

CZECH UNIVERSITY OF LIFE SCIENCES PRAGUE

Faculty of Tropical AgriSciences



**Genetic diversity of hedgehogs from genus
Atelerix and *Erinaceus* on islands.**

BACHELOR'S THESIS

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Declaration

I hereby declare that I have done this thesis entitled Genetic diversity of hedgehogs from genus *Atelerix* and *Erinaceus* on islands independently, all texts in this thesis are original, and all the sources have been quoted and acknowledged by means of complete references and according to Citation rules of the FTA.

In Prague 14.4.2023

.....

Daria Egorova

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Abstract

The main aim of this bachelor's thesis is to investigate the genetic diversity of hedgehogs from the genus *Atelerix* and *Erinaceus* on the islands, which will make it possible to apply effective management strategies to regulate, control, and reduce the impact of these invasive species on local ecosystems. Island ecosystems are vulnerable to biological invasions that can have serious consequences for native species. Within the context of this bachelor's thesis, the genetic diversity of populations of the Algerian hedgehog in Europe, the Canaries, Mallorca, Menorca, Ibiza, Formentera, Cabrera in the Balearic Islands and Malta was studied. Previous studies have shown low genetic diversity in these populations due to founder effects and maternal mtDNA inheritance. In addition, the genetic diversity of European hedgehog populations in New Zealand and on the islands of Sardinia, Elba and Pianosa has been studied and the low genetic diversity among these island populations confirmed the theory of their introduction by humans from the continents.

Key words: genetic diversity, hedgehog, impact of introduction, islands, origin.

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1. Introduction

This Bachelor's thesis is focused on the genetic diversity of hedgehogs from the genus *Atelerix* and *Erinaceus* on islands. Islands are known to have a high degree of endemism and a limited range of species. The Theory of Island Biogeography states that species diversity on islands is dependent on their size, proximity to the mainland, and isolation from other islands. Islands are also vulnerable to biological invasions, which consist of the transport, introduction, establishment and spread of non-native species into an area outside their natural range. Invasive species can cause drastic changes to the local ecosystems, and can cause the extinction of native species. Therefore, understanding and managing the genetic diversity of species on islands is important for the conservation of local biodiversity.

2. Aims of the Thesis

The main objective of this study is to assess the history of the populations and genetic diversity of hedgehogs of the genus *Atelerix* and *Erinaceus* in the islands. Other objectives are to analyse the potential impact of biological invasions on genetic diversity and to identify the main causes of genetic changes, to evaluate the theory of island biogeography and its application to populations of invasive species on islands. Further, to provide an overview of current knowledge on the causes and effects of biological invasions and the management strategies that have been proposed or implemented to prevent or mitigate the impact on islands. Finally, to summarise the results of previous studies on the genetic diversity of the Algerian hedgehog in the Canary and Balearic Islands and Malta, and the European hedgehog in New Zealand and Pianosa Island, and to identify patterns or knowledge gaps that require further investigation.

3. Literature Review

1.1. Genetic diversity on islands

Conservation of genetic diversity is now considered a key concept in Conservation Biology, as it is often thought to be essential for the overall fitness of species and their ability to adapt to environmental changes (Meffe & Carroll 1997). For example, Grant (1998) found that the number of species inhabiting the Galapagos Islands was positively correlated with the size of the islands. This was attributed to the fact that larger islands provide a greater variety of habitats and resources, which can lead to higher levels of genetic diversity (Hartl & Clark 1997). In addition, the geographical isolation of islands has been found to be an important factor in the genetic diversity of species living on them. Grant and Grant (2008) found that species on isolated islands have limited opportunities for gene flow, which can lead to reduced genetic diversity. Furthermore, the physical isolation of islands can lead to the formation of new species, which can also contribute to increased genetic diversity. Human activities can also have a significant impact on the genetic diversity of island species. For example, Losos et al. (1997) found that the introduction of the invasive lizard species *Anolis sagrei* had a negative impact on the genetic diversity of the native species *Anolis conspersus* in the Hawaiian Islands. This was attributed to the fact that invasive species can outcompete native species for resources and can also hybridise with them, leading to the loss of genetic diversity. Finally, the climate of an island can also affect the genetic diversity of species living on it. Pimm and Askins (1995) found that species living on islands with more extreme climates had lower levels of genetic diversity than those living on islands with more moderate climates. This was attributed to the fact that extreme climates can lead to higher levels of environmental stress, which can reduce the ability of species to adapt and survive, thus leading to lower levels of genetic diversity. In conclusion, the physical characteristics of islands, the geographical isolation of islands, the introduction of invasive species, and the climate of an island can all have a significant impact on the genetic diversity of species living on them. Understanding the various ways that these factors can affect genetic diversity is important for developing effective conservation measures for island species (Sax et al. 2002).

1.2. The Theory of Island Biogeography

The Theory of Island Biogeography (TIB) was first proposed by Robert MacArthur and Edward O. Wilson in 1967. The theory is based on the idea that the species richness of an island is determined by the balance between immigration of new species and extinction of existing species. The theory states that the number of species on an island will reach a steady state equilibrium, where the rate of immigration is equal to the rate of extinction. This equilibrium is determined by the distance of the island from the mainland, the size of the island, and the number of species already present on the island. – see Figure 1 (MacArthur & Wilson 1967)

