

Research Article

Alborán Island, a small meeting point for three invasive lizards, whose geographic origin is uncovered by molecular analysisCatarina Rato^{1,6,*}, Valéria Marques^{1,2}, Mariano Paracuellos³, Jorge Tortolero⁴, Juan C. Nevado⁵ and Miguel A. Carretero^{1,2,6}¹CIBIO, Research Centre in Biodiversity and Genetic Resources, InBIO, Universidade do Porto, Campus de Vairão, Rua Padre Armando Quintas nº7, Vairão 4485 - 661, Vila do Conde, Portugal²Departamento de Biologia, Faculdade de Ciências da Universidade do Porto, R. Campo Alegre, s/n, 4169 - 007, Porto, Portugal³Área de Gestión de la Biodiversidad y Geodiversidad, Agencia de Medio Ambiente y Agua, Consejería de Agricultura, Ganadería, Pesca y Desarrollo Sostenible, Junta de Andalucía, C/ California, 2, pl. baja, E-04007, Almería, Spain⁴Destacamento Naval de Alborán, Estación Naval de Puntales, Fuerza de Acción Marítima en Cádiz, Ministerio de Defensa, C/ Salvador Viniegra y Valdés, s/n, E-11011, Cádiz, Spain⁵Dpto. de Geodiversidad y Biodiversidad, Consejería de Agricultura, Ganadería, Pesca y Desarrollo Sostenible, Junta de Andalucía, C/ Hermanos Machado, 4, 4ª pl., E-04004, Almería, Spain⁶BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Campus de Vairão, 4485-661 Vairão, PortugalAuthor e-mails: catarina.rato@cibio.up.pt (CR), valmarques@cibio.up.pt (MP), mariano.paracuellos@juntadeandalucia.es (MP), jtorsar@fn.mde.es (JT), juanc.nevado@juntadeandalucia.es (JN), carretero@cibio.up.pt (MAC)

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Abstract

Alborán is a small volcanic island located in the center of the Alborán Sea, W Mediterranean, 85 km from the Iberian Peninsula (Europe) and 55.5 km from the NW African coast line. Despite its small size (605 × 265 m), four distinct exotic lizard species have already been reported there, one of them presumably extinct (*Saurodactylus mauritanicus*). Throughout history, the island has maintained an intermittent human presence, being now permanently occupied by a military detachment connected to the Iberian Peninsula mainly by means of cargo shipments. Hence, this communication between the island and the continent has fuelled human-mediated species introductions. Populations of the geckos *Tarentola mauritanica* and *Hemidactylus turcicus* and the most recently reported wall lizard *Podarcis vaucheri* still remain in the island. Here, we used molecular tools to assess species identity and putative invasion pathways. As expected, results confirm the initial species assignment and indicate southern Iberia as the source area. However, surprisingly, two clades of *T. mauritanica* were found, the European clade commonly introduced elsewhere, and the Iberian clade, reported here for the first time outside its native distribution. Moreover, the reported southern Iberian lineage of *P. vaucheri* in Alborán, represents the third case of introduction of this species. This amazing concentration of alien species in such a reduced territory highlights how prone small islands are to be successfully invaded, and that these should not be neglected in invasion biology. The effects of these alien reptile species over native taxa are yet unknown, although an impact over several endemic invertebrates cannot be ruled out. As such, regular monitoring should be implemented to prevent they act as hubs for future new introductions.

Key words: *Tarentola mauritanica*, *Hemidactylus turcicus*, *Podarcis vaucheri*, phylogeography, invasion pathways

Introduction

The introduction of new species to areas outside their native range due to deliberate or accidental human transport has been occurring for millennia.

The reshuffling of species ranges is in some cases so great, that it becomes uncertain what is the geographic origin of the introduced taxa. Unfortunately, a fraction of this alien biota may have a major negative impact on native species, causing their extinction, community changes and ecosystem conversion.

