

# The role of island physiography in maintaining genetic diversity in the endemic Tyrrhenian wall lizard (*Podarcis tiliguerta*)

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## Keywords

islands; elevation; insular differentiation; Tyrrhenian wall lizard; *Podarcis tiliguerta*; Mid-Pleistocene; genetic diversity; Mediterranean.

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## Abstract

Sea level oscillations occurred during the Pleistocene have strongly affected islands' physiography by changing area, elevation, and even the number of islands rising above the sea level. Such changes had direct consequences on island genetic diversity by promoting genetic admixture during glacial marine regressions while fragmentation or even extinctions occurred because of marine transgressions. Here we investigated the effect of islands' physiographic changes on the mitochondrial diversity of 84 individuals of the Tyrrhenian wall lizard (*Podarcis tiliguerta*) from different islands and island groups surrounding Corsica and Sardinia. The La Maddalena Archipelago that is the more complex of the studied island groups, showed the highest genetic diversity, while we detected decreasing genetic diversity in island groups with lower number of islands and elevation. The genetic imprint we found seems to have been shaped by eustatic changes occurred in the Mediterranean basin during Mid-Pleistocene times. Indeed, a relevant component of ancient lineages was found on those island groups among which elevation of at least one island allowed populations to survive during the Mid-Pleistocene marine transgressions. In contrast, we found evidence of recent gene flow between populations inhabiting islands or island groups characterized by low elevation. Our results suggest that many features such as number of islands and their elevation, may provide predictive information to identify those islands or "archipelagos" that deserve special attention in terms of conservation priority.

## Introduction

The genetic imprint of continental islands can be traced back principally to the cyclic sea level changes triggering transient vicariant conditions through repeated periods of connection and isolation (Cody, 2006). Indeed, islands located on continental shelves were connected both to the mainland and to each other during glacial phases of sea level dropping, while they emerged forming island or archipelagos during interglacials. Island elevation was also very important in determining the fate of insular biota. In fact, during periods of interglacial marine transgressions, low altitude continental islands may have been totally submerged causing local extinction while islands above a certain elevation might have allowed populations to persist and differentiate.

In the Mediterranean, two episodes of strong marine transgression (at 0.54 and 0.35 Mya) have been reported for the Mid-Pleistocene. These marine transgressions caused a sea level rise of 55–120 m (Malatesta & Zarlenga, 1988; Carrara,

Cremaschi & Dai Pra, 1994). Such strong episodes of sea level rise have been suggested to be the main cause of local extinctions of insular vertebrate populations (Brown *et al.*, 2008; Senczuk *et al.*, 2018a,b,c).

The two Mediterranean islands of Corsica and Sardinia, located in the Tyrrhenian Sea, host several endemic species (Thompson *et al.*, 2005; Grill *et al.*, 2007; Blondel *et al.*, 2010) because of their long and complex geological history of isolation dating back to 24–20 Mya (Carmignani *et al.*, 1995; Robertson & Grasso, 1995). During the counter-clockwise rotation of the Corso-Sardinian microplate these two landmasses underwent repeated land bridge connections to mainland Italy until the last Messinian Salinity Crisis (5.3 Mya) (Duggen *et al.*, 2003). Later, Quaternary cyclic sea level changes produced transient connections between these two islands. Such a complex geological history, parallels an important number of molecular studies, showing a significant variety of species specific responses, including signatures of Miocene and Pliocene divergences (Salvi *et al.*, 2010; Bisconti *et al.*, 2013b;

Ketmaier & Caccone, 2013); as well as complex Pleistocene evolutionary histories similar to those observed for continental species (Ketmaier *et al.*, 2010; Bisconti, Canestrelli & Nascetti, 2013a; Ketmaier & Caccone, 2013; Salvi, Bisconti & Canestrelli, 2016; Thibault *et al.*, 2016). Corsica and Sardinia are surrounded by hundreds of satellite islands, some of which grouped into “archipelagos”. During the interglacials many of the current existing satellite islands were submerged because of their low elevation. On the contrary, during the glacial periods, these islands were connected to each other as well as to the main islands because of the sea level drop (Ulzega, 1996). This let populations move across different land masses promoting either *ex novo* migrations or secondary contacts between formerly separated demes (Mayr, 1944; Hewitt, 2011; Qi *et al.*, 2014). The last glacial maximum (LGM) was the most recent of these events after which the progressive sea level rise led to the current island arrangement.

