Biol Invasions (2026) 28:46
https://doi.org/10.1007/s10530-026-03760-3

ORIGINAL PAPER

From ship to shore: the genetic legacy of the invasive black rat in Atlantic Islands

Maryane Wielewski · Lara Almeida · Sofia I. Gabriel · Raquel Vasconcelos

Received: 17 June 2025 / Accepted: 17 January 2026

Abstract Islands offer unique ecological and evolutionary insights, yet they are fragile ecosystems, particularly vulnerable to invasive species. The present study focused on the origin of an invasive species in Macaronesia and other Atlantic islands, specifically the black rat, *Rattus rattus*. The ability of this species to thrive is attributable to its ability to coexist with humans in a commensal relationship. The objective of this study was to ascertain the origins of these insular rat populations through the analysis of a molecular marker, examining their genetic diversity within the islands and providing information for their management aiming for the conservation of native species. The mitochondrial DNA D-loop region of 41 individuals was sequenced to compare with sequences from public databases in order to infer their most likely origin, using phylogenetic and network analyses. A total of 106 different haplotypes were obtained from combining sequences from GenBank and new sequences, distributed into two distinct haplogroups. The Indian Ocean group included samples from India and a number of other countries and islands in the Indian Ocean region, as well as Italy and Cabo Verde. Meanwhile, the Atlantic Ocean group included samples from Europe, Oceania, Central and South America, and Africa. For the first time, an Indian lineage was found in Cabo Verde. These introductions are strongly linked to European trade routes and human colonisations, Understanding the routes by which these populations arrived on the islands, as well as their origins, is therefore crucial to understanding the patterns of biological invasions.

Keywords Historical trade routes · Invasive black rat · Island Biogeography · Macaronesia · Mitochondrial D-loop region

Communicated by Mariano A. Rodriguez-Cabal.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10530-026-03760-3.

M. Wielewski · L. Almeida · R. Vasconcelos (✉)
CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO, Laboratório Associado, Programa BIOPOLIS em Genómica, Biodiversidade e Ordenamento do Território, Universidade do Porto, Campus de Vairão, 4485-661 Vairão, Portugal
e-mail: raquel.vasconcelos@uc.pt

M. Wielewski · L. Almeida
FCUP, Faculdade de Ciências, Departamento de Biologia, Universidade do Porto, 4169-007 Porto, Portugal

S. I. Gabriel
CE3C, Centro de Ecologia, Evolução e Alterações Ambientais, CHANGE, Faculdade de Ciências da Universidade de Lisboa, 1749-016 Lisbon, Portugal

R. Vasconcelos
DCV, Departamento de Ciência da Vida, Faculdade de Ciências e Tecnologia, Universidade de Coimbra, 3000-456 Coimbra, Portugal

Introduction

Islands, which are often considered to be isolated havens of biodiversity, are not only hotspots of endemism but are also highly vulnerable to the introduction of invasive species (Whittaker and Fernández-Palacios 2007). Introduced species are those that were intentionally or unintentionally introduced into new territories and established populations within the new environment (Feldhaar and Lach 2020), while invasive species are introduced species that, once established, impact the community structure of ecosystems by competing for resources, acting as vectors of diseases, and engaging in predation (Lockwood et al. 2013). Once non-native vertebrates become established, they tend to compete for resources, act as vectors for the transmission of diseases, and engage in predation (Lockwood et al. 2013; Gaiotto et al. 2020). While most native and endemic species often encounter challenges due to their inability to adapt to competitive environments (Alpert 2006), the consequences of invasive species can be particularly severe on islands. This is due to the existence of empty niches as a result of the absence of entire groups of species, high number of endemic species, their relative inexperience with competitors and predators, and their more limited distribution range compared to mainland species (Gaiotto et al. 2020). This renders native island species more vulnerable and at a disadvantage when confronted with invaders (Gaiotto et al. 2020). The isolation of island native populations, both geographically and genetically, serves to amplify the impacts of alien species (Whittaker and Fernández-Palacios 2007). Hence, islands are considered good natural laboratories to study introduced species, especially oceanic ones (Whittaker et al. 2017). This isolation intensifies the vulnerability of species on islands due to low levels of gene flow, low genetic variation, as well as their unique speciation traits. This increases their susceptibility to extinction caused by environmental changes, such as the introduction of invasive species. (Frankham 1997). Oceanic islands, particularly those with a documented human colonisation history and that were recently colonised provide a conducive environment for tracking the origins of introduced biodiversity (Whittaker and Fernández-Palacios 2007).

The Macaronesia region, situated in the northeastern Atlantic Ocean, comprises five oceanic archipelagos: the Azores, Madeira (including Selvagens Archipelago), the Canary Islands and Cabo Verde. The climate and biodiversity in this region are quite distinct (Fernández-Palacios 2011). These systems are all extremely vulnerable to invasive species due to low levels of gene flow within populations of different islands, low genetic variation of island species (Vasconcelos et al. 2010a), and an increased tendency of extinctions caused by changes in the environment, diseases, predators, competitors and climate (Cropper and Hanna 2014; Patiño et al. 2016; Wood et al. 2017). An example of a native species threatened by invasive vertebrates in Macaronesia is *Pipistrellus maderensis* in Madeira Archipelago, frequently predated by introduced domestic cats (Russo and Cistrone 2023). In addition to those interesting factors, the history of human colonisation of these archipelagos is considered very recent and relatively well-studied (Barcellos, 1899, 1904; Dall'Angola 1990; Rodrigues et al. 2015). All Macaronesian islands were found uninhabited in the fifteenth century, except the Canary Islands (Fernández-Palacios et al. 2011), making it easier to track human history in the region and also the origin of the study species.

During the fifteenth century, navigation through the oceans became more common in Europe, especially by Spanish and Portuguese navigators. The purpose was to establish new trade routes, exploit resources and build new colonies. Historically, the first Macaronesian archipelago these navigators reached was the Canary Archipelago in the beginning of the fourteenth century. However, the islands had already been settled by the indigenous Guanche population. Consequently, under orders from the Castilian king Henry III, Jean de Béthencourt and Gadifer de La Salle initiated hostilities over the territory, which continued until the end of the fifteenth century (Rodrigues 2016; Bühner 2024). The second was Madeira, discovered by João Gonçalves Zarco and Tristão Vaz Teixeira in 1418 (Veríssimo 2016). Later, Azores was first visited by Gonçalo Velho in 1431 (Rodrigues et al. 2015). The final archipelago to be discovered was Cabo Verde, which was found by António da Noli and Diogo Gomes in 1460 (Barcellos, 1899; Dall'Angola 1990).

Throughout these travels, there is evidence to suggest that not only were humans the occupants of the ships, but there is also documentation of the presence of introduced small terrestrial mammals. In the Canary Islands, that lead to the introduction, for example, of the greater white-toothed shrew *Crocidura russula,* the pygmy white-toothed shrew *Suncus etruscus*, the Barbary ground squirrel *Atlantoxerus getulus*, the North African hedgehog *Atelerix algirus*, the black rat *Rattus rattus*, the brown rat *Rattus norvegicus*, and the house mouse *Mus musculus*, some of them invasive (Nogales et al. 2006; Whittaker and Fernández-Palacios 2007). The last three rodents are also present in the Azores Archipelago (Borges, 2010), in the Madeira Archipelago (Borges et al. 2008) and in Cabo Verde (Martinez et al. 2021). The European hedgehog *Erinaceus europaeus* is the only species that has not been identified as a threat to local biodiversity (Borges, 2010). Besides the species mentioned above, in Cabo Verde, the bats identified in the archipelago include *Hypsugo savii, Pipistrellus kuhlii, Miniopterus schreibersii, Plecotus austriacus,* and *Taphozous nudiventris*. The question of whether these species are indigenous or non-indigenous remains uncertain (Borloti et al. 2020).

The present study aimed to understand the patterns of colonisation of three Macaronesian archipelagos by the black rat, *R. rattus*, which was hypothesised to have arrived at a similar time as the human population, around 550 years ago (Borges, 2010; Masseti 2010). The black rat is one of the mammals that was unintentionally transported to the Macaronesian Islands (Borges, 2010). In the Azores, it is indicated that it arrived with the first settlers, and is present on all the islands (Borges, 2010; Masseti 2010; Mathias et al. 1998). In the Madeira Archipelago, the species began to colonise immediately after human arrival and is present on the island of Madeira and Porto Santo (Borges, 2010; Zino et al. 2001), and absent in Selvagens (Sequeira et al. 2023). In Cabo Verde, the presence of the species on the islands of Santiago, Brava, Santo Antão, São Nicolau, Boavista, Maio and Fogo probably coincides with the first human colonisations (Hazevoet and Masseti 2011). The species arrived in the other Atlantic Islands, such as São Tomé and Príncipe, during the fifteenth century, with the Portuguese ships according with Dutton (1994). There is no information about the arrival of *R. rattus* in Guinea-Bissau.