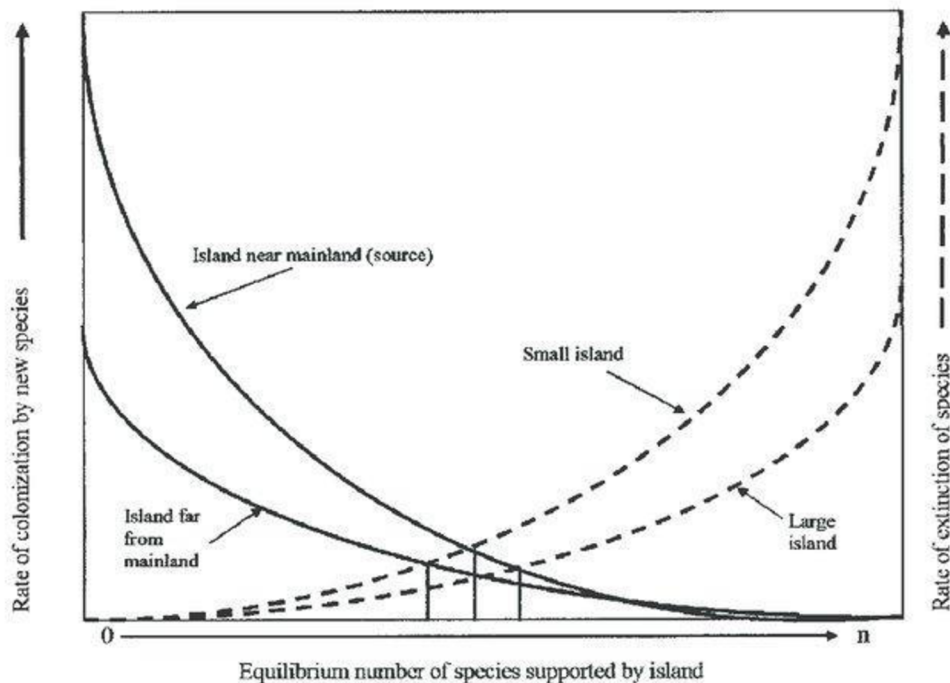


Figure 1 The graph illustrates the theory of island biogeography, which suggests that large islands situated close to a possible source of colonisers are expected to have a higher number of species at equilibrium. This is because they experience increased immigration rates and decreased extinction rates. In contrast, small and isolated islands are predicted to have the lowest number of species due to their lower rates of colonisation and higher rates of extinction. Therefore, the graph represents the relationship between island size, proximity to a source of colonisers, and the predicted number of species present on the island (MacArthur and Wilson 1967).

The original TIB was based on the idea that immigration was the most important factor in determining species richness on an island. However, subsequent research has shown that the extinction rate can be just as important as the immigration rate in determining species richness. Losos and Ricklefs (2009) proposed a revised version of the TIB, which takes into account the role of extinction in determining species richness on an island. According to the revised TIB, the species richness of an island is determined by a balance between the immigration and extinction rate, which is determined by the factors mentioned above.

The Theory of Island Biogeography (TIB) has been used to explain a variety of patterns in the distribution of species on islands, such as the pattern of species richness increasing with island size (MacArthur & Wilson 1967) and the pattern of species richness decreasing with distance from the mainland (Simberloff 1998). The TIB has also been used to explain the patterns of species richness on oceanic islands, which are typically much more species-rich than continental islands (Whittaker 1972). The TIB has been used to explain the patterns of species richness on isolated islands, as well as the patterns of species richness on islands that are connected to the mainland (Brown & Wilson 1956). The TIB has been used to explain the patterns of species richness in a variety of ecosystems, including terrestrial, freshwater, and marine ecosystems (Ricklefs 1987). Additionally, the TIB has been used to explain the patterns of species richness in different types of habitats, such as forests, grasslands, deserts, and wetlands (Ricklefs 1987). The TIB has also been used to explain the patterns of species richness in different types of communities, such as communities of plants, animals, and microorganisms (Ricklefs 1987).

1.3. The biological invasion

Biological invasions are a major global environmental issue that has become increasingly important in recent years (Pimentel et al. 2001). Biological invasions occur when a non-native species is introduced into a new environment and subsequently spreads (Simberloff 2006). These invasions can have a wide range of impacts on the environment, ranging from changes in the structure of the local ecosystem to the introduction of new diseases (Mack et al. 2000). Human activities are the primary cause of biological

invasions, including the intentional or unintentional introduction of species into new areas, the spread of species through the transport of goods and people, and the destruction of habitats that allow invasive species to thrive (Simberloff et al. 2000). Climate change is also a major factor in the spread of invasive species, as rising temperatures enable species to survive in areas that were previously too cold for them (Mack et al. 2000). Natural processes, such as the spread of species through birds and other animals, can also contribute to the spread of invasive species (Simberloff et al. 2000).

The proposed unified framework for biological invasions by Blackburn et al. (2011) provides a comprehensive overview of the processes that lead to successful invasions and the potential impacts of biological invasions. The framework outlines the various stages of the invasion process and the factors that influence the success of invasions. These stages include introduction, establishment, spread and impact. The framework also highlights the importance of understanding the environmental and ecological context in which invasions take place and the potential for management interventions to reduce the impacts of invasions. The framework provides a useful tool for researchers to better understand the dynamics of biological invasions and the potential impacts they may have on the environment – See Figure 2 (Blackburn et al. 2011).