The present work focuses on the Tyrrhenian wall lizard, *Podarcis tiliguerta*, a paleo-endemic species to Corsica, Sardinia and their satellite islands (Bruschi *et al.*, 2006; Corti, 2006; Bruschi, Corti & Capula, 2010). The evolutionary history of *P. tiliguerta* is characterized by the presence of four differentiated lineages with parapatric distribution (Pinho *et al.*, 2004; Harris *et al.*, 2005; Podnar, Mayer & Tvrtković, 2005; Vasconcelos *et al.*, 2006). Noteworthy, two recent phylogeographic studies using mitochondrial and nuclear sequences came to different conclusions. Rodríguez *et al.* (2017) found a remarkable differentiation between the Corsican and Sardinian lineages even in the nuclear markers, therefore recommending a taxonomic revision of the species, whereas Salvi, Pinho & Harris (2017) found an evident mito-nuclear discordance. These conflicting results could be the outcome of different sampling efforts the authors used. Indeed, although Rodríguez *et al.* (2017) used six nuclear markers in contrast to two used by Salvi *et al.* (2017), the latter handled a denser sampling (81 against 32 populations), which may have provided higher phylogeographic resolution.

Species distribution modelling (SDM) indicates that during the LGM the species was probably able to inhabit large parts of the coastal areas emerged by the sea level drop (Salvi *et al.*, 2017). In the light of this, *P. tiliguerta* represents a good model to study how the sea-level changes contributed in shaping the current insular genetic diversity.

By studying *P. tiliguerta* populations on the main islands of Sardinia and Corsica and a number of satellite islands surrounding these two islands we expected to find a genetic imprint tracing the phylogeography of all these island populations. In particular, we tried to understand the role of some island related variables (e.g. elevation, number of islands) in favouring genetic diversity during the different phases of the Pleistocene.

The Mediterranean sea level changes occurred during the last 0.5 Mya allow to relate genetic diversity with the regressions and transgressions occurred in the studied island systems.

Indeed, if marine transgression occurred before LGM matters the most, we expect distinct lineages to occur on islands with elevation >150 m a.s.l. (that is the largest Pleistocene sea level rise in the Mediterranean). Otherwise, if LGM marine

regression shapes current genetic diversity in these islands, we predict strong evidence for both genetic admixture and haplotype sharing among populations.

Hence, in this paper, we also aim to provide predictive geographic features such as island setting, number of islands, and relative elevation that can be integrated on the identification of island conservation priorities.

## Materials and methods

### Sampling area and data analysis

The samples analysed in this study belong to nine islands and four island groups/archipelagos (hereafter “island groups”) surrounding Corsica and Sardinia (all sample sites are reported in Table 1; Table S1). In northern Corsica (Cape Corse), the studied islands (hereafter “Northern Islands”) include: Isolotto di Capense Islet, Giraglia Island, Isolotto di Terra Islet, and Isolotto Finocchiarola Islet. In southern Corsica we studied the Lavezzi Islands and the Îles Cerbicales, consisting of 23 and 11 islands respectively (Table 1 for the island names). In northern Sardinia we focused on La Maddalena Archipelago, a complex island system made of more than 70 islands, islets and rocks. The other sampled Sardinian satellite islands are isolated ones or belonging to other island groups (e.g. Il Toro Island, Asinara and Piana dell’Asinara islands) (Fig. 1).

We collected and stored in pure ethanol 84 tail tip tissues of *P. tiliguerta*, following rigorous guidelines and in full accordance with all specific permits. DNA was extracted by means of the universal protocol of Salah & Martinez (1997) with incubation at 56°C with proteinase K and DNA precipitation with isopropanol. Mitochondrial gene fragments of the NADH dehydrogenase subunit 4 with flanking tRNAs (*nd4*) were amplified using standard PCR techniques with primers: (forward) ND4 5' - TACTTAAACTAGGGGGCTACGGCCTAATCCGCATT and (reverse) Leu 5' - CATTACTTTTACTTGGATTTGCACCA - 3' (Arevalo, Davis, & Sites, 1994). PCR products were purified using Sureclean (Bioline) and sequenced by Macrogen (www.macrogen.com). The electropherograms were checked for quality and the software BioEdit 7.2 (Hall, 1999) was used to compute a consensus alignment. We also included sequences of the same fragment from 149 individuals’ retrieved from GenBank (Salvi *et al.*, 2017, see Table S1 for accession numbers).

The number of haplotypes (*n*), as well as nucleotide ( $\pi$ ) and haplotype (*h*) diversity was calculated for the whole dataset, for each island group and for single islands with sample size larger than  $N = 3$  using DNASP 5.1 (Librado & Rozas, 2009). The number of shared haplotypes between island groups and the respective main islands was calculated. We expected to find a lower number of shared haplotypes and a higher genetic divergence in those islands/island groups that are believed not to have been completely submerged during interglacials. These populations have indeed been able to avoid extinction maintaining unique and/or differentiated haplotypes.