Most of the current research and management efforts on terrestrial invaders are dedicated to mammals, plants and insects, and less on reptiles and amphibians, for instance. Although largely sedentary, reptiles are frequently introduced by humans during transport of building material, soil or cultivated plants (Kraus 2009). Islands, in particular, often host a large number of alien reptiles (Pitt et al. 2005), which are among the most successful and abundant vertebrates in small islands (Novosolov et al. 2016). Moreover, small islands appear to be more prone to be successfully invaded than larger masses (references in Kraus 2009). Because insular ecosystems are unbalanced often leaving empty niches, and many insular native species have evolved for a long time without competitors, predators or parasites, islands and island-like mainland areas seem to be more amenable to herpetofaunal invasion (Whittaker and Fernández-Palacios 2007).

The Mediterranean region, in particular, has one of the longest histories of human settlements and trade, as well as of interaction between humans and biodiversity, with multiple biological introductions occurring over thousands of years (Blondel et al. 2010). In that sense, humans have been key drivers of the dispersal of alien reptiles on Mediterranean islands. However, their distributions are determined by a complex interplay between human activities, geographic factors and species features (Silva-Rocha et al. 2019). The Balearic Islands, for instance, once harboured considerable levels of endemism, as evidenced by the rich fossil record, have now more alien than native reptiles and amphibian species (e.g., Pinya and Carretero 2011; Silva-Rocha et al. 2015). In such Mediterranean islands, it is sometimes challenging to ascertain the native status of species, and many reptiles are traditionally assumed as natives. Fortunately, the advance of molecular genetics and phylogeographic tools have greatly improved our understanding of invasion dynamics and the demography of biological invasions, allowing a more accurate determination of alien status (Le Roux and Wiczorek 2009). However, in cases where the obtained genetic diversity is low and divergence shallow, the distribution of the species can be either explained by human introductions or recent natural colonization by very small propagules (e.g., Bisbal-Chinesta et al. 2020; Graciá et al. 2013; Salvi et al. 2011, 2014; Silva-Rocha et al. 2012). Moreover, while Mediterranean reptiles have been the target of multiple phylogeographic studies, molecular data are still lacking for most insular species. In fact, although the Mediterranean is one of the most studied regions of the world, genetic evidence is available for less than 10% of the species-by-island combinations (see Silva-Rocha et al. 2019).

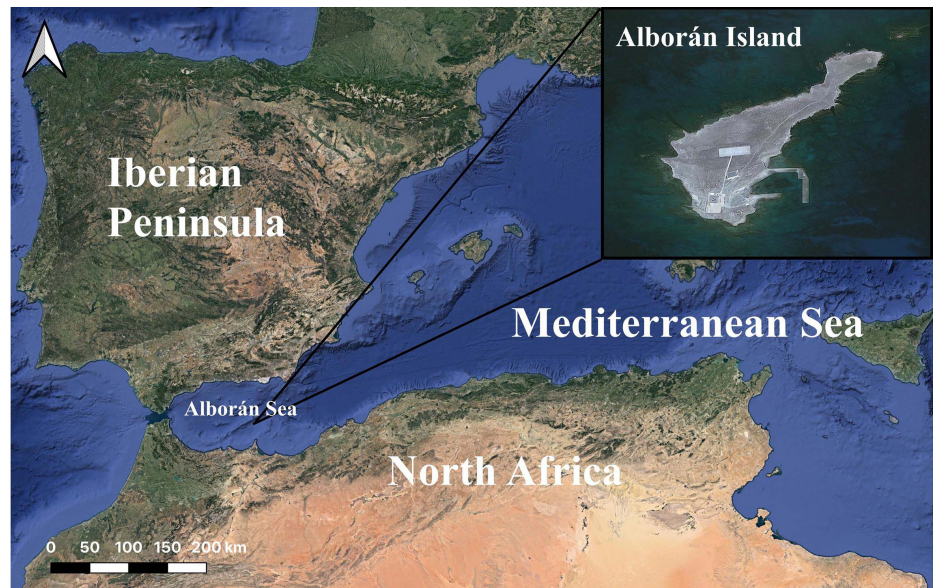


Figure 1. Map depicting the geographic location of Alborán Island.