This species is native to Asia, but is distributed across most of the world (Baig et al. 2019). It exhibits a remarkable degree of phenotypic plasticity in its adaptations that explains its fast dispersal, with the ability to inhabit a diverse range of environments, adapting to a broad omnivorous diet, and to urban ecosystems (Borroto-Páez and Woods 2012). The species also has high reproductive levels and short generation time, which can vary with temperature and food availability on the islands (Harper and Bunbury 2015). As an invasive species, its aggressive and territorial behaviour is one of the causes of decline of native fauna and flora richness, especially on island biotas (Borroto-Páez and Woods 2012). As an example, Gaiotto et al. (2020) indicated that the black rat has negatively affected the populations of Noronha skinks in the Fernando de Noronha Archipelago. The species also negatively impact humans in urban areas, once it is a vector of some diseases like leptospirosis, infection by hepatic capillariasis, bubonic plague, leprosy, among others (Babolin et al. 2016; Enscore et al. 2020; Lima et al. 2022).

The specific objectives of this study were to determine the provenance of *R. rattus* in Macaronesia and its potential introduction events, i.e. whether islands within archipelagos have divergent origins and their relationships with mainland populations. It was hypothesised that there is a strong identity of these populations with mainland Portugal and coastal Africa and other African Atlantic Islands, such as Guinea-Bissau and São Tomé and Príncipe, like what was observed in other invasive species in the region (Förster et al. 2009; Gabriel et al. 2013, 2015, 2024). In the case of Cabo Verde, no previous studies were performed with invasive vertebrates, so it was hypothesised that a similar pattern will be observed as in the other regions of Macaronesia, based on the available historical indications. This correlation is attributed to the trends and colonisation from the mainland to the islands. Also, it was aimed to characterise the genetic structure of this invasive species. It is anticipated that the degree of genetic diversity shared among the rats from the archipelagos and those from the mainland will be low. This information will provide fundamental insights into the mechanisms underlying its invasion success and is essential for designing evidence-based management interventions (Du et al. 2021).

For achieving these objectives, molecular methods were used as they are proven to be important for understanding the colonisation pathways of introduced species in this region (Cristescu 2015). A molecular marker that has been used in studies of this nature is the D-loop mitochondrial region, which possesses both conserved regions and hypervariable regions (Larizza et al. 2002; Nyunja et al. 2017).

Methodology

Study area

The Macaronesian region, located in the northeastern Atlantic Ocean, comprises five volcanic archipelagos (Fig. 1): the Azores, the Madeira Islands, the Selvagens (belonging to Madeira), the Canary Islands and the Cabo Verde Islands. The oldest subaerial lavas are on the Selvagem Grande, estimated to be 26 million years old (my), in the Selvagens Archipelago (with no rats), while the youngest are on Pico Island in the Azores, with 0.19 my (Florencio et al. 2021). Despite their volcanic origin, only the Azores, the Canary Islands and Cabo Verde maintain active volcanism (Fernández-Palacios 2011). Of this region, Azores, Madeira and Cabo Verde were sampled, and these are described in more detail below. The Azores Archipelago, located approximately 1,370 km from Lisbon in between the North American and the Eurasian plate, is a Portuguese territory and consists of nine islands: Santa Maria, São Miguel, Terceira, Graciosa, São Jorge, Pico, Faial, Flores and Corvo. The region experiences a temperate climate, characterised by cool and humid conditions throughout the year (Fernández-Palacios 2011; Florencio et al. 2021). The Madeira Archipelago, made up of Madeira Island, Porto Santo and Ilhéu da Cal (the oldest with around 19 my) and

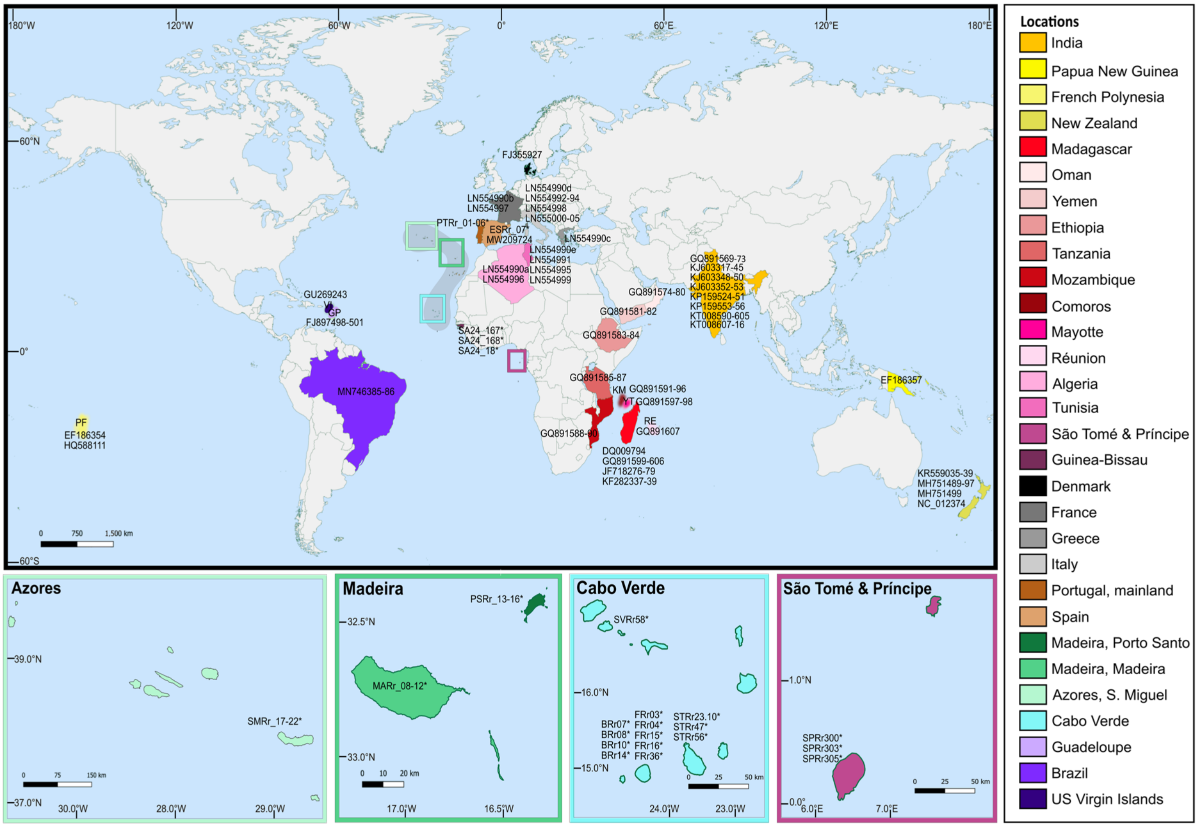

Fig. 1 Maps representing the geographical location of the samples of *R. rattus* used in this study for D-loop mitochondrial DNA region. The upper image represents the worldwide samples. The grey area delineates the Macaronesia region. The bottom images represent samples from Azores, Madeira, Cabo Verde, and São Tomé and Príncipe archipelagos, respectively. Samples retrieved from GenBank are represented by accession numbers and the new samples from this study are represented by asterisks (*) and voucher codes. For further details, please check Table S1

Desertas, with three other uninhabited islands and islets: Ilhéu Chão, Deserta Grande and Bugio (Florencio et al. 2021). The climate present in the Archipelago is classified as Mediterranean, bearing a resemblance to that of the Canary Islands. During the winter months, the archipelago experiences mild and humid weather, while in summer, the weather is dry and warm (Fernández-Palacios 2011). Cabo Verde, on the other hand, has a warm and dry climate, due to its location closer to the Sahel, about 570 kms from the coast of Senegal (Duarte and Romeiras 2009). The archipelago is made up of ten main islands: Santo Antão, São Vicente, Santa Luzia, São Nicolau, Sal, Boavista, Maio, Santiago, Fogo and Brava, and several islets of which Boavista is the oldest considering its subaerial lavas, with around 18 my (Florencio et al. 2021).