The phylogenetic relationship of insular lizards and their position with respect to the main island lineages was investigated constructing a time-calibrated tree in BEAST v.1.8

**Table 1** Sampling localities with the relative code, island/island group and haplotype

Locality code	Locality	Island/island group	Haplotype
1a	Isolotto di Terra Islet	Northern Islands	1H4
2a	Finocchiarola Islet	Northern Islands	1H3
	Finocchiarola Islet	Northern Islands	1H3
3a	Giraglia Is.	Northern Islands	1H1
	Giraglia Is.	Northern Islands	1H1
	Giraglia Is.	Northern Islands	1H1
	Giraglia Is.	Northern Islands	1H1
4a	Isolotto di Capense Islet	Northern Islands	1H2
	Isolotto di Capense Islet	Northern Islands	1H2
1b	Toro Grande Is.	Cerbicale	1H44
2b	Pietricaggiosa Is.	Cerbicale	1H44
	Pietricaggiosa Is.	Cerbicale	1H44
3b	Piana Is.	Cerbicale	1H44
	Piana Is.	Cerbicale	1H46
4b	Maestro Maria Is.	Cerbicale	1H46
5b	Forana Is.	Cerbicale	1H44
1c	Porraggia Piccola Is.	Lavezzi	1H52
	Porraggia Piccola Is.	Lavezzi	1H52
2c	Ratino Is.	Lavezzi	1H52
3c	Piana Is.	Lavezzi	1H56
4c	Camaro Canto Is.	Lavezzi	1H52
5c	San Bainsu Is.	Lavezzi	1H50
	San Bainsu Is.	Lavezzi	1H51
6c	Isolotto nord-est Lavezzi	Lavezzi	1H53
	Isolotto nord-est Lavezzi	Lavezzi	1H54
7c	Silene Islet	Lavezzi	1H54
	Silene Islet	Lavezzi	1H54
	Isolotto Piccolo di Cala Chiesa	Lavezzi	1H55
8c	Lavezzu Is.	Lavezzi	1H54
	Lavezzu Is.	Lavezzi	1H54
	Lavezzu Is.	Lavezzi	1H54
	Lavezzu Is.	Lavezzi	1H54
	Lavezzu Is.	Lavezzi	1H54
	Lavezzu Is.	Lavezzi	1H54
	Lavezzu Is.	Lavezzi	1H54
9c	Semillante Islet	Lavezzi	1H54
	Semillante Islet Est	Lavezzi	1H54
	Isolotto est (Corsica)	Lavezzi	1H54
1C	Trinité (Bonifacio)	Corsica	1H44
2C	Bonifacio	Corsica	1H44
1d	Razzoli Is.	La Maddalena	3H5
	Razzoli Is.	La Maddalena	3H9
2d	Capicciolu Is.	La Maddalena	3H5
	Capicciolu Is.	La Maddalena	3H5
3d	La Presa Is.	La Maddalena	3H5
	La Presa Is.	La Maddalena	1H46
4d	S. Maria Is.	La Maddalena	3H5
	S. Maria Is.	La Maddalena	3H5
5d	Isolotto meridionale di Paduleddi Islet	La Maddalena	3H7
	Isolotto meridionale di Paduleddi Islet	La Maddalena	3H7
6d	Budelli Is.	La Maddalena	3H5
7d	Piana Is.	La Maddalena	3H11
8d	Barrettini Is.	La Maddalena	3H5
	Barrettini Is.	La Maddalena	3H10
9d	Abbatoggia Islet	La Maddalena	3H1
	Abbatoggia Islet	La Maddalena	3H2
10d	Colombi Islet	La Maddalena	3H5

**Table 1** Continued.

Locality code	Locality	Island/island group	Haplotype
11d	Maddalena Is. (Bassa Trinità)	La Maddalena	3H4
	Maddalena Is. (Bassa Trinità)	La Maddalena	3H5
	Maddalena Is. (Cala Francese)	La Maddalena	3H5
12d	Isolotto degli Italiani Islet (Caprera)	La Maddalena	3H2
13d	Caprera Is.	La Maddalena	3H2
	Caprera Is.	La Maddalena	3H5
14d	Isolotto di Stagnali Islet (Caprera)	La Maddalena	3H6
15d	Isolotto di Cala Scavicchio Islet (Caprera)	La Maddalena	3H5
16d	Santo Stefano Is.	La Maddalena	3H2
	Santo Stefano Is.	La Maddalena	3H5
17d	Spargi Is.	La Maddalena	3H5
	Spargi Is.	La Maddalena	3H7
18d	Spargiotto Is.	La Maddalena	3H29
	Spargiotto Is.	La Maddalena	3H30
19d	Mortorio Is.	La Maddalena	3H12
	Mortorio Is.	La Maddalena	3H13
20d	Capo d'Orso	Sardinia	3H3
1S	Capo Testa	Sardinia	3H27
2S	Isola Rossa di Trinità d'Agultu Is.	Isola Rossa di Trinità d'Agultu	3H28
3S	Asinara Is.	Asinara	3H32
4S	Piana dell'Asinara Is.	Asinara	3H31
5S	Piana di Tavolara Is.	Tavolara	3H26
6S	Cavoli Is.	Isola dei Cavoli	4H1
7S	Flumini maggiore	Sardinia	4H12
8S	Il Toro Is.	Il Toro	4H16
	Il Toro Is.	Il Toro	4H16
	Il Toro Is.	Il Toro	4H16