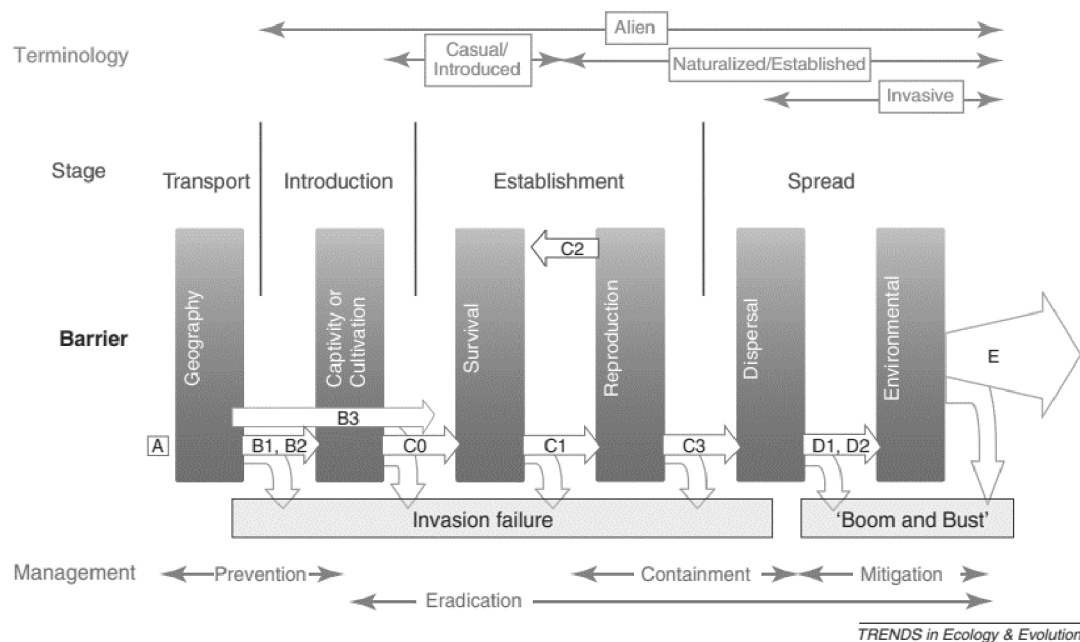


Figure 2 The graph serves to illustrate the proposed unified framework's main components, including the invasion stages, associated barriers, species categorization, and the need for different management interventions at each stage (Blackburn et al. 2011).

The consequences of biological invasions can be far-reaching and have a significant impact on the environment (Mack et al. 2000). Non-native species can compete with native species for resources, resulting in a decrease in local biodiversity (Pimentel et al. 2001). In addition, invasive species can introduce new diseases and parasites into an area, which can cause significant damage to local ecosystems (Mack et al., 2000). Invasive species can also alter the physical environment, leading to changes in water or soil chemistry (Simberloff 2006). The presence of invasive species can lead to changes in the food web, which can have a significant impact on ecosystem balance (Mack et al., 2000). Invasive species are also capable of causing economic impacts, such as the estimated \$10 billion loss due to the emerald ash borer (Mack et al. 2000).

In order to reduce the impact of biological invasions, it is important to take steps to reduce the spread of non-native species (Simberloff et al. 2000). This may include controlling the movement of commodities to prevent the spread of species as well as increasing public awareness of the risks associated with the introduction of non-native species (Simberloff et al. 2000). In addition, it is important to take steps to control and manage existing populations of invasive species as well as to restore populations of native species (Simberloff et al. 2000). Understanding the causes of biological invasions is essential for effective management and prevention strategies (Mack et al. 2000).

1.3.1. Management of invasive species on islands

Islands are particularly vulnerable to invasion species, as they are isolated and have limited resources to respond to the impacts of introduced species (McGeoch et al. 2010). Invasion species can cause significant damage to island ecosystems, reducing biodiversity, altering habitats, and reducing the availability of ecosystem services (Vilà et al. 2010). For this reason, it is important for islands to have effective management strategies in place to prevent, control, and reduce the impact of invasive species.

The first step in managing invasive species on islands is to identify the pathways of introduction, as this will inform the prevention and control strategies that are most appropriate for the island (Hulme et al. 2008). Pathways of introduction can include intentional or unintentional release, natural dispersal, and transfer of species from one island to another (McGeoch et al. 2016). Once the pathways of introduction are identified,

a risk assessment can be carried out to identify the species that are most likely to become invasive on the island (Dawson et al. 2015).

Once the pathways and species of concern have been identified, the next step is to develop a management plan. This plan should include strategies to prevent the introduction of invasive species, such as biosecurity measures, and strategies to control and reduce the impact of existing invasion species, such as eradication or population reduction (Harvey-Samuel et al. 2017). The Global Invasive Species Programme (GISP) provides a toolkit with best practice recommendations for the management of invasive species on islands (Wittenberg & Cock 2001). In addition, the Biotope Good Practice Guide provides specific recommendations for the management of invasive species in Seychelles, which can be applied to other islands (Rocamora & Henriette 2015).

1.4. Subfamily *Erinaceinae*

Subfamily *Erinaceinae* (G. Fischer 1814) is a group of small to medium-sized mammals that are part of the family *Erinaceidae* (G. Fischer 1814). This subfamily is widely distributed across Europe, Africa, and Asia and is characterised by several distinct features. Their spines are modified hairs called quills, acts as a dual-purpose defence mechanism against predators and insulation for thermoregulation in cold environments (Corbet 1988; Macdonald 2006). They have small eyes and a keen sense of smell that they use to locate their prey, which primarily consists of insects, snails, and other invertebrates (Macdonald 2006). Hedgehogs are also known to consume some small vertebrates, such as lizards and frogs (Nowak 1991). The subfamily *Erinaceinae* comprises around 17 species that are classified into five genera: *Atelerix* (Pomel 1848), *Erinaceus* (Linnaeus 1758), *Hemiechinus* (Fitzinger 1866), *Mesechinus* (Ognev 1951), and *Paraechinus* (Trouessart 1879) (Wilson & Reeder 2005).

1.4.1. Genus *Atelerix*

Genus *Atelerix* includes four species of hedgehog, which are native to Africa and the Middle East. The species of this genus are the Four-toed hedgehog (*Atelerix albiventris* Wagner 1841), the North African hedgehog (*Atelerix algirus* Lereboullet

1842), the Southern African hedgehog (*Atelerix frontalis* Smith 1831) and the Somali hedgehog (*Atelerix sclateri* Anderson 1895) (HE et al. 2012).