The Alborán Island ($35^{\circ}56'24''\text{N}$; $3^{\circ}02'04''\text{W}$) is located in the center of the Alborán Sea, 85 km from Punta Entinas (Spain) and 55.5 km from Cabo Tres Forcas (Morocco), the two closest continental shores in the enclave (Figure 1). This small volcanic island is only 7.12 ha, with an average 15 m altitude, 605 m long and 265 m wide. The emerged part of the island is from the late Early Pleistocene (800,000 years) but the volcanic base is from the Middle-Late Miocene (7–18 Mya). It is surrounded by sea depths of 1.000–2.000 m and has not been connected to the mainland since the Messinian Salinity Crisis, 5–6 Mya (Yus et al. 2013).

Due to its geostrategic position and rich fishing grounds, this island has been frequently visited throughout history by fishermen, pirates, explorers and travelers from both coasts of the Alborán Sea. In this sense, throughout history the island has maintained an intermittent human presence. The first permanent settlers on the island arrived with the construction of the lighthouse in 1860, being abandoned again when it was automated in 1936. Since then, the human presence in Alborán has been mainly of military installed there since late 1930s. With an absence of several years since 1992, in 1997 the Alborán Military Detachment became permanent on the island, composed of an average of 11–12 soldiers. Furthermore, since 1997 the enclave became protected as a Marine Reserve and Fishing Reserve, and since 2003 as Natural Area. Such events have meant that, to this day, there are constant movements of cargo shipments between Alborán and, mainly, the south of the Iberian Peninsula (highlighting Cádiz, Málaga and Almería) to the transportation of personnel, building materials and equipment (Acosta 1996; Cano et al. 2006; Rubio 2001; Salvator 1898; Sola et al. 2006).

Although initial surveys to the Alborán Island were unable to record any introduced reptile species (except the reference of the occasional presence of “wall lizards” by Candela and Geiger 1982, of which no more information

was ever obtained afterwards), the Maghreb gecko *Saurodactylus mauritanicus* Dumeril & Bibron, 1836 (Barbadillo et al. 1999), the Moorish gecko *Tarentola mauritanica* (Linnaeus, 1758) (Paracuellos and Nevado 2004), the Mediterranean house gecko *Hemidactylus turcicus* (Linnaeus, 1758) (Paracuellos et al. 2016), and the Vaucher's wall lizard *Podarcis vaucheri* (Boulenger, 1905) (Tortolero et al. 2020) have been successively identified. Currently, *S. mauritanicus* is thought to have gone extinct, since there were no individuals found during the latest surveys to the island (Paracuellos et al. 2005).

Tarentola mauritanica is the most common gecko in the Western Mediterranean Basin, geographically distributed across southern Europe (Iberian Peninsula, France, Italian Peninsula, coastal Balkans, and insular and continental Greece), Northwestern Africa (Morocco, Algeria and Tunisia), and most of the Mediterranean islands (Vogrin et al. 2017). Genetic studies confirm the existence of six different lineages composing this taxon (Harris et al. 2004a, b, 2009; Perera and Harris 2008; Rato et al. 2010, 2012), suggested to represent six putative distinct species of *Tarentola* (Rato et al. 2016). All lineages have fairly restricted and well defined geographic ranges, except the “European/North African” clade, that is widespread across the entire western and central Mediterranean Basin.

Hemidactylus turcicus has a mainly circum-Mediterranean distribution, including many islands and with populations extending to the south along the Nile River upstream to the border with Sudan (Mateus and Jacinto 2008; Sindaco and Jeremcenko 2008). Phylogeographic studies by Rato et al. (2011) confirm the existence of two distinct western Mediterranean mitochondrial lineages originated very rapidly from the east, where one has moved to Europe and the other to North Africa spreading latter into Europe.

Both *H. turcicus* and *T. mauritanica* are frequently associated to humanized environments, living around or inside houses and stone walls, especially near artificial lights that attract insect prey. Not surprisingly, this close relationship with humans has led to several accidental anthropogenic introductions of the Moorish gecko into new areas such as Madeira and Porto Santo Islands (Báez and Biscoito 1993; Jesus et al. 2008), Azores (Barreiros et al. 2010; Rato et al. 2015), South America (Chile, Argentina, Uruguay, Mexico) and the United States (e.g., Achaval and Gudynas 1983; Ortiz-Medina et al. 2019; Vogrin et al. 2017); and *H. turcicus* has also been introduced in the Canary islands (Geniez 2002), Mexico, Cuba, Florida (Smith 1946), and in other areas of the United States (Pianka and Vitt 2003; White and Tumlison 1999).