(Drummond *et al.*, 2012). To find the best evolutionary substitution model to be implemented in the coalescent analysis we used the software JModeltest (Durrba *et al.*, 2012) which suggested HKY+I+G under the Akaike Information Criterion (AIC) as the most reliable substitution model. To estimate the age of the most recent common ancestor (MRCA) of the main islands and “island groups” we employed a combination of biogeographic and secondary calibrations. First, we applied a normal prior distribution ( $\mu = 5.325$ ,  $SD = 0.05$ ) to calibrate the split between *P. lilfordi* endemic to the Balearic Islands and *P. pytiusensis* endemic to the Pytiusic Islands which probably occurred after the Messinian Salinity Crisis (Brown *et al.*, 2008; Rodríguez *et al.*, 2017). In addition, we incorporated a lognormal distribution prior ( $\mu = 0.0115$ ,  $SD = 0.5$ ) on the *nd4* substitution rate which was previously estimated in other *Podarcis* lizards from the Siculo-Maltese region (Salvi *et al.*, 2014). We used a lognormal relaxed-clock under a constant coalescent model as tree prior, running the analysis for  $3 \times 10^8$  generations sampling every  $3 \times 10^4$  steps. The software tracer 1.6 (Rambaut *et al.*, 2014) was used to evaluate the stationary of the run and the convergence of each parameter. The final consensus tree was summarized from the stationary distribution (burn-in = 25%) in TreeAnnotator 1.8.1 (Drummond *et al.*, 2012).

In addition, to explore gene genealogies we reconstructed statistical parsimony networks employing the software POPART (Leigh & Bryant, 2015) using the TCS

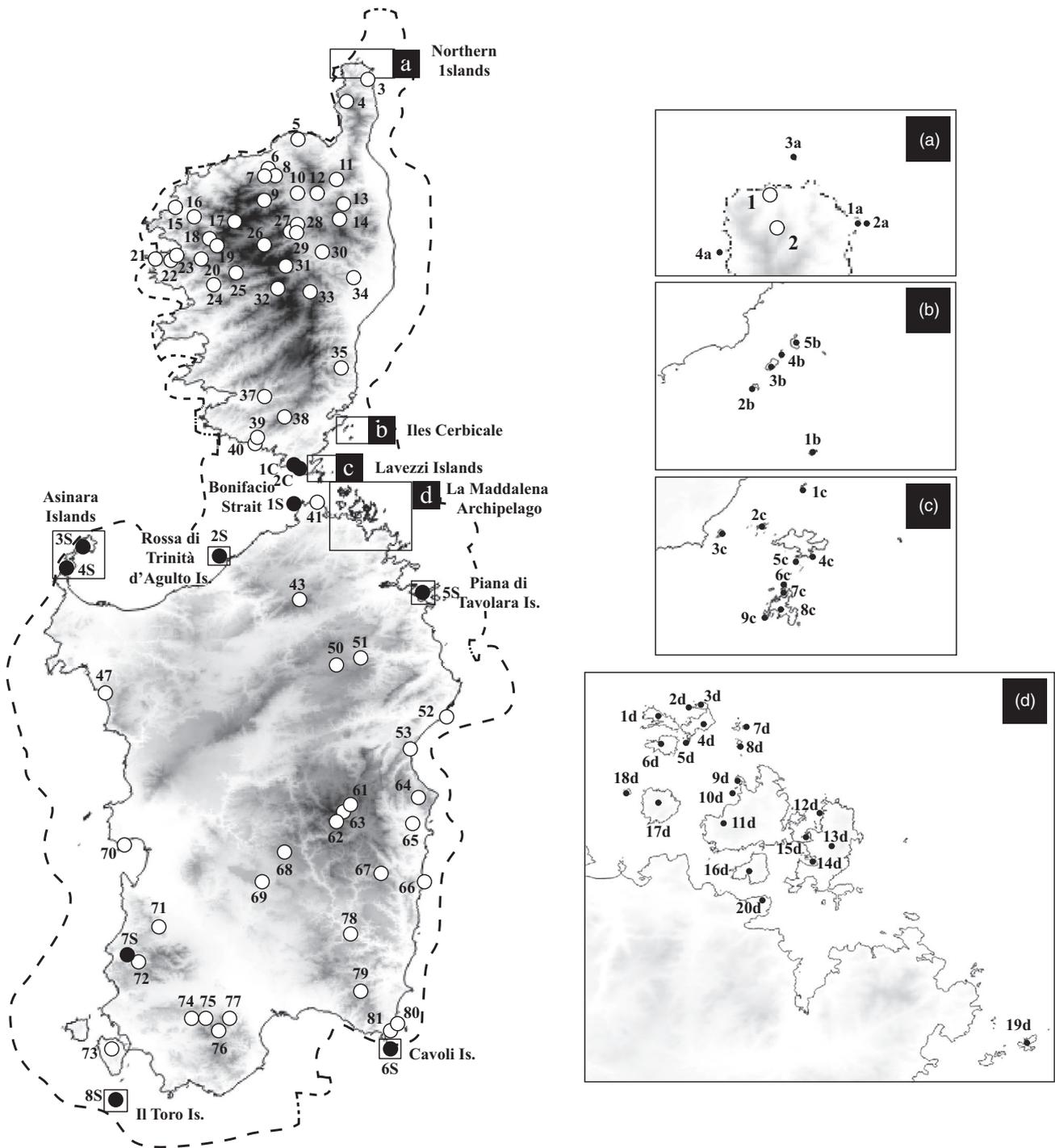
statistical parsimony procedure (Clement, Posada & Crandall, 2000). Because of the presence of strong genetic structuring, we built separate parsimony networks for each main lineage.