1.4.1.1. The Algerian hedgehog

The Algerian hedgehog, also known as *Atelerix algirus*, is an animal endemic to the northern Maghreb region which includes Tunisia, Algeria, Morocco, and Libya (Best 2018). Although it was once found in France, it is now extinct (Heim de Balsac 1936). In continental Spain, this species can be found along the Mediterranean coast, from Catalonia (Girona, Barcelona) to Valencia, Murcia, and Andalusia (Malaga, Almeria) (García-Rodríguez & Puig-Montserrat 2014). The Algerian hedgehog is also found in other regions such as the Balearic, Canary, and Maltese islands (Best 2018). The Algerian hedgehog may have been introduced into Spain, Southern France, and possibly the Maltese Islands around 1000 BC during the Phoenician's maritime expeditions (Borg 2005). This species inhabits dry and rocky habitats, such as shrublands, grasslands, and deserts (García-Rodríguez & Puig-Montserrat 2014). Unfortunately, the Algerian hedgehog is threatened by various anthropogenic factors, including road mortality, habitat loss, and illegal hunting (Sayah et al. 2009). Despite this, it has been listed as "Least Concern" on the IUCN Red List of Threatened Species (Amori et al. 2022).

The study of Algerian hedgehogs has revealed several subspecies and forms that can be differentiated based on their morphometric data and pelage coloration. Hutterer (2005) proposed a classification system that includes three subspecies within *Atelerix algirus*. The first subspecies, *A. algirus algirus* (Lereboullet, 1842), is found in North Africa and has been associated with four synonyms: *caniculus* (Thomas, 1915), *diadematus* (Dobson, 1882), *fallax* (Dobson, 1882), and *lavaudeni* (Cabrera, 1928). The second subspecies, *A. a. girbaensis* (Vesmanis, 1981), is found only on Djerba Island in Tunisia. The third subspecies, *A. a. vagans* (Thomas, 1901), inhabits various islands including Spain and Minorca, and is associated with one synonym, *krugi* (Peters, 1877). These subspecies differ in their physical characteristics and geographical distribution (Hutterer 2005).

Genetic diversity in *Atelerix algirus* was investigated by several researchers using different DNA markers. Khaldi et al. (2016) analyzed mitochondrial (Cytochrome b) and nuclear (BFIBR) genes, and reported low genetic diversity across the geographic range

of the species. Based on these results, Best (2018) suggested merging *A. a. algirus* and *A. a. vagans* into a single subspecies. However, Derouiche et al. (2016) examined a fragment of the control region and found low genetic diversity within the species in Algeria. In contrast, Velo-Antón et al. (2019) analyzed the same DNA fragment and identified three distinct genetic lineages within *A. algirus*. Lineages 1 and 2 differed by at least 22 mutations, indicating that the control region may be a useful marker for studying the species' phylogeography and evolutionary history. Recently, El-Farhati et al. (2021) identified two distantly related lineages (lineages I and II) within *A. algirus*, which were not found in previous studies. Despite showing low mitochondrial diversity across the continent, previous phylogeographic studies of North African organisms have revealed a marked east-west divergence and identified two common disjunction areas. These disjunction areas were located around the Algeria-Morocco border and in Kabylia (central Algeria) (Nicolas et al. 2015; Beddek et al. 2018). Interestingly, the two haplogroups co-occur in Atlas and Rif mountains (El-Farhati et al. 2021). Authors proposed two hypotheses to explain this pattern: (i) vicariance of an eastern and a western haplogroup followed by secondary expansion, or (ii) retention of deep mitochondrial DNA diversity in Morocco followed by loss of diversity during eastward expansion of the species out of Morocco. Both scenarios imply a population expansion of haplogroup 2, for which there is evidence only with Fu's F_s test. Climatic niche modelling results support the first hypothesis, showing that during the Last Glacial Maximum, there were several disconnected areas of high climatic suitability for *A. algirus*: one in South-West Morocco, one at the coastal Moroccan-Algerian border, and one in Tunisia-coastal Libya (El-Farhati et al. 2021).

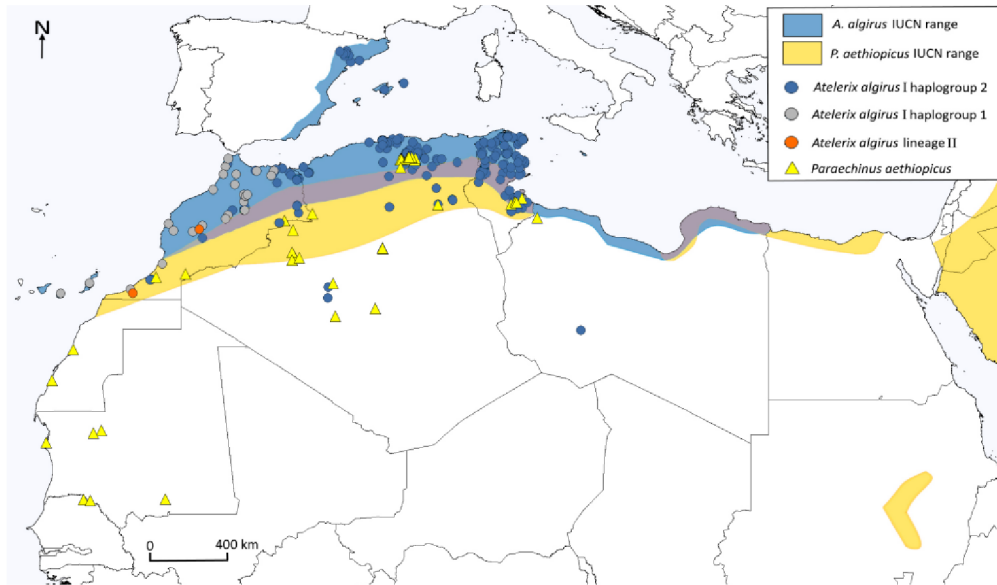


Figure 3 The figure depicts the geographical distribution of hedgehog DNA samples utilised in a particular study alongside the distribution of the analysed taxa based on the International Union for Conservation of Nature (IUCN) 2015 classification (El-Farhati et al. 2021).