São Tomé and Príncipe comprise two oceanic islands, São Tomé Island and Príncipe Island, and several islets, situated in the Gulf of Guinea, in western equatorial Africa. The local climate is oceanic equatorial and is divided into rainy and dry seasons (Ceríaco et al. 2022). The first continental nation included in this study was Guinea-Bissau, located in West Africa. The climate in the region is classified as tropical, also exhibiting a distinct dry season during the winter months, and a rainy season during the summer months (Myers et al. 2000; Mendes and Fragoso 2023). The Iberian Peninsula is constituted by two countries, Portugal and Spain, which share borders with the Atlantic Ocean and the Mediterranean Sea. The majority of the territory is influenced by the Mediterranean climate, which is wet during the winter months and dry during the summer months (Vide and Cantos 2001; Mora and Vieira 2020). The samples from São Tomé and Príncipe, Guinea-Bissau, Portugal and Spain were used for comparison purposes, as they are a potential source for the introduction of the species in the Macaronesian region.

Study species

Rattus rattus has variable dorsal and ventral fur colouration, ranging from greyish black to brown, and typically displaying shades of grey, yellow or white, respectively. The presence of prominent ears, which can reach and cover the eyes, is notable. The tail is significantly longer than the body and head and is usually slender and lighter in colouration (Yiğit et al. 1998; Islam et al. 2021). The species exhibits nocturnal activity patterns and possesses advanced climbing abilities, both of which are key characteristics that facilitate its invasive behaviour (Štolhoferová et al. 2024). It is a prominent example of a terrestrial species that has become invasive on islands, ranking among the top 10 most invasive species on these islands (Spatz et al. 2017).

Data collection

The tissue samples were collected in the Macaronesian region, São Tomé and Príncipe and on mainland Europe and Africa (Fig. 1). All samples were collected far from airport and port areas, in humid habitats, to avoid recently introduced individuals. In the Azores Archipelago, six samples were obtained from the island of São Miguel. In the Madeiran Archipelago, five samples were collected from Madeira Island and four from Porto Santo Island. Sample from Azores and Madeira Archipelagos were opportunistically collected from roadkills. Samples from Cabo Verde were collected opportunistically as bycatches of mouse sampling with Sherman traps (23×9×8 cm, H. B. Sherman traps Inc., Tallahassee, Florida), namely on the islands of São Vicente (one sample), Fogo (five samples), Santiago (three samples) and Brava (four samples). The Cabo Verdean samples were deposited in the Biocatalog collection at the Technical University of the Atlantic, Mindelo, São Vicente, using the same codes as for genetics. In mainland Portugal (six samples) and in Spain (one sample), roadkills were also used. From São Tomé Island and Guinea Bissau three samples were collected from each country using Sherman traps. All the information about the samples can be found in Supplementary Table S1. Some of these animals were photographed for morphological identification and those photographs were deposited in the Morphobank project 5896 (codes M957008–M957063).

DNA extraction, amplification and sequencing

The DNA was extracted with the saline technique outlined in Borloti et al. (2020). The mitochondrial D-loop region was amplified using the primers EGL4L (5’ CCACCATCAACACCCAAAG 3’) and RJ3R (5’ CATGCCTTGACGGCTATGTTG 3’)

(Robins et al. 2007). The PCR was configured with the initial activation temperature of 95 °C for 15 min, followed by 35 cycles of denaturation at 95 °C for 60 s, annealing at 64 °C for 60 s and extension at 72 °C for 90 s with a touchdown of -0.5 °C in the annealing temperature in each cycle until the temperature reached 58 °C, followed by a 10-min extension at 72 °C. The products of the PCR process were then subjected to Sanger sequencing at the CIBIO facilities, and the chromatograms of forward and reverse sequences were subsequently reviewed using Geneious Prime 2024.0.7 (Kearse et al. 2012).

Data analysis

Phylogenetic and network analyses can yield insights into the origin of populations, the number of introductions, the dispersal mechanisms, the genetic diversity, and the establishment of species in novel ecosystems (Cristescu 2015). The consensus of the sequences was used to perform a Basic Local Alignment Search Tool (BLAST) to identify similar sequences available on GenBank. The selection criteria included sequences with 96% similarity, and the geographic origin of these sequences and their GenBank accession codes were also documented in the Supplementary Table S1.

A total of 532 sequences from 23 countries were downloaded from GenBank and included in the study (Fig. 1) together with 41 new samples from 5 countries, in a total of 573 samples from 28 countries. The new sequences were deposited on GenBank with the codes PX508128–PX508168 (check Supplementary Table S1 for details). A Clustal alignment was assembled using the sequences from GenBank reference and the new samples dataset, employing the software Geneious Prime (Kearse et al. 2012). An alignment with 273 base pairs was recovered.to maximise the number of sequences of different lengths available in GenBank.

A phylogenetic tree was constructed using unique haplotypes created on TCS. All the 106 sequences had the same length and a sample of *R. norvegicus* was added as outgroup, in a total of 107 sequences with 273 base pairs (indels included). The method of phylogenetic analysis employed was the Bayesian analysis. In order to ascertain the most appropriate model for the Bayesian tree, the software MEGA v11.0.13 (Tamura et al. 2021) was used to provide the maximum likelihood (ML) tree with 1,000 bootstrap replicates. The optimal model sequence evolution was determined to be HKY + G + I. The reconstruction of the tree was facilitated by MrBayes 3.2.7. (Ronquist et al. 2012), which executed simulations of Markov Chain Monte Carlo (MCMC) with 10^6 generations, producing 20,000 trees saving a tree every 100 generations. The bootstrap value ≥ 95% was considered as evidence for highly supported branches. The software Fig Tree v.1.4.3 (https://github.com/rambaut/figtree/releases/tag/v1.4.5pre) was employed to visualise the tree.

The 573 sequences were then used to reconstruct a haplotype network using TCS (Clement et al. 2000), treating indels as a fifth state, with a 95% connection limit, to comprehend and visualise the relationships among all the populations. To visualise the results, tcsBU (Santos et al. 2016) was employed.

Finally, indices of genetic diversity were calculated, i.e. haplotype diversity (Hd) and nucleotide diversity (π), for all the samples, for the two main detected haplogroups (the Indian Ocean group and the Atlantic Ocean group) and for the Macaronesian samples. Those calculations were performed using the DnaSP 6.12.03 software. (Rozas et al. 2017).

Results

Phylogenetic tree

The phylogenetic tree was divided into two clusters (Fig. 2). The larger cluster, named Indian Ocean, comprised samples from India, Madagascar, Oman, Yemen, Ethiopia, Tanzania, Mozambique, Grande Comoro and Mayotte, Italy, and Cabo Verde. The second cluster was divided in two clades, a small clade called Madagascar, which consisted of samples from New Zealand and Madagascar, and the Atlantic Ocean clade, which consisted of samples from Denmark, France, Guadeloupe, French Polynesia, Italy, Portugal (mainland, Madeira and the Azores), Spain, New Zealand, Papua New Guinea, Brazil, US Virgin Islands, Réunion, Madagascar, Cabo Verde, Algeria, Tunisia, São Tomé and Príncipe, and Guinea-Bissau.