The wall lizard, *Podarcis vaucheri*, has a wide native distribution range comprising southern Spain, central and northern Morocco, northern Algeria and northern Tunisia (Mateo et al. 2009). Up till now, records of this wall lizard species outside its native range include Athens (continental Greece) (Spilani et al. 2018) and Asilah (Morocco) (Busack et al. 2005), apart from

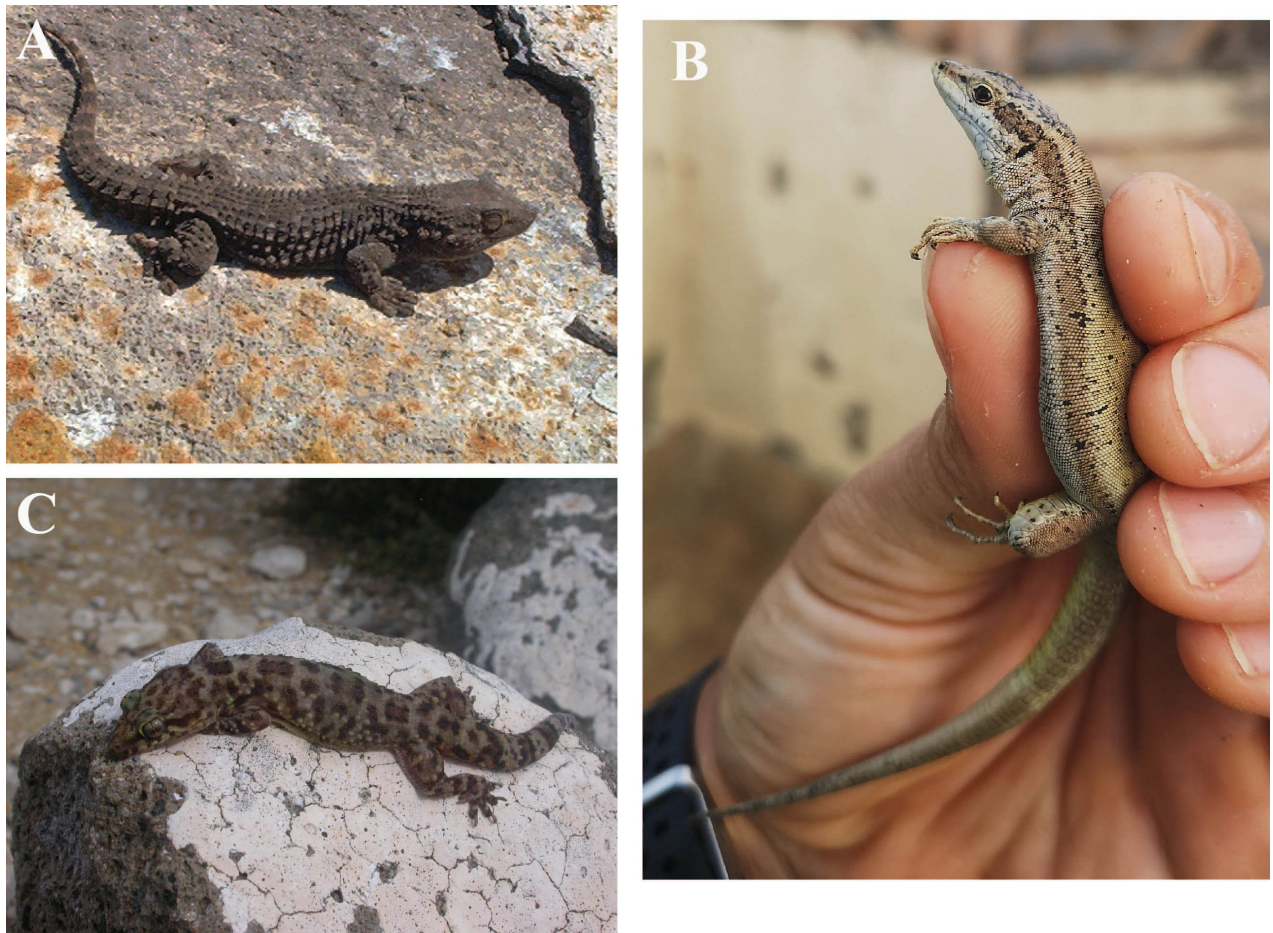


Figure 2. Pictures of the species from Alborán Island: A) Moorish gecko, *Tarentola mauritanica*; B) Vaucher's wall lizard, *Podarcis vaucheri*; and C) Mediterranean house gecko, *Hemidactylus turcicus*. Photos: J. Valero, J. Tortolero and M. Paracuellos, respectively.

Alborán. However, a population of *P. vaucheri* clustering with North African individuals was once found in southeastern Iberia, resulting from human-mediated introductions (Renoult et al. 2010).

Considering the recent findings in Alborán Island of several specimens from the aforementioned reptile species, this study aims to make a preliminary inference on the geographic origin of these introduced individuals by assessing the genetic lineage they belong to. As such, several mitochondrial genetic markers and phylogeographic tools will be implemented to determine the genetic relationships between the specimens from Alborán and those from the native range of each species.

Materials and methods

DNA extraction, amplification and sequencing

In 2020, three specimens identified as *Tarentola mauritanica*, three as *Hemidactylus turcicus* and other three as *Podarcis vaucheri* were collected in the Alborán Island (Figure 2). All animals were collected in and around the military installations, either in the natural habitat or (except for *H. turcicus*) in man-made structures. Tissue from tail tip muscle was collected from each individual and preserved in 96% ethanol. Later, the specimens were