1.4.1.1.1 *Atelerix algirus* in the Canary Islands

Atelerix algirus, the Algerian hedgehog, is an introduced species in the Canary Islands with a hundred-eight km distance from the continent and is currently present on the islands of Fuerteventura, Lanzarote, Gran Canaria and Tenerife. (Medina 2016). It is believed that a pair of hedgehogs brought from Morocco to Fuerteventura in 1892 led to the introduction of the species to the Canary Islands (Hutterer 1983). All four hedgehog individuals from the Canary Islands share the same mtDNA haplotype, which suggests that the hedgehog pair was introduced from Morocco to Fuerteventura and then spread to other islands (Khaldi et al. 2016). Founder effects and maternal inheritance of mtDNA could be the reason behind the low genetic diversity observed for the Cytb gene in the Canary Islands (Khaldi et al. 2016). Subspecies recognition may not be necessary as there is no genetic discontinuity between different populations (Khaldi et al. 2016). Human activity may be responsible for the introduction of *A. algirus* to Europe and the Canary Islands as this species is kept as a domestic animal in some areas and used for medicinal and witchcraft purposes in Morocco (Farhati et al. 2021). Ecological niche modelling analyses suggest that favourable climatic conditions have existed in most of the southern and eastern lowland areas of the Iberian Peninsula over the last 6000 years to support the spatial expansion of the Algerian hedgehog following its arrival in Europe (Farhati et al.

2021). Despite these favourable conditions, the current distribution of the Algerian hedgehog in Spain is smaller than expected on the basis of climate niche modelling, probably due to interactions between species such as competition, predation, parasitism, and mutualism, which may play an important role in determining the distribution of the species (Farhati et al. 2021). The European hedgehog, *Erinaceus europaeus*, which was already well distributed in Spain before the introduction of the Algerian hedgehog, may have contributed to its limited distribution in Spain due to competition between the two species (Pearman et al. 2008; Sinclair et al. 2010; Giannini et al. 2013). Hedgehogs could affect endemic invertebrates such as *Coleoptera* and some vertebrate groups such as ground-nesting birds and endemic reptiles (Nogales et al. 2006; Domínguez & Bacallado 1944). They can also disrupt ecological processes such as mutualism between animals and plants, as observed in the Canary Islands during the dispersal of seeds of the endemic fleshy fruit fly species *Plocama pendula* (Barquín et al. 1986). Furthermore, hedgehogs can transmit parasites of importance to human health (Khaldi et al. 2012).

1.4.1.1.2 *Atelerix algirus* in Balearic Islands

The species of interest can be found in several Balearic Islands, namely Mallorca, Minorca, Ibiza, Formentera, and Cabrera in the Balearic Islands (Alcover et al. 1993; Johnson et al. 2012). Recently, genetic evidence from Farhati et al. (2021) indicates that the Algerian hedgehog (*Atelerix algirus*) has colonized the Balearic Islands, likely due to human intervention. Evidence of the Algerian hedgehog's presence in Minorca was discovered by Morales and Rofes (2008), who attribute its introduction to Muslims from the Almohad Empire. Radiocarbon dating from the Balearic Islands by Valenzuela et al. (2022) confirms that the Algerian hedgehog was deliberately introduced, occurring simultaneously in Mallorca and Menorca, and slightly later in Eivissa. Valenzuela et al. (2022) suggest that the introduction of mammals to islands often leads to evolutionary changes in body size as species adapt to new ecological conditions. The new ¹⁴C ages presented in the study could be used to investigate the rate at which evolutionary body size changes occur in islanders. The introduction of Algerian hedgehogs to the Balearic Islands was part of a broader phenomenon of animal translocation in the Almohad period that included dromedaries and hyenas (Delort 1978; Morales 1994; Delibes et al. 2019). The current fauna of terrestrial non-aquatic mammals in the Balearic Islands was introduced by human intervention, intentional or unintentional (MacKinnon 2014).

However, the Algerian hedgehog's historical distribution is strongly associated with intentional human movement, given the sociocultural values and human use documented for the species (Valenzuela et al. 2022).

1.4.1.1.3 *Atelerix algirus* on Malta

Historical records indicate that the Algerian hedgehog has been present in Malta and the neighbouring island of Gozo since the time of the Phoenicians, approximately 1000 years before the common era (Borg, 2005). This species was likely introduced to the islands for pest control purposes, as it was commonly used as a weapon against various agricultural pests at the time (Borg, 2005). In fact, it has been suggested that the Algerian hedgehog may have been introduced specifically to combat cockroach infestations on the island of Comino, which led to an overpopulation of these insects in the 19th century (Borg, 2005).

1.4.2. Genus *Erinaceus*

The members of Genus *Erinaceus* are widely distributed across a range of habitats in Eurasia. The species of this genus are the Amur hedgehog (*Erinaceus amurensis*, Schrenk 1858) found in northern China and the Russian Far East, the southern white-breasted hedgehog (*Erinaceus concolor*, Martin 1838) in the Middle East, Central Asia and South-Western China, the European hedgehog (*Erinaceus europaeus*, Linnaeus 1758) throughout Europe, and the northern white-breasted hedgehog (*Erinaceus roumanicus*, Barrett-Hamilton 1900) in Eastern Europe and Western Russia (HE et al. 2012).

1.4.2.1. *Erinaceus europaeus*

The European hedgehog (*Erinaceus europaeus*) is a nocturnal predator species that inhabits various regions across the British Isles, New Zealand, and continental Europe, ranging from Iberia and Italy to Scandinavia (Reeve 1994; Morris 2014). It is essential to maintain gene flow across fragmented landscapes to avoid the negative effects of genetic drift, reduced genetic diversity, and inbreeding depression (Lacy 1997; Keller & Waller 2002). The application of conservation genetics, including genetic rescues, is beneficial in assessing, preserving, and managing populations that are genetically susceptible (Ralls et al. 2018). Researchers are particularly interested in the levels of

heterozygosity and inbreeding, with some studies suggesting that promiscuity and superfecundation in hedgehogs may decrease inbreeding (Moran et al. 2009). Although the species is classified as a Least Concern on the IUCN Red List of Threatened Species, conservation measures are still necessary to protect hedgehogs from habitat loss, road mortality, and other anthropogenic threats (Amori 2016).

