous ages due to the absence of previous palynological data on the same area. Despite the incomplete information, the continuity of vegetation during the last Mesolithic and early Neolithic at Sa Curcurica and the absence of Cerealia at the earlier Neolithic site studied (the open-air site of Sa Punta, Pittau et al., 2012, 2018) could be a significant reflection of the limited human impact on the vegetation at that time. Consequently, the available palynological record points to an apparent higher capacity to cope with the human impacts in Sardinia than in Mallorca, corresponding with the vertebrate extinction pattern outlined here.

On Mallorca, the pre-human Mallorcan terrestrial vertebrate fauna only included three non-volant mammals (plus one reptile and one amphibian), while there were at least seven, and probably eleven or more, non-volant mammals (and a still undetermined number of reptiles and amphibians)in Sardinia immediately before the human arrival. The sudden extinction of mammals on Mallorca contrasts with the delayed extinction (scattered over seven millennia) on Sardinia. The archaeological record for other animal groups is still very fragmentary. The Mallorcan lizard (*Podarcis lilfordi* [Günther 1874]) survived on the island shortly after the introduction of the weasel, which is documented before 206 cal BC (Valenzuela and Alcover, 2013). The Mallorcan midwife toad (*Alytes muletensis* [Sanchíz and Adrover 1979]) still survives in a very few isolated places in Mallorca. On Sardinia, no records exist on reptilian and amphibian extinction after the human arrival. The attested divergent response of Mallorcan and Sardinian vertebrate fauna could be an indication of the different levels of vulnerability that each insular ecosystem had. On the ecological-level scale, throughout the Holocene up to the present, Mallorca appears to have been more vulnerable than Sardinia to the external disturbances introduced by humans. Smaller areas, lower biodiversity and longer isolation could be decisive factors to explain the reduced capacity of the Mallorcan ecosystems to absorb external perturbations, thereby retain the highly modified species.

Conclusions

A new chronological framework for the extinction of the endemic small mammals of Mallorca and Sardinia is provided. The implementation of a hygienic protocol based on new direct radiocarbon dates and the careful scrutiny of the archaeological evidence allows the accurate comparison of both extinction processes. A comparison of the trends outlined for Sardinia and Mallorca established a divergent or asynchronous pattern. On Mallorca, the small size and less ecological variability of the island led to a catastrophic and rapid process of extinction, whereas the more extensive and heterogeneous territory of Sardinia enabled the endemic small mammals to cope, at least for a while, with the disturbances introduced by humans. Therefore, the zooarchaeological record emerges as an essential proxy for the elucidation of past extinction events and to approach future challenges.

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