released, in good health, again in the same places where they were captured. Genomic DNA was extracted using a standard high-salt protocol (Sambrook et al. 1989). For both *T. mauritanica* and *H. turcicus* was performed the amplification of the 12S rRNA gene fragment by Polymerase Chain Reaction (PCR), using the primers 12Sa/12Sb from Kocher et al. (1989). PCR conditions were the same as those described in Harris et al. (1998). Regarding *P. vaucheri*, a fragment including the terminal portion of the ND4 gene and the tRNAs for Serine, Histamine and Leucine was amplified using the primers published by Arévalo et al. (1994). Amplification conditions were the same as described in Pinho et al. (2006). All amplified fragments were sequenced in a Sanger sequencer and deposited to GenBank database with accession numbers from MZ388480 to MZ388488.

Gene genealogies

Additional sequences assigned to each of the studied taxa and target gene fragment were downloaded from GenBank (Albert et al. 2009; Beddek et al. 2018; Busack et al. 2005; Carranza et al. 2002; Carvalho et al. 2017; Garcia-Porta et al. 2019; Harris et al. 2004a, 2009; Jesus et al. 2008; Kaliontzopoulou et al. 2011; Lamb and Bauer 2006; Lima et al. 2009; Mačát et al. 2014; Nogales et al. 1998; Perera and Harris 2008; Pinho et al. 2006, 2007; Rato et al. 2010, 2011, 2012, 2013, 2015; Šmíd et al. 2013). The obtained sequences were imported into the software Geneious Prime v.2021.0.3 (<https://www.geneious.com>) where alignment was performed with MAFFT v.7.017 (Katoh and Standley 2013), under the default parameters (auto algorithm; scoring matrix = 200PAM/k = 2; gap open penalty = 1.53; and offset value = 0.123).

To determine the genetic affinities of the specimens, phylogenetic analyses were carried out for each of the three taxa under a Bayesian Inference (BI) methodology. To build these genealogies, distinct GenBank sequences were integrated as outgroups taxa; *Phyllopezus maranjonensis* and *Phyllodactylus thompsoni* (Koch et al. 2016) for *T. mauritanica*'s phylogeny; *Hemidactylus mindiae*, *H. lavadeserticus* and *H. dawudazraqi* (Šmíd et al. 2013) for *H. turcicus*'; and *Podarcis hispanica*, *P. bocagei* and *P. carbonelli* (Kaliontzopoulou et al. 2011; Pinho et al. 2006) to build the *P. vaucheri*'s ND4 genetic topology.