Finally, to assess a possible effect of both number of islands per island group and maximum elevation, we reported a scatter plot comparing these variables with the nucleotide diversity found for each island group. For this analysis, we used only islands where the species is found according to Biaggini & Corti (2019) and (Corti, 2006; Corti *et al.*, 2014). If island groups' complexity, both due to number of islands and elevation, play a role in maintaining species' genetic diversity we expect to find an increase of genetic diversity corresponding to a larger number of islands and higher altitude.

## Results

We obtained a final alignment of 623 bp from 233 individuals (84 collected for the present study and other 149 reported in Salvi *et al.*, 2017). For the entire dataset we found 133 haplotypes (30 original haplotypes found in this study and 103 already published) with 220 polymorphic sites ( $h = 0.98 \pm 0.002$ ;  $\pi = 0.095 \pm 0.001$ ). The number of haplotypes, nucleotide and haplotype diversity for each island group are reported in Table 2.

The phylogenetic analysis allowed to assign the island samples to one of the four main lineages. All the estimated



**Figure 1** Geographic position of the collected *Podarcis tiliguerta* tissue samples (black circles) and those originating from literature (white circles, Salvi *et al.*, 2017). The dashed outline approximately represents coastlines during the Last Glacial Maximum.

parameters of the diverging time analysis showed good chain mixing and stationary posterior distributions with effective sample size (ESS) >200.

The estimated time of the most common ancestor (TMRCA) with the relative 95% high posterior density (HPD) per island group is reported in Table 2.

All Corsican satellite island samples fall within lineage 1 (Fig. 2). Individuals of the Northern Islands (Finocchiarola, Isolotto di Terra, Giraglia and Isolotto di Capense islands) form the distinct haplogroup N (1H1-1H4) with two haplotypes shared with Corsica (main Island). The two southern Corsican island groups, the Îles Cerbiciale and the Lavezzi Islands,

**Table 2** Geographic and genetic characteristics of the analysed island groups

Island groups	Tot N° Isl. (N° Isl.)	N°	Max elev.	Haplogroup(s)	TMRCAs (Mya)	95% HPD	Shared Hap.	H	h ± sd	π ± sd
Asinara Islands	2 (2)	2	408	A	0.86–4.02		0	2	-	-
La Maddalena	38 (19)	31	212	M1	0.26–1.18		0	2	0.742 ± 0.07	0.013 ± 0.0071
				M2	0.45–1.77		0	10		
				M3	0.21–1.09		1	3		
Îles Lavezzi	23 (9)	23	40	L	0.09–0.65		1	0.701 ± 0.10	0.005 ± 0.0019	
Îles Cerbicale	11 (5)	6	36	C	0.07–0.43		2	0.709 ± 0.13	0.002 ± 0.0008	
Northern Islands	5 (4)	9	65	N	0.06–0.51		1	0.778 ± 0.11	0.002 ± 0.0004	

Number of islands within each island group where the species *Podarcis tiliguerta* is present (Tot N° Isl.); the total number of the samples per island group (N°); maximum elevation per island group (Max elev.); haplogroup names; the time of the most recent common ancestor in million years per haplogroup (TMRCAs); the number of shared haplotypes between island haplogroups and main islands; number of haplotypes (H); haplotype diversity (h) and nucleotide diversity (π) and relative standard deviations.

resulted in a differentiated monophyletic assemblage including several haplotypes from the southernmost portion of the main island of Corsica. Concerning the Lavezzi Islands, all individuals but one (1H56) form the monophyletic haplogroup L (1H50–1H55) while individuals from the Îles Cerbicale are part of the haplogroup C that also includes haplotypes shared with the main Island (Fig. 2, Table 2). Although lineage 2 is distributed in southern Corsica (Fig. 2), no new haplotype, neither from islands nor main island was found from this lineage.