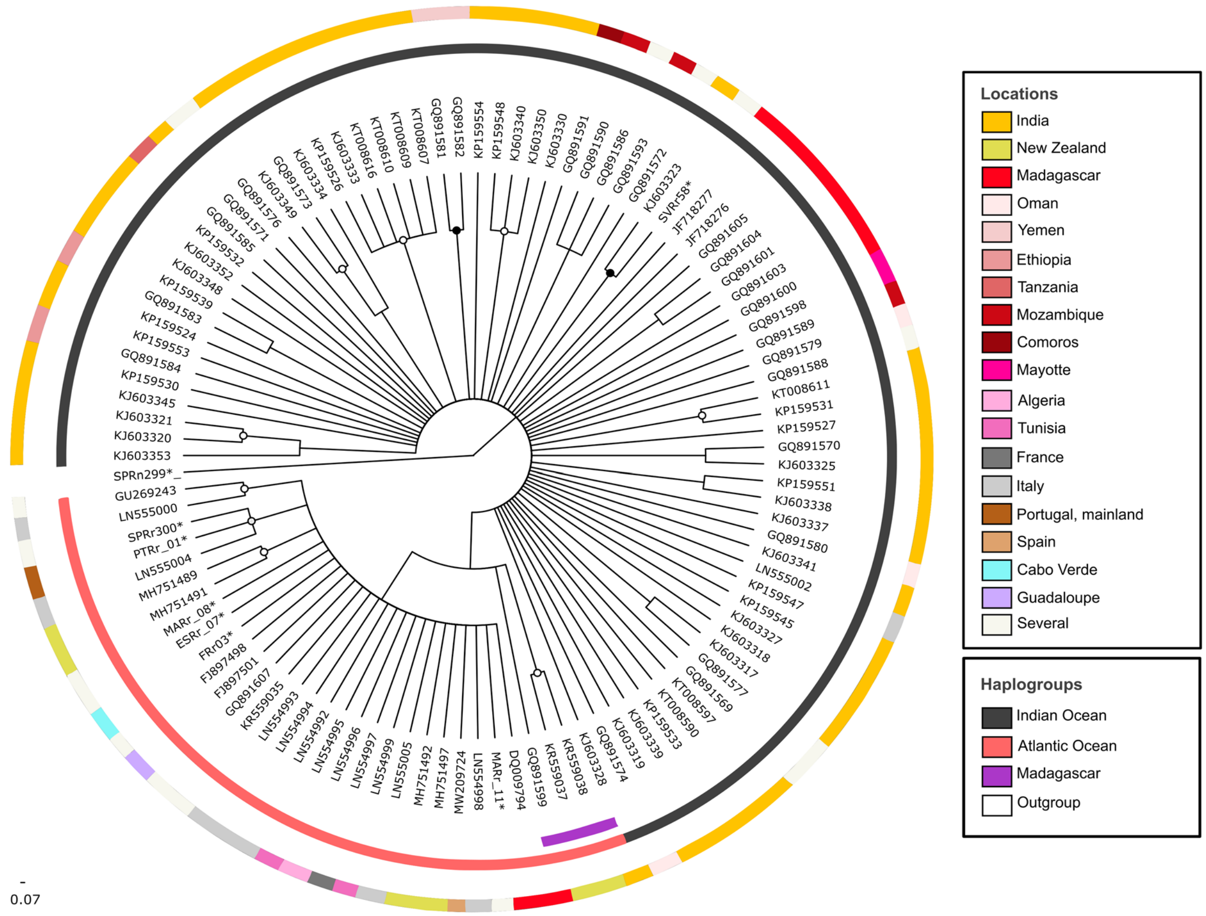

Fig. 2 A Bayesian phylogenetic tree of D-loop region (273 base pairs) of *R. rattus* rooted with *R. norvegicus* (outgroup). The white dots on the nodes indicate the bootstraps value between 75 and 95% and the black dots indicate bootstraps value ≥ 95%. The codes of the new samples of this study are marked with asterisks (*). Colours in the inner circle represent the haplogroups and in the outer circle the locations of the selected individual of each clade

Haplotype network

The samples from Macaronesia and the mainland were represented in seven haplotypes of the 106 obtained on the haplotype network (Fig. 3). Two haplotypes were recovered in the Madeira Archipelago, one haplotype in Azores, and four in Cabo Verde. Two well defined haplogroups were evident. The Indian Ocean haplogroup, included samples from India and several countries and islands in the Indian Ocean region (Madagascar, Oman, Yemen, Ethiopia, Tanzania, Mozambique, Comoros and Mayotte), as well as Italy and Cabo Verde. The Atlantic Ocean haplogroup, meanwhile, included samples from Europe (Denmark, France, including Réunion, Guadeloupe and French Polynesia, Italy, Portugal, including Madeira and Azores, and Spain), Oceania (New Zealand and Papua New Guinea), America (Brazil and the US Virgin Islands), and Africa (Madagascar, Cabo Verde, Algeria, Tunisia, São Tomé and Príncipe, and Guinea-Bissau). Finally, the Madagascar subgroup, included samples from Madagascar and New Zealand. For further details regarding the locations and references, please refer to Table S1 in the Supplementary Material. This finding was further corroborated by the phylogenetic tree (Fig. 2).

The Indian Ocean haplogroup exhibited a higher degree of genetic diversification, characterised by a greater degree of intrapopulation and interpopulation genetic diversity, with a much higher number

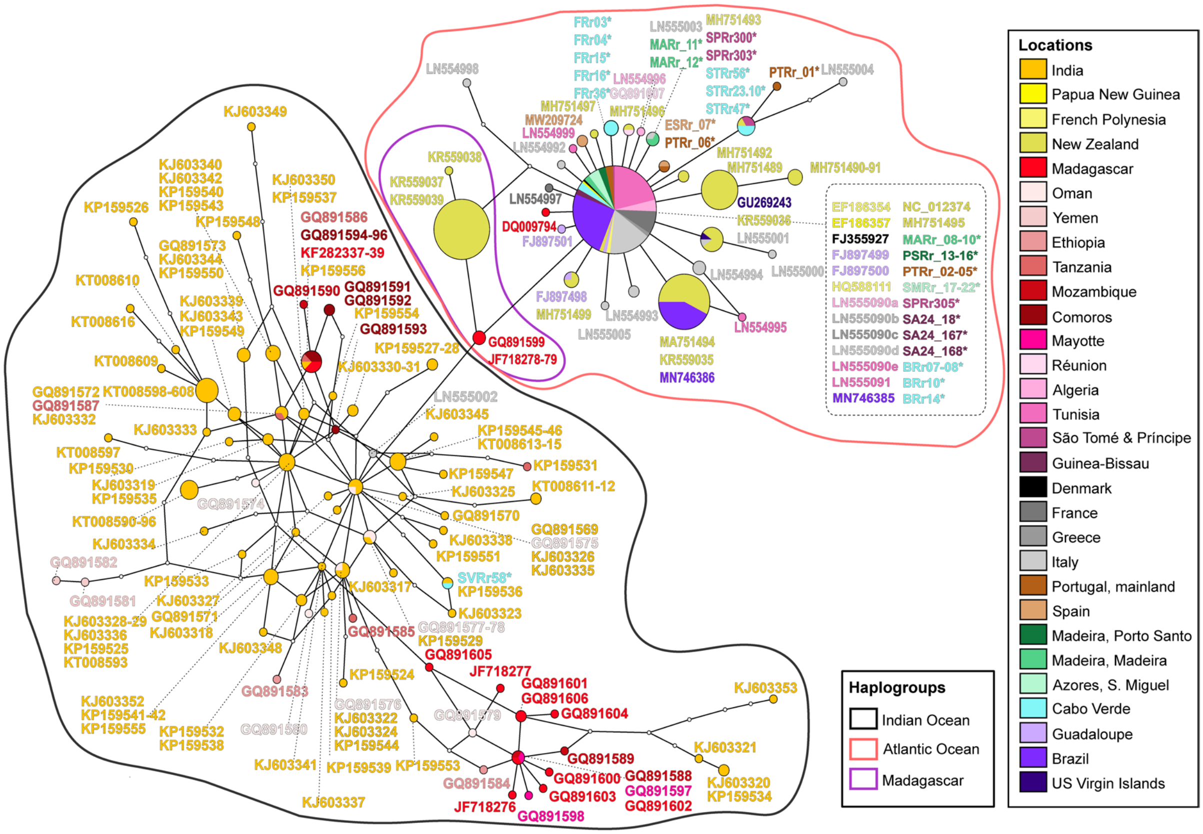

Fig. 3 Haplotype network for D-loop mitochondrial region (273 base pairs) of *R. rattus*. The lines represent mutational steps, the coloured circles represent haplotypes, and the open dots represent missing or unsampled haplotypes. The size of the circle is proportional to the number of individuals within the haplotype, and different colours of the haplotypes and the sample codes correspond to different locations indicated on the list on the right side. The haplotypes are divided in two haplogroups indicated with coloured lines. The codes with asterisks (*) represent the new samples from this study

of different haplotypes than the Atlantic Ocean haplogroup per country population and in total. In the Indian Ocean haplogroup, it was observed that a sample from São Vicente (Cabo Verde), shared the same haplotype with a sample from India. Madagascar haplotype connected the two haplogroups, as it was connected to an Indian haplotype by one mutation and to a frequent haplotype comprising 27 sequences from Papua New Guinea, French Polynesia, New Zealand, Algeria, Tunisia, Denmark, France, Greece, Italy, Guadeloupe, Brazil, Madeira, Porto Santo Island, Azores, São Tomé and Príncipe, mainland Portugal, and Guinea-Bissau from the Atlantic Ocean haplogroup. Evidence of genetic variation is indicated by the presence of a distinct haplotype shared by Portuguese and Spanish individuals, and another of Madeira Island shared with Italy. The Fogo Island in Cabo Verde exhibits a unique haplotype, and there is evidence of genetic similarity between New Zealand, São Tomé and Príncipe, and Santiago Island in Cabo Verde. A Portuguese unique haplotype is also present, suggesting further genetic variation after the introduction to Europe.