To determine the best fitting nucleotide model for each phylogenetic analysis, the software PartitionFinder v.1.1 was used (Lanfear et al. 2012). Parameters used were *branchlengths* = linked and *modelselection* = BIC.

The software BEAST v.2.6.3 (Bouckaert et al. 2019) was used for the BI analyses. All analyses were run twice for 10×10^6 generations with a sampling frequency of 5.000 generations. Models and prior specifications applied were as follows (otherwise by default): Strict Clock; Coalescent with Constant Population Size; random starting tree. The implemented nucleotide models based on PartitionFinder were: *T. mauritanica* – HKY + G;

H. turcicus – HKY+ I; and in *P. vaucheri* – TN93 + G. Convergence for all model parameters was assessed by examining trace plots and histograms in Tracer v.1.7 (Rambaut et al. 2018) after obtaining an effective sample size (ESS) > 200. The initial 10% of samples were discarded as burn-in. Runs were combined using LogCombiner, and maximum credibility trees with divergence time means and 95% highest probability densities (HPDs) were produced using Tree Annotator (both part of the BEAST package). Trees were visualized using FigTree v.1.4.4 (Rambaut 2009).

Results

According to the obtained genealogy for *H. turcicus*, two of the collected specimens (DB31624 and DB31625) are more closely related to individuals from the European/North African clade, while the specimen DB31623 to the European clade (Figure 3). Similarly, the *T. mauritanica* specimens DB31620 and DB31621 belonged to the clade comprising individuals from Europe/North Africa, as expected. However, DB31622 was phylogenetically related to the Iberian clade. Finally, all specimens assigned as *Podarcis vaucheri* clustered with the clade containing individuals from the southern Spain.

Discussion

While some studies consider that alien richness is related mostly to human population size, in addition to island size (e.g., Ficetola and Padoa-Schioppa 2009; Roura-Pascual et al. 2016; Spatz et al. 2017), others give precedence to the human factor compared to the island traits (Helmus et al. 2014; Silva-Rocha et al. 2019). In any case, all studies confirm the keystone importance of human activities on island biotas and their distributions. Not surprisingly, the results obtained in this study for the Alborán Island confirm the human footprint on biological invasions, which has led to an increase of reptile richness in this minute piece of land over the past 20 years.

Taking into account that most of the current trips between the island and the continent are with the southern seaports of the Iberian Peninsula, ship arrivals from North Africa are practically non-existent nowadays. In fact, it was in the years prior to the sighting of *Saurodactylus mauritanicus* in Alborán (in 1997, Barbadillo et al. 1999), that the military garrison abandoned permanently the insular facilities (between 1992 and 1997), favouring the visit to the island by clandestine fishing boats coming from North Africa (Rubio 2001). Indeed, the survey carried out by Paracuellos et al. (2005) between 1994 and 2005 in Alborán to assess the vertebrate fauna in the island found no evidence of *S. mauritanicus*. This could mean that the few specimens reported by Barbadillo et al. (1999) were most likely introduced when ship traffic between Alborán and North Africa was frequent, but once that was interrupted, the vestigial gecko population went extinct (Paracuellos et al. 2005).