Lineage 3 is distributed in northern and central Sardinia and includes samples from La Maddalena Archipelago, Asinara and Piana dell'Asinara islands, Isola Rossa di Trinità d'Agultu and Piana di Tavolara islands (Fig. 2). Asinara islands' lizards are the most differentiated (haplogroup A) resulting in a basal position within lineage 3 (Fig. 3). La Maddalena Archipelago harbours three differentiated haplogroups (M1, M2 and M3). The haplogroup M1 includes only two haplotypes (3H29–3H30) found on Spargiottu Island (18d, Fig. 2) separated from the nearest Sardinian (main Island) haplotype (3H26) by eight substitutions. The haplogroups M2 and M3 also form a monophyletic assemblage separated by nine substitution steps with other Sardinian haplotypes and from each other by six substitutions. However, while all M2 individuals belong to La Maddalena Archipelago, the haplogroup M3 includes one haplotype from Sardinia (3H3). All other insular samples (Isola Piana di Tavolara and Isola Rossa di Trinità d'Agultu) slightly differ from the Sardinian main island haplotypes. Finally, lineage 4 is distributed from central to southern Sardinia including the southernmost Sardinian islands Isola dei Cavoli and Il Toro islands, showing a separation of one and two mutation steps respectively with respect to the closest Sardinian haplotype. The scatter plot comparing the nucleotide diversity with the number of islands showed the highest genetic diversity in La Maddalena Archipelago. On the other hand, high genetic diversity was found only for those islands with elevation exceeding 150 m a.s.l. (La Maddalena Archipelago), while all the other "island groups" showed reduced genetic variability (Fig. 3).

## Discussion

Past climate changes extensively shaped islands' physical environment such as area, elevation, and isolation that are the main drivers of islands' genetic differentiation (Wilson & MacArthur, 1967; Wright, 1983; Kalmar & Currie, 2006; Kreft *et al.*, 2008; Whittaker, Triantis & Ladle, 2008). Sea level rising following the up warming phases usually led to a reduction of islands' size increasing isolation among islands and submerging those characterized by low elevation. Our findings seem to confirm such scenario indicating the presence of ancient lineages on those island groups that at least include one island with elevation >150 m (La Maddalena and the Asinara islands). The estimated time divergence of these endemic haplotypes dates older than the Mid-Pleistocene 0.35 Mya (Table 2; Fig. S1). Most likely, they diversified during the Mid-Pleistocene and persisted during the LGM in coastal areas close to the area of origin, seemingly with limited secondary contact between islands and main island haplogroups. Such a result is fairly surprising taking into account the vast coastal

plains emerged during the LGM that should have favoured extensive genetic exchange between satellite islands and the main islands of Corsica and Sardinia, as observed for other endemic species (Ketmaier *et al.*, 2010; Salvi *et al.*, 2010; Bisconti *et al.*, 2011). On the contrary, the persistence of ancient lineages close to the area of origin, mirrors the results found for *Podarcis siculus* (Senczuk *et al.*, 2017), where the presence of 4 mitochondrial lineages in strict parapatry persisted over the LGM in a restricted area of southern Italy (Calabria). These results suggest that dispersal ability of *Podarcis* lizards may be more limited than expected. As alternative explanations should be also considered that *Podarcis* insular endemics often tend to be more aggressive than mainland counterparts (Raia *et al.*, 2010) and often display different ecologies because of insular specialization (e.g. Pérez-Mellado & Corti, 1993). Therefore, local adaptation and direct intraspecific competition may also be involved to limit the secondary genetic exchange.

La Maddalena Archipelago that represents the most complex system among the studied island groups shows the highest genetic diversity with three differentiated lineages (M1, M2 and M3). According to the MRCA, these lineages originated before the LGM in different time frames during the Mid-Pleistocene (Table 2, Fig. S1). It should be noted that time estimates relying on molecular clocks must be taken with caution taking into account the uncertainty related to the coalescent processes as calibrations are based on *a priori* biogeographic assumptions (Kodandaramaiah, 2011; Hipsley & Müller, 2014). The La Maddalena island system is made of more than 70 islands, islets and rocks including three islands exceeding 150 m in elevation (Caprera,  $H_{\max} = 212$  m; La Maddalena,  $H_{\max} = 156$  m; Spargi,  $H_{\max} = 153$  m). It is interesting to note that a recent work by Sillero, Biaggini & Corti (2018) analysed the herpetofauna species–area relationship and structural connectivity among islands of La Maddalena Archipelago, suggesting that the number of unique habitats and relatively high mean elevation are the most important factors explaining the species richness across different species groups.