Diversity analysis

The genetic diversity (haplotypic diversity and nucleotide diversity) of all sequences was high (Hd = 0.875, π = 0.011). The Indian Ocean haplogroup presented the highest values (Hd = 0.975, π = 0.014), indicating an elevated proportion of unique haplotypes and a considerable number of nucleotide differences within the group. In contrast, the Atlantic Ocean group exhibited lower values than the latter (Hd = 0.761, π = 0.005). The levels of diversity of the samples of Macaronesia were the lowest (Hd = 0.405, π = 0.002).

Discussion

In this study, the colonisation history of *R. rattus* in Macaronesia provided a historical perspective on European navigations. It was hypothesised that over 500 years ago, the presence of boats along the coast of the Atlantic and Indian oceans for the purpose of replenishing supplies and human colonisation may have facilitated the dispersal of the study species. This is based on the premise that the Atlantic Islands in question, excluding the Canary Islands, were uninhabited by humans and other rodents at the time (Whittaker and Fernández-Palacios 2007; Borges et al. 2008; Borges 2010; Masseti 2010). The archipelago of the Canary Islands is distinguished from other Macaronesia islands in that it was first colonised by humans and rats before Renaissance. This process was particularly evident on the islands of Lanzarote and Fuerteventura, which are geographically closest to the African continent (Gaspar and Vallejo 1992). As demonstrated in the study by Rando et al. (2012), the presence of fossils of *R. rattus* on the islands has been dated between 580 to 980 AD, proving a pre-European occupation. The islands later experienced another reintroduction of species with the Portuguese and Spanish occupation in the fifteenth century (López et al. 2013).

The colonisation patterns exhibited by *R. rattus* in the other Macaronesia archipelagos demonstrated diversity within the populations. Evidence suggested the presence of two distinct haplogroups. Analysis of the phylogenetic tree indicated that the sample from Madagascar reveals a link between the Indian Ocean and the Atlantic Ocean haplogroups, suggesting this island acted as a stepping-stone in the colonisation of the species. This finding aligns with the hypothesis proposed by Russell et al. (2011), which hypothesised Madagascar as a satellite colony. As the island shows a high diversity and different haplotypes, this may be an indication of an old colonization. In fact, Madagascar played a very significant role as a trade hub during the navigation era (Pollini 2018; Tollenaere et al. 2010).

The Indian Ocean haplogroup exhibited a high degree of genetic diversity both within and between populations. It is evident that the haplotypes exhibited a high degree of interconnectedness, suggesting a history of multiple introductions into the populations and gene flow. This phenomenon is indicative of the origin of the species and a larger ancestral population as supported by previous studies (Baig et al. 2019; Gregorius 1987). In contradistinction to the other samples from Macaronesia, the pattern of colonisation exhibited by São Vicente Island in Cabo Verde is distinct. This is the first occasion on which a direct connection with the indigenous populations of India has been observed in the region, rather than with Portuguese rats as historically expected, as it were the Portuguese who discovered the uninhabited islands around 1460 (Barcellos, 1899). As historical records demonstrate, Portugal established colonies in India, in the late fifteenth century. The expeditions were led by Vasco da Gama with the help of Ahmad Ibn Majid. Portugal established connections with several coastal regions in India, such as Calicut, Goa, Daman and Diu, driven by the imperatives of maritime expansion and controlling commercial trade routes mainly for spices and tea (Tripati and Godfrey 2007; Cunliffe 2025). Portugal held a monopoly on the maritime region for at least 100 years until other European nationalities arrived (Tripati and Godfrey 2007). Following Varudkar and Ramakrishnan (2015), the Indian sample which shared the same haplotype with S. Vicente Island (Cabo Verde), was collect approximately 60 km NE from Cannanore, a port city in domain of Portugal between 1505 and 1663 (Barcellos, 1899). It has been established that this specific haplotype was connected to other haplotypes that exhibit a single mutation of difference. This mutation has been identified in a region approximately 300 km south of the Western Ghats, where *R. rattus* is native. This shared Cabo Verdean haplotype with India, suggests that an alternative lineage was introduced into those islands due to their strategic position. In fact, Vasco da Gama, in his famous first voyage to India, made a halt in Santiago, a strategic location for navigating the treacherous waters towards the Indian subcontinent (Barcellos, 1899). In a similar manner, Afonso de Albuquerque, on his return journey from India in 1512, chose Cabo Verde as a rest stop (Barcellos, 1899). This island was also visited by Nunes da Cunha, the Governor of India, who, having departed Lisbon in 1528, made of Cabo Verde his temporary residence (Barcellos, 1899). Furthermore, Cabo Verde and India have historically enjoyed significant connections (Barcellos, 1899). The two nations were frequently under the command of the same captain or family. For example, João Corrêa de Sousa, the captain of Calecut, got married in India. His son subsequently assumed the role of captain in Cabo Verde (Barcellos, 1899).

With three mutational steps of difference from the samples of São Vicente and one from an Indian sample in the Indian Ocean haplogroup there is a haplotype from Italy. In the Atlantic Ocean haplogroup there is another haplotype with two mutational steps from Santiago Island samples, there are two singletons from Italy. Those are, again, probably connected to European navigations to India. Antonio da Noli, an Italian navigator, was famous for exploring the seas. Together with Diogo Gomes, he discovered the islands of Santiago in Cabo Verde, pursuant to the demise of his descendant, D. Branca de Aguiar, the right of possession and control of the island (Barcellos, 1899; Dall'Angola 1990). At the time, Italian ports served also as stopping points of trips between Europe, Africa and India. Furthermore, Italy used to trade with India as well (Dall'Angola 1990; Gupta et al. 2001).

The Atlantic Ocean haplogroup presented a star-shaped phylogeny indicating a founder effect, as well as bottleneck events (Austerlitz et al. 1997; Du et al. 2021). Furthermore, it suggests that there was a recent colonisation and population expansion (Colangelo et al. 2015). Most of the samples analysed in this study (supplementary Table S1) were found to belong to the Atlantic Ocean haplogroup. The samples from the Madeira Archipelago, the Azores, São Tomé and Príncipe, and Brava Island (Cabo Verde) were found to have the same haplotype as those from mainland Portugal. Also, it is possible to see some similarities between mainland and island populations, particularly associated with samples from Portugal and coastal Africa, such as Guinea-Bissau. This finding suggests again the possibility of a colonisation event from the Portuguese mainland and the Mediterranean region population due to European navigations (Colangelo et al. 2015; Russell et al. 2019). The hypothesis was also advanced that the expected patterns of origin of the Atlantic Islands were related to populations from Europe (Portugal) and Africa (Guinea-Bissau), due to the existence of extensive trade relations across these regions (Barcellos, 1899).

During the fifteenth century, Portugal travelled across the oceans and reached the Azores, Madeira, Cabo Verde, Guinea-Bissau, and São Tomé. The Portuguese then began the process of colonising these areas and exploiting their natural resources. Agriculture was introduced to the islands, particularly in the Azores, Madeira and Cabo Verde, and they were established as trading points (Barcellos, 1899; Rodrigues et al. 2015; Vieira 2015). The haplotype represented by samples from Madeira and Italy suggests that voyages from the Mediterranean to the Atlantic Ocean in search of trade opportunities in coastal Africa likely introduced the black rat to that archipelago as well (Colangelo et al. 2015). Dall'Angola (1990) also indicates that Antonio da Noli made stops at Madeira Archipelago to seek shelter from storms in the region.

This pattern was also evident in the Mediterranean populations and in the Canary Islands. A star-shaped phylogeny was observed in samples from the Mediterranean Basin, the Antilles, the Canary Islands and West Africa in the studies of Colangelo et al. (2015), Aplin et al. (2011) and by López et al. (2013), using the D-loop region and the cyt *b* gene. Samples from Europe, the Americas, and Oceania shared the same haplotype, indicating that the same lineage of *R. rattus* colonised Europe, the Americas, Oceania, and West Africa aided by human navigations (Baig et al. 2019). A similar pattern was also seen with different vertebrates, such as with the introduction of the tropical house gecko *Hemidactylus mabouia*, and the Moorish gecko *Tarentola mauritanica*, and associated with European trade routes (Pinho et al. 2023; Rato et al. 2023).