Bolfiková et al. (2013) reported negative effects of hedgehog introductions outside their native range, including the decline of endemic invertebrates, small reptiles, and ground-nesting birds due to predation. This invader's increase in population density, despite reduced genetic variability compared to the mainland, can have serious consequences for the survival of native species (Jackson 2001; Bolfikova et al. 2013, 2017). Intensive studies in Scotland (Jackson 2001; Travis and Park 2004; Bremner and Park 2007) and New Zealand (Bolfiková et al. 2013, 2017; Jones et al. 2013) support these findings. Jackson (2001) conducted experiments at two sites in Western Isles, Scotland, to measure hedgehog impact on waders (Charadrii). The removal of hedgehogs resulted in a 2-4-fold increase in nest success of waders compared to control areas with high hedgehog densities (Jackson 2006).

1.4.2.1.1 *Erinaceus europaeus* in New Zealand

New Zealand has an interesting history of animal introduction, and the *Erinaceus europaeus* is no exception. Historical evidence indicates that European hedgehog was initially introduced to New Zealand's South Island in the 19th century, and they were not present on the North Island before the 20th century. It was believed that they were transported from the South Island to the North Island (Thomson 1922; Wodzicki 1950; Brockie 1975; Long 2003; King 2005). However, a recent study by Bolfiková et al. (2013) using molecular data has challenged this view. Authors utilised a control stretch of mitochondrial DNA and 11 microsatellite loci to compare populations from different regions of New Zealand with individuals from the UK. The study found that the hedgehog population genetically similar to the British one was located near Palmerston North on the North Island. Bayesian cluster analysis revealed that the genotypes were structured into four clusters, with one cluster containing hedgehogs from the UK and the three others consisting of individuals from New Zealand. (See Fig 5). However, 77% individuals showed admixed origin, suggesting that the establishment phase of the western hedgehog took place on the North Island, from where the hedgehog subsequently spread to the rest

of New Zealand and recolonized the South Island. Furthermore, hedgehogs were deliberately transported between the islands by people, and the study revealed the possibility of the South Island hedgehog lineage becoming extinct and being replaced by individuals dispersing from the north (Brockie, 1975; Bolfiková et al. 2013). The molecular data indicated that the hedgehog population inhabiting New Zealand is purely British (Bolfiková et al. 2013). Additional research by Pipek et al. (2020) identified several previously unknown overseas shipments of hedgehogs to the North Island. They found that hedgehogs also appeared as pets in areas where no previous shipment was noted, such as in Auckland and Wellington in the 1880s. The data in the newspapers supported some but not all of the findings from molecular data, demonstrating that historical analysis can provide new insights into the history of animal introductions and spread in New Zealand. The study by Pipek et al. (2020) suggests that newspapers can be valuable in capturing early occurrences of species that may have been missed by previous research. Improved historical records can also assist in clarifying the history of animal introductions and spread in New Zealand (Jones & Sanders 2005).

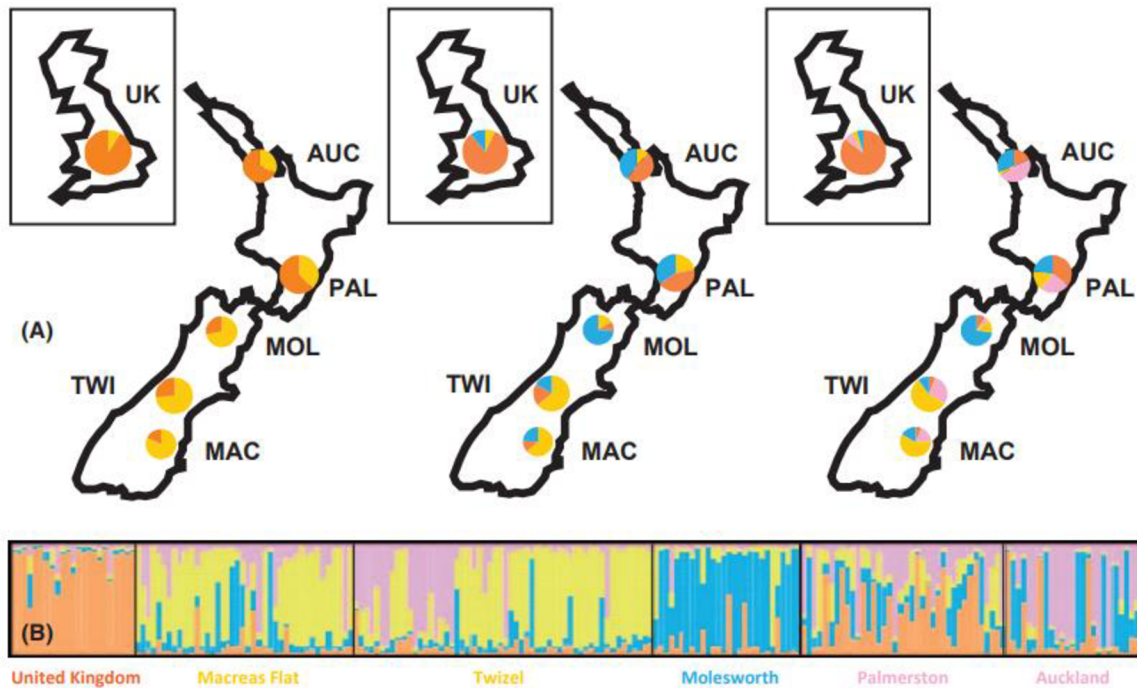


Figure 4 The study used the software STRUCTURE for $K = 2, 3,$ and 4 to infer the population structure of New Zealand hedgehogs, with the distribution of specific clusters in various locations, including the United Kingdom, Auckland, Palmerston North, Molesworth, Twizel, and Macreas Flat, represented in panel A, while panel B shows the outcome of the best-supported sorting, with each vertical bar representing an individual and divided into segments based on the probability of assignment to each cluster for $K = 4$. (Bolfiková et al. 2013).