Such circumstances may have favoured relict populations to persist and differentiate *in situ* during the Mid-Pleistocene marine transgressions (Malatesta & Zarlenga, 1988; Carrara *et al.*, 1994). A similar explanation was also suggested for other Mediterranean insular *Podarcis* to explain their genetic Mid-Pleistocene make up (Brown *et al.*, 2008; Senczuk *et al.*, 2018b). The mitochondrial genetic admixture found for the populations within La Maddalena Archipelago, characterized by a high number of shared haplotypes, would suggest the relevant role of the LGM coastal expansions in favouring diffusion processes. On the other hand, on La Maddalena Archipelago we found only one haplotype shared with the main island of Sardinia (3H3 from Capo d'Orso). Nevertheless, the genetic differentiation of this haplotype would seem to date back prior to the LGM (0.05 Mya). Most likely, it is not by chance that the other well differentiated haplogroup (A) found within lineage 3, belongs to the Asinara islands. This

insular setting is made of two islands: Piana dell'Asinara, which is a flat island and Asinara a large rocky island with maximum elevation of 408 m a.s.l. Although we just analysed two samples from these islands, a Mid-Pleistocene, or even a more ancient origin occurred on the Asinara “paleo-island” seems to be the most reasonable interpretation that explains the centre of origin of this ancient lineage of *Podarcis tiliguerta*.

On the other hand, all other insular populations from Sardinian satellite islands that are characterized by low elevation (Il Toro, Cavoli, Piana di Tavolara and Isola Rossa di Trinità d'Agulto islands) reflect a recent evolutionary history compatible with the vicariant processes that occurred during or after the LGM.