Samples from Fogo and Santiago islands in Cabo Verde showed mutations that were specific to each island. These mutations derived from a central haplotype and only differed by one mutational step in each case. The haplotype from Fogo Island represented a singleton, indicating possible in situ diversification of this population. The haplotype detected in Santiago was shared with samples from São Tomé and Príncipe, as well as with those from New Zealand. This supported the hypothesis of Russell et al. (2019) that European navigators carried the species across the oceans, probably when coming from East to West. However, this pattern differed from the others mentioned because connected to this haplotype there is a singleton from Portugal, likely indicating a posterior introduction to the mainland from the Atlantic Islands. It was also different from other terrestrial vertebrates introduced in Cabo Verde, which presented the same mutation as Guinea-Bissau samples, as the case of the African common toad *Sclerophrys regularis* and the green monkey *Chlorocebus sabaeus* (Vasconcelos et al. 2010b; Almeida et al. 2024). Finally, in this study, the Latin American population showed similarities with the Macaronesian population as well. Similar patterns of colonisation from southern Europe towards Latin America have been observed in *R. rattus* and *M. musculus* in previous studies (Aplin et al. 2011; Gatto-Almeida et al. 2020; Gabriel et al. 2024). In this study, it was possible to identify sequences from Brazil (Gatto-Almeida et al. 2020) in the central haplotype of Atlantic Ocean group, as well as a haplotype that was shared with New Zealand (Robins et al. 2016; Russell et al. 2019). This can be explained because during the era of European navigations, the Macaronesia region was a strategic stopover on routes to Brazil (Barcellos, 1899).

This study yielded valuable insights into the origin and colonisation patterns of *R. rattus* in Macaronesia, with a focus on its association with human navigation. Notably, this study used opportunistic sampling in a poorly sampled area for the first time. However, the intentional collection of samples from all the islands in these regions would provide more conclusive evidence as to how the species arrived in the archipelagos. Some new haplotypes might be discover, especially if the species is found in other unsampled islands. As some were colonised in different years, they may have a different link with either close islands from these Macaronesian or other Atlantic archipelagos, with European or African sources and provide a better idea of the human history of this region. Consequently, further research is required to investigate and monitor the presence of *R. rattus* within the archipelagos and to achieve a more profound comprehension of the impact exerted. There is already evidence of the negative ecological and economic impact of *M. musculus* in Cabo Verde (Pinho et al. 2022). A further study has indicated that *R. rattus* has had the greatest impact on the fauna and flora of the Canary Islands (Traveset et al. 2009). Morphological analyses are also required to ascertain whether there are any morphological adaptations of the species to the archipelagos, as previously suggested for the black rat introduced to Pacific Ocean islands (Pergams et al. 2015). The maternally inherited mitochondrial marker furnished one segment of the data necessary to trace the colonisation of the black rat (Tollenaere et al. 2010). Nevertheless, the incorporation of nuclear markers would furnish additional biparental information concerning the number of introductions on the islands.

Finally, it is imperative to devise a management plan with the objective of eradicating this invasive species from the islands. It is thus recommended to include regular surveys to detect the species in the conservation action plans of all the protected areas of this region, especially in those where these surveys were never conducted and have higher conservation importance, such as in the integral reserves of the Cabo Verde Islands. The genetic material collected in this study can be used for conservation purposes. If eradication occurs on the islands, there will be genetic material to monitor new reintroductions and provide clues to the sources of introduction, especially if recovered haplotypes are common in specific locations. In a study by Olivera et al. (2010), the *M. musculus* was successfully eradicated from Selvagens Islands. This was achieved through the use of baits and traps, followed by a significant period of monitoring to ensure the complete eradication of the species. It is therefore theoretically possible to eradicate the black rats in the Macaronesia Islands which are small and uninhabited, such as on Rombo's islets in Cabo Verde, if their presence is confirmed.

Acknowledgements We thank to the following individuals for their invaluable contributions to the collection of samples in Cabo Verde: the farm owners Sr. Mundinho and Nadi Delgado, Albertino Santos (aka General), Jorge Tavares (INIDA), Cátio de Pina, Yannick Gomes, and Herculano Dinis (Projecto Vitó), and Evandro Lopes (UTA). We are also thanking to João Soares and Filipa Palmeirim for providing samples from Guinea-Bissau, and to Vanessa Mata, Amalia de la Torre, and Daniel Velarde Garcéz for provision of samples from São Tomé. We thank Ana Cerveira, Rita Monarca, and Joaquim Tapisso for their support in collecting samples from Portugal. Finally, we would like to thank Dr. David Gonçalves, Dra. Fernanda Almeida-Gatto, the editor-in-chief, Dr. Mariano Rodriguez-Cabal, and three anonymous reviewers for the suggestions to improve this work.

Author contributions Raquel Vasconcelos (RV) and Sofia Gabriel (SG) contributed to the study conception and design. Material preparation and data collection were performed by RV, SG, Lara Almeida (LA). Data analyses were performed by Maryane Wielewski (MW) under the supervision of RV. The first draft of the manuscript was written by MW and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Funding Open access funding provided by FCT|FCCN (b-on). This research was funded by “Gabinete de Ensino Superior, Ciência e Tecnologia do Ministério da Educação, Governo de Cabo Verde” (to RV) and partially by the project NORTE-01–0145-FEDER-000046, supported by Norte Portugal Regional Operational Programme (NORTE2020), under the Portugal 2020 Partnership Agreement, through the European Regional Development Fund (ERDF). This research was also funded by Portuguese funds through the ‘Fundação para a Ciência e a Tecnologia (FCT) BigFit project EXPL/BIA-EVL/0470/2021 and contracts under the ‘Norma Transitória’ DL57/2016/CP1440/CT0002 and DL57/2016/CP1440/CP1646/CT0003 to RV and CE3C (https://doi.org/10.54499/UID/00329/2025) to SG. LA was supported by a PhD grant (PRT/BD/154373/2022) funded by the Portuguese FCT, financed by the CEBiCNa Programme.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

References

Almeida L, Colmonero-Costeira I, da Silva MJF et al (2024) Insights into the geographical origins of the Cabo Verde Green Monkey. Genes 15:504. https://doi.org/10.3390/GENES15040504/S1

Alpert P (2006) The advantages and disadvantages of being introduced. Biol Invasions 8:1523–1534. https://doi.org/10.1007/S10530-005-5844-Z/METRICS

Aplin KP, Suzuki H, Chinen AA et al (2011) Multiple geographic origins of commensalism and complex dispersal history of black rats. PLoS ONE 6:11. https://doi.org/10.1371/journal.pone.0026357

Austerlitz F, Jung-Muller B, Godelle B, Gouyon P-H (1997) Evolution of coalescence times, genetic diversity and structure during colonization. Theor Popul Biol 51:1488164. https://doi.org/10.1006/tpbi.1997.1302

dos Babolin LS, de Almeida-Silva MJF, Potenza MR et al (2016) Zoonosis associated to *Rattus rattus* and the impacts of the public actions to control the species. Arq Inst Biol (Sao Paulo). https://doi.org/10.1590/1808-1657000832014

Baig M, Khan S, Eager H et al (2019) Phylogeography of the black rat *Rattus rattus* in India and the implications for its dispersal history in Eurasia. Biol Invasions 21:417–433. https://doi.org/10.1007/S10530-018-1830-0/METRICS

Barcellos CJ de S (1899) Subsídios para a história de Cabo Verde e Guiné: memória apresentada à Academia Real das Sciencias de Lisboa. Typographia da Academia Real das Sciencias, Lisboa

Barcellos CJ de S (1904) Cabo-Verde: Alguns apontamentos sobre as fomes em Cabo-Verde desde 1719 a 1904. Typographia da Cooperativa Militar, Lisboa

Borges P, Abreu C, Aguiar AF, et al (2008) A list of the terrestrial fungi, flora and fauna of Madeira and Selvagens archipelagos. Tipografia Peres, Amadora

Borloti I, Dinis H, Vasconcelos R (2020) Bats out of Africa: disentangling the systematic position and biogeography of bats in Cabo Verde. Genes 11:877. https://doi.org/10.3390/GENES11080877

Borroto-Páez R, Woods CA (2012) Status and Impact of Introduced Mammals in the West Indies. In: Borroto-Páez R, Woods CA, Sergile FE (eds) Terrestrial Mammals of the West Indies. Florida Museum of Natural History And Wacahoota Press, Florida, pp 241–257

Bühner J (2024) The Conquest of the Canary Islands (1402–1409). An Alternative History of International Law. Elsevier BV, Frankfurt am Main