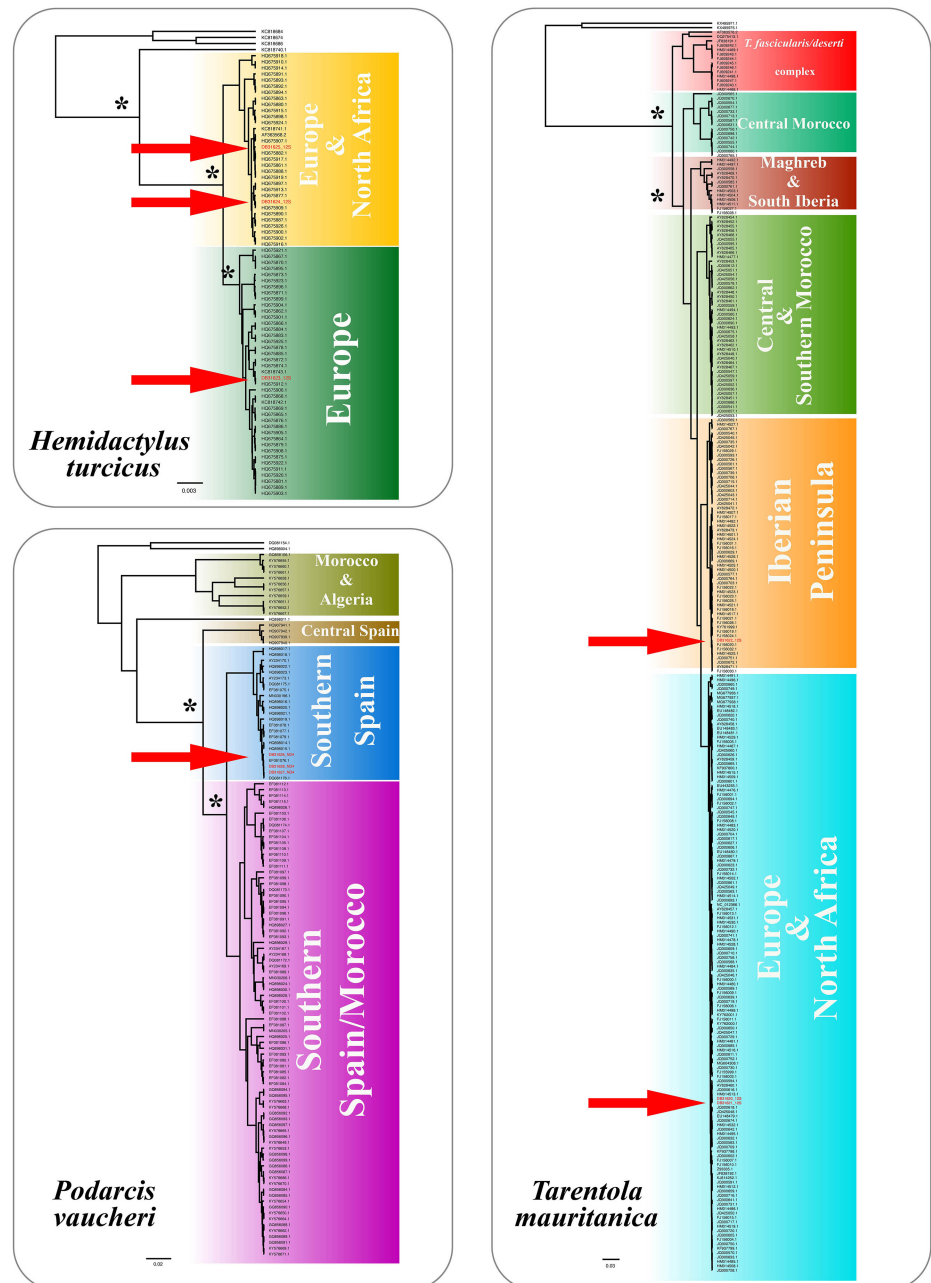


Figure 3. Mitochondrial phylogeographic analyses for each of the recorded species in Alborán Island; 12SrRNA for both *H. turcicus* and *T. mauritanica*, and ND4 for *P. vaucheri*. Red arrows denote the phylogenetic position of each specimen, and asterisks the nodes with >95% posterior probability.

According to the results found here, both *T. mauritanica* and *H. turcicus* geckos from Alborán have phylogenetic affinities with populations from both Europe and North Africa (Figure 3). However, in both species's phylogenies, there is not an exclusive North African clade, meaning that these populations always share the same haplotypes with southern Iberia. Taking this into consideration and the current reduced communication between Alborán and North Africa, these gecko specimens most likely arrived from southern Spain. This same geographic origin of introduction is clearer and unequivocal with respect to *Podarcis vaucheri*, since the

specimens collected in Alborán cluster exclusively with the populations found in southern Spain.