1.4.2.1.2 *Erinaceus europaeus* in Pianosa Island (Tuscan Archipelago)

The presence of the European hedgehog on Pianosa Island in the Tuscan Archipelago is interesting in terms of invasion. The study of the genetic diversity of *E. europaeus* on this island provides a valuable opportunity to trace the process of human-mediated invasion and understand the implications of such invasions for the resident species. Although the species is not native to Pianosa Island, it has been observed on Elba Island, the closest island to Pianosa, for over a century (Damiani 1923; Vesmanis & Hutterer 1980). During the last glacial period, when Elba Island was more extensive and connected to the mainland, hedgehogs had the opportunity to colonize it naturally (Bossio et al. 2000). However, due to the lack of a permanent human population on Elba Island and high staff turnover rates resulting from the island's use as a state prison until 2011,

detailed information about the timing and circumstances of the hedgehog's introduction was difficult to obtain (Iannucci et al. 2018). Archaeological evidence suggests that hedgehogs were present on Pianosa Island during the Neolithic era, along with other species that are no longer found, such as the red fox (*Vulpes vulpes*), water vole (*Arvicola terrestris*), and imported *Ovicaprinae* (Ducci et al. 2000). The cause and timing of their disappearance are unknown.

It is hypothesized that the current hedgehog population on Pianosa Island originated from individuals recently moved by humans from Elba to Pianosa, either unintentionally or for unknown purposes (Amori et al. 2008). A recent genetic study compared the genetic diversity of European hedgehogs from four different regions of Italy, including the mainland, Sardinia, and the islands of Elba and Pianosa (Iannucci et al. 2018). The genetic data indicated a high similarity between the Pianosa and Elba populations, supporting the hypothesis that the Pianosa hedgehog originated from a pool of individuals translocated by humans from Elba to Pianosa (See Fig.6). A unique haplotype in the Sardinian population suggests a genetic relationship with other unexplored Mediterranean populations, possibly from Sicily, France, or Iberia (Amori et al. 2008; Iannucci et al. 2018). However, human-induced translocation should be considered a crucial factor in characterizing the Sardinian fauna (Scandura et al. 2010).

Eradication plans supported by genetic analysis have been successful in Italian islands, as evidenced by the successful removal of the black rat from the Tavolara archipelago, which increased the reproductive success of dive birds on the islands (Sposimo et al. 2012; Iannucci et al. 2018). However, plans to eliminate species that are attractive to humans, such as hedgehogs, often encounter ethical disagreements that can lead to project failure (Iannucci et al. 2018).

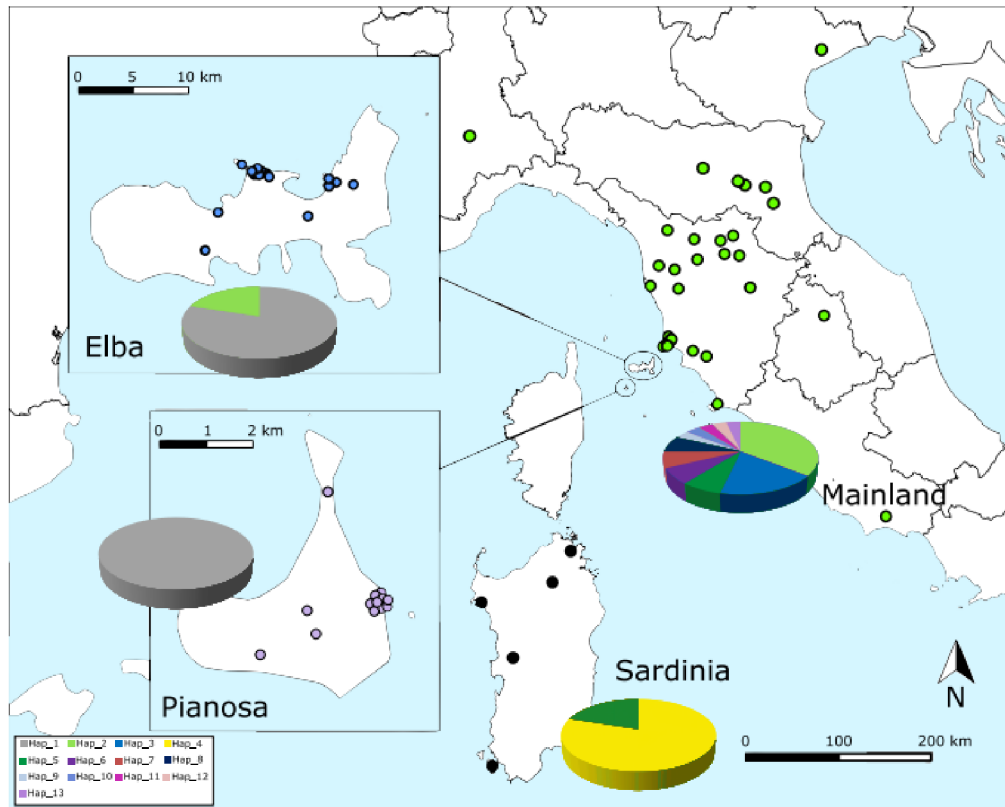


Figure 5 The figure displays the geographic distribution of the sampling localities, namely Pianosa, Elba, Mainland, and Sardinia, and the frequency pies of the 13 haplotypes representing the four population groups (Iannucci et al. 2018).