Ceríaco LMP, Santos BS, Lima RF et al (2022) Physical Geography of the Gulf of Guinea Oceanic Islands. Biodiversity of the Gulf of Guinea Oceanic Islands: Science and Conservation. Springer International Publishing, Cham, pp 13–36

Clement M, Posada D, Crandall KA (2000) TCS: a computer program to estimate gene genealogies. Mol Ecol 9:1657–1659. https://doi.org/10.1046/j.1365-294X.2000.01020.x

Colangelo P, Abiadh A, Aloise G et al (2015) Mitochondrial phylogeography of the black rat supports a single invasion of the western Mediterranean basin. Biol Invasions 17:1859–1868. https://doi.org/10.1007/s10530-015-0842-2

Cristescu ME (2015) Genetic reconstructions of invasion history. Mol Ecol 24:2212–2225. https://doi.org/10.1111/mec.13117

Cropper TE, Hanna E (2014) An analysis of the climate of Macaronesia, 1865–2012. Int J Climatol 34:604–622. https://doi.org/10.1002/joc.3710

Cunliffe B (2025) The World Encircled 1490–1602. Driven by the Monsoons. Oxford University Press, Oxford, pp 278–311

Dall’Angola M (1990) La scoperta dell’Arcipelago di Capo Verde da parte del navigatore veneziano Alvise Da Mosto. Eres Arqueología/ Bioantropología 1:105–117

Du Z, Wu Y, Chen Z et al (2021) Global phylogeography and invasion history of the spotted lanternfly revealed by mitochondrial phylogenomics. Evol Appl 14:915–930. https://doi.org/10.1111/eva.13170

Duarte MC, Romeiras MM (2009) Cape Verde Islands. In: Gillespie R, Clague D (eds) Encyclopedia of Islands. University of California Press, USA, California, pp 143–148

Dutton J (1994) Introduced mammals in São Tomé and Príncipe: possible threats to biodiversity. Biodivers Conserv 3:927–938. https://doi.org/10.1007/BF00129667

Enscore RE, Babi N, Amatre G et al (2020) The changing triad of plague in Uganda: invasive black rats (*Rattus rattus*), indigenous small mammals, and their fleas. J Vector Ecol 45:333–355. https://doi.org/10.1111/jvec.12404

Feldhaar H, Lach L (2020) Introduced and Invasive Species. In: Starr CK (ed) Encyclopedia of Social Insects. Springer International Publishing, Cham, pp 1–10

Fernández-Palacios JM, Nascimento L, Otto R et al (2011) A reconstruction of Palaeo-Macaronesia, with particular reference to the long-term biogeography of the Atlantic island laurel forests. J Biogeogr 38:226–246. https://doi.org/10.1111/j.1365-2699.2010.02427.x

Fernández-Palacios J (2011) The islands of Macaronesia. In: Serrano ARM, Borges PAV, Boieiro M, Oromí P (eds) Terrestrial arthropods of Macaronesia. Biodiversity, ecology and evolution. Sociedade Portuguesa de Entomologia, Lisboa, pp 1–30

Florencio M, Patiño J, Nogué S et al (2021) Macaronesia as a fruitful arena for ecology, evolution, and conservation biology. Front Ecol Evol 9:718169. https://doi.org/10.3389/fevo.2021.718169

Förster DW, Gündüz İ, Nunes AC et al (2009) Molecular insights into the colonization and chromosomal diversification of Madeiran house mice. Mol Ecol 18:4477–4494. https://doi.org/10.1111/j.1365-294X.2009.04344.x

Frankham R (1997) Do island populations have less genetic variation than mainland populations? Heredity 78:311–327. https://doi.org/10.1038/hdy.1997.46

Gabriel SI, Mathias MDL, Searle JB (2013) Genetic structure of house mouse (*Mus musculus* Linnaeus 1758) populations in the Atlantic archipelago of the Azores: colonization and dispersal. Biol J Linn Soc 108:929–940. https://doi.org/10.1111/bij.12015

Gabriel SI, Mathias ML, Searle JB (2015) Of mice and the ‘Age of Discovery’: the complex history of colonization of the Azorean archipelago by the house mouse (*Mus musculus*) as revealed by mitochondrial DNA variation. J Evol Biol 28:130–145. https://doi.org/10.1111/jeb.12550

Gabriel SI, Hughes JJ, Herman JS et al (2024) House mice in the Atlantic region: genetic signals of their human transport. Genes 15:1645. https://doi.org/10.3390/genes15121645

Gaiotto JV, Abrahão CR, Dias RA, Bugoni L (2020) Diet of invasive cats, rats and tegu lizards reveals impact over threatened species in a tropical island. Perspect Ecol Conserv 18:294–303. https://doi.org/10.1016/J.PECON.2020.09.005

Gaspar AT, Vallejo EA (1992) Lessons from the Canaries: the first contact between Europeans and Canarians c. 1312–1477. Antiquity 66:120–129. https://doi.org/10.1017/S0003598X00081138

Gatto-Almeida F, Pichlmueller F, Micheletti T et al (2020) Using genetics to plan black rat (*Rattus rattus*) management in Fernando de Noronha archipelago, Brazil. Perspect Ecol Conserv 18:44–50. https://doi.org/10.1016/j.pecon.2020.01.001

Gregorius HR (1987) The relationship between the concepts of genetic diversity and differentiation. Theor Appl Genet 74:397–401. https://doi.org/10.1007/BF00274724

Gupta S, Williams D, Peacock D (2001) Dressel 2–4 amphorae and Roman trade with India: the evidence from Nevasa. South Asian Stud 17:7–18. https://doi.org/10.1080/02666030.2001.9628589

Harper GA, Bunbury N (2015) Invasive rats on tropical islands: their population biology and impacts on native species. Glob Ecol Conserv 3:607–627. https://doi.org/10.1016/j.gecco.2015.02.010

Hazevoet CJ, Masseti M (2011) On the history of the green monkey *Chlorocebus sabaeus* (L., 1766) in the Cape Verde Islands, with notes on other introduced mammals. Zool Caboverdiana 2:12–24

Islam MM, Farag E, Mahmoudi A et al (2021) Morphometric study of *Mus musculus*, *Rattus norvegicus*, and *Rattus rattus* in Qatar. Animals 11:2162. https://doi.org/10.3390/ani11082162

Kearse M, Moir R, Wilson A et al (2012) Geneious basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. Bioinformatics 28:1647–1649. https://doi.org/10.1093/BIOINFORMATICS/BTS199

Larizza A, Pesole G, Reyes A et al (2002) Lineage specificity of the evolutionary dynamics of the mtDNA D-loop region in rodents. J Mol Evol 54:145–155. https://doi.org/10.1007/s00239-001-0063-4

de Lima MF, do Silvestre MPSA, dos Santos EC et al (2022) The Presence of Mycobacterium leprae in Wild Rodents. Microorganisms 10:1114. https://doi.org/10.3390/microorganisms10061114

Lockwood J, Hoopes M, Marchetti M (2013) Invasion ecology. Wiley-Blackwell, West Sussex

López M, Foronda P, Feliu C, Hernández M (2013) Genetic characterization of black rat (*Rattus rattus*) of the Canary Islands: origin and colonization. Biol Invasions 15:2367–2372. https://doi.org/10.1007/s10530-013-0466-3

Martinez J, Melo T, Wong LJ, Pagad S (2021) Global Register of Introduced and Invasive Species - Cabo Verde. In: Invasive Species Specialist Group ISSG. https://www.gbif.org/dataset/4c575729-705c-47b8-adad-f1f2410395aa. Accessed 17 Jun 2025

Masseti M (2010) Mammals of the Macaronesian islands (the Azores, Madeira, the Canary and Cape Verde islands): redefinition of the ecological equilibrium. Mamm 74:3–34. https://doi.org/10.1515/MAMM.2010.011

Mathias ML, Ramalhinho MG, Santos-Reis M et al (1998) Mammals from the Azores islands (Portugal): an updated overview. Mamm 62:397–408. https://doi.org/10.1515/mamm.1998.62.3.397

Mendes O, Fragoso M (2023) Assessment of the record-breaking 2020 rainfall in Guinea-Bissau and impacts of associated floods. Geosciences 13:25. https://doi.org/10.3390/geosciences13020025

Mora C, Vieira G (2020) The climate of Portugal. In: Vieira G, Zêzere J, Mora C (eds) Landscapes and landforms of Portugal. Springer, Cham, pp 33–46

Myers N, Mittermeier RA, Mittermeier CG et al (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858. https://doi.org/10.1038/35002501