The assignment of Alborán's Moorish gecko to the European/North African genetic clade is not a surprise, and had already been uncovered by Rato et al. (2010). Apart from that, this clade is characterized by its wide distribution range (Rato et al. 2016), being recurrently introduced in several Mediterranean islands (e.g., Deso et al. 2020). In contrast, this is the first record of the Iberian clade outside its native range, suggesting either at least two different waves of colonisation by *T. mauritanica* (already suggested by Paracuellos et al. 2005) or from a single locality in Iberia where both clades are sympatric. Remarkably, Harris et al. (2009) already reported a similar case in the tiny islet of Conigli near Lapedusa island in the central Mediterranean.

Previous ecophysiological studies on *T. mauritanica* revealed that the European/North African clade presents high plasticity levels regarding water loss (Rato and Carretero 2015), which might explain its invasive success. In fact, when *T. mauritanica* was first discovered in Alborán in 2003 (Paracuellos and Nevado 2004) some animals were marked, and recaptured a few months later. However, when a new sampling was carried out in 2004, the researchers detected an increase in the initial population, with at least 14 new specimens, which given their ages, most probably must have come from later colonizations (Paracuellos et al. 2005). The more animals are introduced, the more likely is the population to thrive and extend its geographic range across the island.

Apart from the populations discovered in Greece (Spilani et al. 2018) and Morocco (Busack et al. 2005), Alborán now represents the third locality where *P. vaucheri* is found outside its native geographic range. Surprisingly, both the Greek and Moroccan wall lizard specimens belong also to the Southern Spain clade, hence, like the individuals from this study. These results suggest that this lineage might be more prone to be introduced elsewhere, compared to other clades also occurring across the African Mediterranean coast. Certain *Podarcis* species (e.g., *P. sicula*, *P. muralis* and *P. pityusensis*) are known to be introduced by direct or indirect anthropogenic means of dispersal such as railways, pet trade, cargo, merchant or touristic vessels, timber trade, plant trade and building materials (e.g., Hodgkins et al. 2012; Rivera et al. 2011; Silva-Rocha et al. 2012, 2014; Valdeón et al. 2010). In the case of Alborán, *P. vaucheri* was certainly introduced from southern Iberia during vessel traffic.

All this evidence configures a scenario of repeated introductions and some species/lineage turnover. It seems that the three introduced species are thriving on the island, in view of its increasing area of occupied land and the presence of eggs and neonates (Tortolero et al. 2020; J. Tortolero and M. Paracuellos *unpublished own data*). However, it is unknown if competitive interactions among them exist, although a decline in the

population of *T. mauritanica* has been estimated after the introduction of *H. turcicus*, the latter being currently the most abundant in Alborán (*pers. obs.*). Nonetheless, all three species live frequently in syntopy in Southern Iberia where diurnal in *P. vaucheri*, cathemeral in *T. mauritanica* and nocturnal *H. turcicus* activity patterns may contribute to some niche partitioning (González de la Vega 1988). At least in Croatia, it is documented that competition with *T. mauritanica* induces a spatial shift on populations of *H. turcicus* (Lisičić et al. 2012). However, such ecological relations in such a small area may become more unstable. The effects of these alien species over native taxa have not yet been sufficiently evaluated, and impacts on Alborán's exclusive and endemic invertebrates such as the coleopterans *Zoophosis alborana* and *Erodius proximus* (Aguirre 2006), cannot be ruled out (Hóðar et al. 2009; Paracuellos et al. 2008a, b). Beyond that, the largest threat for biodiversity is probably the risk that the islet could act as an invasion hub for future introductions (Morel-Journel et al. 2019). All these questions are indeed worth investigating and a continuous monitoring protocol should be implemented to provide valuable information in that sense.

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Author's contribution

CR: conceptualization, methodology, software, validation, formal analysis, writing – original draft, writing – review and editing, project administration, funding acquisition; VM: laboratory work, writing – review and editing; MP: sample collection, writing – review and editing; JT: sample collection; JCN: sample collection; MAR: conceptualization, writing – review and editing, project administration, funding acquisition.

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