2. Discussion

The theory of island biogeography (MacArthur & Wilson 1967) can be applied to the genetic diversity of hedgehog populations on islands. The genetic diversity of the *Erinaceus europaeus* population in New Zealand was influenced by the introduction of this species to the island, which isolated it from other populations of the same species (Bolfiková et al. 2013). Pianosa Island, home to the European hedgehog, is also isolated, potentially limiting gene flow and reducing genetic diversity (Iannucci et al. 2018). The forty-nine km isolation of Pianosa Island from the mainland may also increase the risk of local adaptation to the Pianosa environment and the evolution of unique traits in the Pianosa hedgehog population (Iannucci et al. 2018). The introduction of *Atelerix algirus* to the Canary Islands as a result of human activity can be seen as a process of colonization of the new "island" by the "founder" population (Khaldi et al. 2016). The distance of one hundred and eight kilometres between the Canary Islands and the continent, combined with the absence of natural predators and competitors, creates a unique set of environmental conditions that can affect the genetic diversity of the introduced species (Nogales et al. 2006). Previous studies have shown that populations of *A. algirus* show a potential cryptic differentiation within the taxon *Atelerix*, with three distinct genetic lineages and two distantly related lineages (Velo-Antón et al. 2019). However, there is no genetic gap between populations from Algeria, Morocco, Tunisia, Spain, the Balearic and Canary Islands, indicating that other factors, such as founder effect, historical population dynamics and gene flow between populations, may play a greater role in determining genetic diversity. (Khaldi et al. 2016).

The introduction of Algerian Hedgehog to the Canary Islands has been found to have negative effects on endemic invertebrates and vertebrates, including ground-nesting birds and endemic reptiles, and can disrupt ecological processes such as mutualism between animals and plants reptiles (Nogales et al. 2006; Domínguez & Bacallado 1944). Additionally, hedgehogs can transmit parasites of importance to human health (Khaldi et al. 2012). Negative effects of European hedgehog introduction outside their native range have been observed in several areas worldwide, including a decline in endemic invertebrate species, small reptiles, and ground-nesting birds due to predation (Bolfiková et al. 2013). Intensive studies have been conducted in Scotland and New Zealand to

measure hedgehog impacts on native species, and the removal of hedgehogs has been found to increase the nest success of waders by 2–4 times (Jackson 2001; 2006; Travis & Park 2004; Bremner & Park 2007; Bolfíková et al. 2013). However, plans to eliminate invasive species often encounter ethical disagreements that can lead to project failure (Iannucci et al. 2018).

To effectively manage invasive species on islands, it is crucial to first identify the pathways of introduction, which can include intentional or unintentional release, natural dispersal, and transfer of species from one island to another (McGeoch et al., 2016; Hulme et al., 2008). Once the pathways of introduction have been identified, a risk assessment can be conducted to determine which species are most likely to become invasive on the island (Dawson et al., 2015). With this information, a management plan can be developed that includes both prevention strategies, such as biosecurity measures, and control measures, such as eradication or population reduction (Harvey-Samuel et al., 2017). The Global Invasive Species Programme (GISP) offers a toolkit with best practice recommendations for the management of invasive species on islands (Wittenberg & Cock, 2001), while the Biotope Good Practice Guide provides specific recommendations for invasive species management in Seychelles that can be applied to other islands (Rocamora & Henriette, 2015).

The genetic diversity of the Algerian hedgehog (*Atelerix algirus*) has been investigated by several studies. Khaldi et al. (2016) found no genetic discontinuity between different populations from Algeria, Morocco, Tunisia, Spain, Balearic and Canary Islands, suggesting that subspecies recognition may not be necessary. El-Farhati et al. (2021) discovered two distantly related lineages (lineages I and II) within *A. algirus*, which were not recovered in the phylogenetic tree. These results suggest that the mitochondrial phylogeographic structure of the species has a recent origin. The minimum number of mutations observed between haplotypes of these two lineages was only three mutations, and they could only be identified in the haplotype network.

The genetic structure of European hedgehog populations in New Zealand most closely resembles that of the UK population, located near Palmerston North on the North Island (Bolfíková et al. 2013). As the study suggests, this species has undergone a major genetic drift and is significantly different from the original population (Bolfíková et al. 2013).

The genetic diversity of the European hedgehog population on Pianosa is highly similar to the population on Elba, suggesting that the hedgehog population on Pianosa originated from a group of individuals translocated by humans from Elba to Pianosa (Iannucci et al. 2018). The different haplotype of the Sardinian population suggests a genetic relationship with other unexplored Mediterranean populations, potentially Sicilian, French or Iberian, given the absence of the species in North Africa (Iannucci et al. 2018).

4. Conclusions

The aim of this study was to assess the genetic diversity of hedgehogs of the genus *Atelerix* and *Erinaceus* on the islands and to evaluate the potential impact of biological invasions on their genetic diversity. The study also aimed to identify the main causes of genetic changes and to evaluate the theory of island biogeography applied to populations of invasive species on islands. The results of this study show that the size and geographic isolation of islands have a significant effect on the genetic diversity of island species. In addition, invasive species pose a serious threat to the genetic diversity of native species on islands, and the climate of an island can also affect the genetic diversity of its species. The theory of island biogeography is an important concept that explains patterns of species richness on islands and has been used to explain various patterns in the distribution of species on islands. Biological invasions are a major environmental problem that pose a significant threat to native biodiversity and ecosystem services. Effective management strategies are essential to prevent, control and reduce the impact of invasive species on islands. Understanding the causes of biological invasions and developing effective management and prevention strategies is essential to mitigate the impact of invasive species on native ecosystems, biodiversity and economic systems. Previous studies on the genetic diversity of the Algerian hedgehog in the Canary and Balearic Islands and Malta, and the European hedgehog in New Zealand and Pianosa Island have contributed to our understanding of the genetic diversity of hedgehogs on the islands. However, further research is needed to identify patterns and gaps in knowledge that require further investigation. This study has provided valuable insights into the genetic diversity of hedgehogs on the islands and highlighted the importance of understanding and managing the impact of biological invasions on native species.

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