Nogales M, Rodriguez-Luengo J, Marrero P (2006) Ecological effects and distribution of invasive non-native mammals on the Canary Islands. Mamm Rev 36:49–65. https://doi.org/10.1111/j.1365-2907.2006.00077.x

Nyunja C, Maina J, Amimo J et al (2017) Stock structure delineation of the African Catfish (*Clarius gariepinus*) in selected populations in Kenya using mitochondrial DNA (Dloop) variability. J Aquac Res Dev 08:1000485. https://doi.org/10.4172/2155-9546.1000485

Olivera P, Menezes D, Trout R et al (2010) Successful eradication of the European rabbit (*Oryctolagus cuniculus*) and house mouse (*Mus musculus*) from the island of Selvagem Grande (Macaronesian archipelago), in the Eastern Atlantic. Integr Zool 5:70–83. https://doi.org/10.1111/j.1749-4877.2010.00186.x

Patiño J, Mateo RG, Zanatta F et al (2016) Climate threat on the Macaronesian endemic bryophyte flora. Sci Rep 6:29156. https://doi.org/10.1038/srep29156

Borges P, Costa A, Cunha R, Gabriel R, et al (eds.) (2010) A list of the terrestrial and marine biota from the Azores. Príncipia Editora, Cascais

Pergams ORW, Byrn D, Lee KLY, Jackson R (2015) Rapid morphological change in black rats (*Rattus rattus*) after an island introduction. PeerJ 3:e812. https://doi.org/10.7717/peerj.812

Pinho CJ, Lopes EP, Paupério J et al (2022) Trust your guts? The effect of gut section on diet composition and impact of *Mus musculus* on islands using metabarcoding. Ecol Evol 12:1–20. https://doi.org/10.1002/ece3.8638

Pinho CJ, Cardoso L, Rocha S, Vasconcelos R (2023) Aliens on boats? The eastern and western expansion of the African House Gecko. Genes 14:381. https://doi.org/10.3390/genes14020381

Pollini J (2018) Feeding globalization: Madagascar and the provisioning trade, 1600–1800. CJAS 52:255–256. https://doi.org/10.1080/00083968.2018.1435162

Rando JC, Alcover JA, Michaux J et al (2012) Late-holocene asynchronous extinction of endemic mammals on the eastern Canary Islands. Holocene 22:801–808. https://doi.org/10.1177/0959683611430414

Rato C, Deso G, Renet J et al (2023) Colonization routes uncovered in a widely introduced Mediterranean gecko, *Tarentola mauritanica* (Squamata: Phyllodactylidae). Sci Rep 13:16681

Robins JH, Hingston M, Matisoo-Smith E, Ross HA (2007) Identifying *Rattus* species using mitochondrial DNA. Mol Ecol Notes 7:717–729. https://doi.org/10.1111/j.1471-8286.2007.01752.x

Robins J, Miller S, Russell J et al (2016) Where did the rats of Big South Cape Island come from? N Z J Ecol 40:229–234. https://doi.org/10.20417/nzjecol.40.26

Rodrigues JD (2016) Widening the Ocean: Eastern Atlantic Islands in the Making of Early-Modern Atlantic. Comparativ 26:76–89

Rodrigues AF, Martins NO, Ribeiro N, Joaquinito A (2015) Early Atlantic navigation: pre-Portuguese presence in the Azores Islands. Archaeol Discov 03:104–113. https://doi.org/10.4236/ad.2015.33010

Ronquist F, Teslenko M, Van Der Mark P et al (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Syst Biol 61:539–542. https://doi.org/10.1093/SYSBIO/SYS029

Rozas J, Ferrer-Mata A, Sánchez-DelBarrio JC et al (2017) DnaSP 6: DNA sequence polymorphism analysis of large data sets. Mol Biol Evol 34:3299–3302. https://doi.org/10.1093/molbev/msx248

Russell JC, Gleeson DM, Le Corre M (2011) The origin of *Rattus rattus* on the Îles Éparses, Western Indian Ocean. J Biogeogr 38:1834–1836. https://doi.org/10.1111/J.1365-2699.2011.02574.X

Russell JC, Robins JH, Fewster RM (2019) Phylogeography of invasive rats in New Zealand. Front Ecol Evol 7:409196. https://doi.org/10.3389/FEVO.2019.00048/BIBTEX

Russo D, Cistrone L (2023) *Pipistrellus maderensis*. IUCN Red List of Threatened Species https://www.iucnredlist.org/species/17315/211010717. Accessed 27 September 2025

Santos AM, Cabezas MP, Tavares AI, Xavier R, Branco M (2016) tcsBU: a tool to extend TCS network layout and visualization. Bioinformatics 32:627–628. https://doi.org/10.1093/bioinformatics/btv636

Sequeira MM, Góis-Marques CA, Gouveia M et al (2023) Contribution to the flora of the Selvagens archipelago (Portugal) (I). Bot Complut 47:e88585. https://doi.org/10.5209/bocm.88585

Spatz DR, Zilliacus KM, Holmes ND et al (2017) Globally threatened vertebrates on islands with invasive species. Sci Adv 3:e1603080. https://doi.org/10.1126/sciadv.1603080

Štolhoferová I, Rudolfová V, Skalíková H et al (2024) How to explore a new environment: exploratory tactics of the black rat (*Rattus rattus*). Curr Zool 70:371–382. https://doi.org/10.1093/cz/zoae015

Tamura K, Stecher G, Kumar S (2021) MEGA11: molecular evolutionary genetics analysis version 11. Mol Biol Evol 38:3022–3027. https://doi.org/10.1093/MOLBEV/MSAB120

Tollenaere C, Brouat C, Duplantier JM et al (2010) Phylogeography of the introduced species *Rattus rattus* in the western Indian Ocean, with special emphasis on the colonization history of Madagascar. J Biogeogr 37:398–410. https://doi.org/10.1111/J.1365-2699.2009.02228.X

Traveset A, Nogales M, Alcover JA et al (2009) A review on the effects of alien rodents in the Balearic (western Mediterranean sea) and Canary islands (eastern Atlantic ocean). Biol Invasions 11:1653–1670. https://doi.org/10.1007/s10530-008-9395-y

Tripati S, Godfrey I (2007) Studies on elephant tusks and hippopotamus teeth collected from the early 17th century Portuguese shipwreck off Goa, west coast of India: evidence of maritime trade between Goa, Portugal and African countries. Curr Sci 92:332–339

Vasconcelos R, Carranza S, Harris DJ (2010a) Insight into an island radiation: the *Tarentola* geckos of the Cape Verde archipelago. J Biogeogr 37:1047–1060. https://doi.org/10.1111/j.1365-2699.2009.02254.x

Vasconcelos R, Froufe E, Brito JC et al (2010b) Phylogeography of the African common toad, *Amietophrynus regularis*, based on mitochondrial DNA sequences: inferences regarding the Cape Verde population and biogeographical patterns. Afr Zool 45:291–298. https://doi.org/10.3377/004.045.0207

Veríssimo N (2016) Descobrimento e povoamento do arquipélago da Madeira. In: Franco JE, Trindade C (eds) Grande Dicionário Enciclopédico da Madeira. Theya Editores, Lisboa, pp 18–22

Vide JM, Cantos JO (2001) Climas y tiempos de España. Alianza, Madrid

Vieira A (2015) As Ilhas e a expansão da cultura e tecnologia da cana-de-açúcar no Atlântico nos séculos XV a XIX. Lab Eng 1:1–20. https://doi.org/10.20396/lobore.v1i1.227

Whittaker RJ, Fernández-Palacios JM (2007) Island biogeography: ecology, evolution, and conservation. Oxford University Press, New York

Whittaker RJ, Fernández-Palacios JM, Matthews TJ et al (2017) Island biogeography: taking the long view of nature's laboratories. Science 357:eaam8326. https://doi.org/10.1126/science.aam8326

Wood JR, Alcover JA, Blackburn TM et al (2017) Island extinctions: processes, patterns, and potential for ecosystem restoration. Environ Conserv 44:348–358. https://doi.org/10.1017/S037689291700039X

Yiğit N, Çolak E, Sözen M, Özkurt Ö (1998) The taxonomy and karyology of *Rattus norvegicus* (Berkenhout, 1769) and *Rattus rattus* (Linnaeus, 1758) (Rodentia: Muridae) in Turkey. Turk J Zool 22:203–212

Zino F, Oliveira P, King S et al (2001) Conservation of Zino's petrel *Pterodroma madeira* and Veitch in the archipelago of Madeira. Oryx 35:128–136. https://doi.org/10.1046/j.1365-3008.2001.00165.x