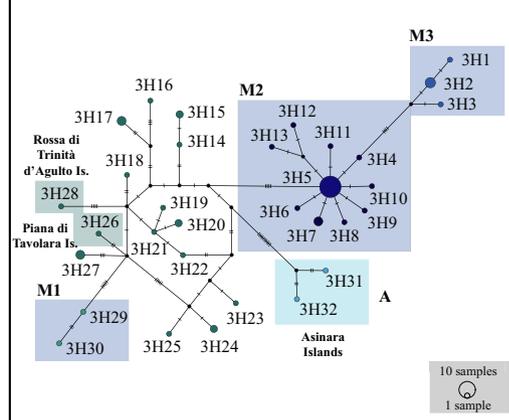
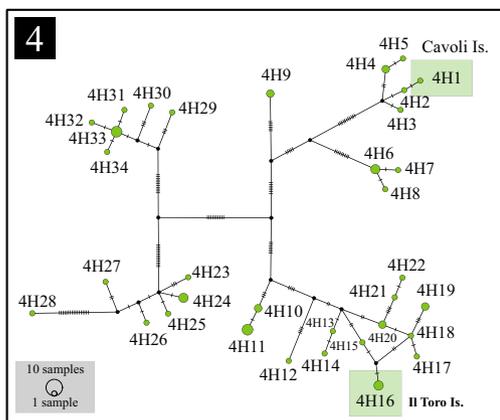
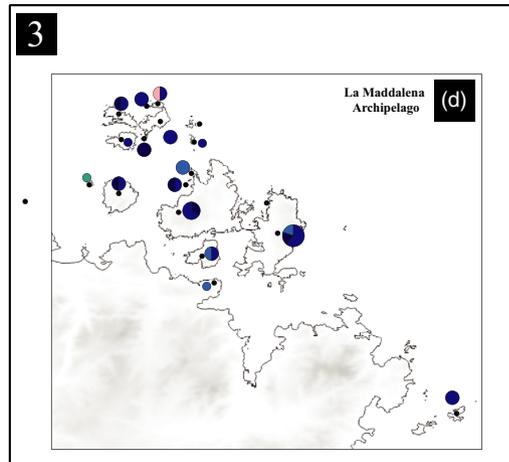
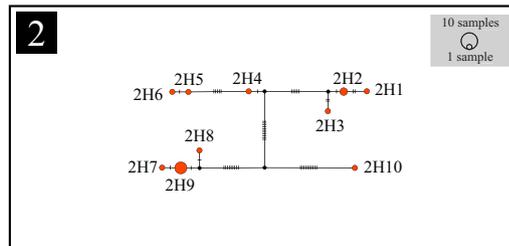
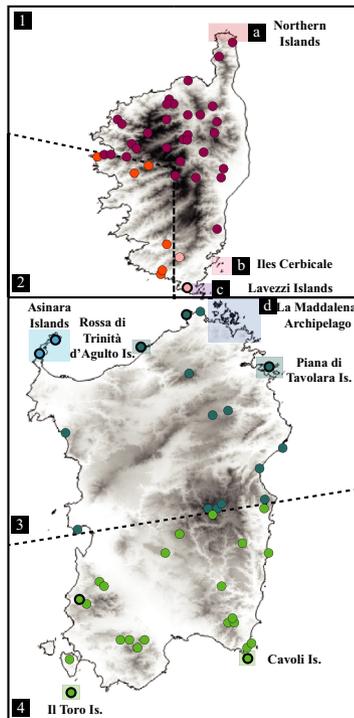
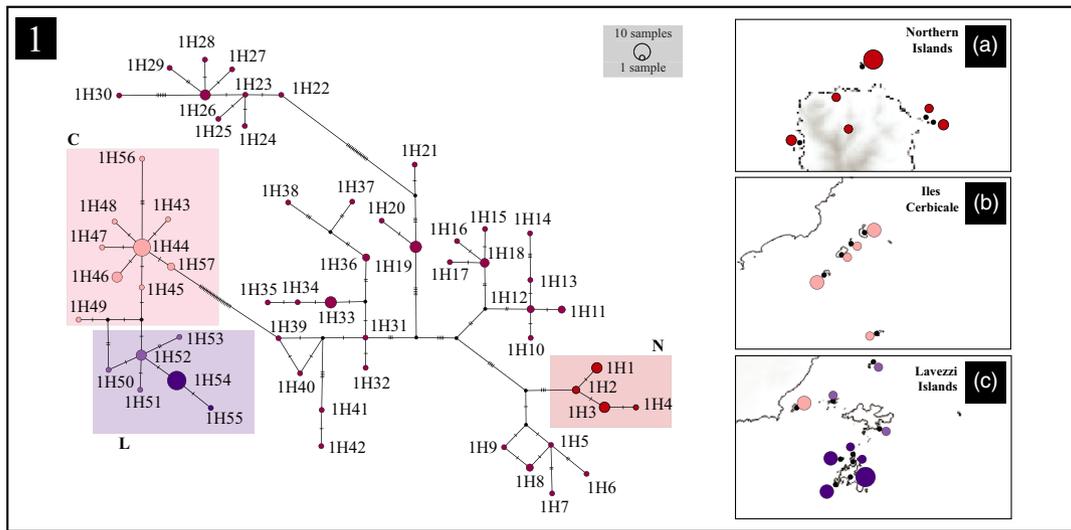
Concerning the Corsican islands, an endemic lineage was found on the Lavezzi Islands that likely originated over the last 0.2 Mya (Table 2). For this island group all samples, except one (1H56, from Piana Island, an islet very close to Corsica main island), form a monophyletic assemblage. Although during the LGM all islands should have been connected to each other, as well as to the main island, the genetic pattern observed for the Lavezzi Islands would seem to suggest a stepping stone colonization model rather than a vicariant process (Fig. 2).

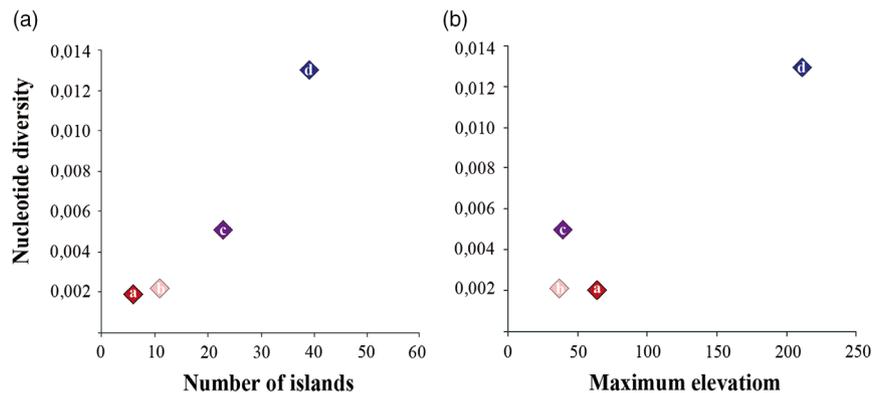
Lizard populations of the other Corsican island groups (Îles Cerbicale and the Northern Islands), show a genetic differentiation level corresponding to a recent separation, most likely by vicariance, as a result of the sea level rise following the LGM. Here the lack of a more ancient genetic signature is not surprising. Indeed, almost all islands below a certain elevation were totally submerged during the Mid-Pleistocene marine transgressions.

The present study, based on mtDNA, allows reconstructing past evolutionary dynamics, but lacks nuclear information that limits the comprehension of possible ongoing or past gene flow processes at the contact zones. Though, the use of nuclear markers can fairly increase the resolution of the overall phylogeography paralleling or adding new information to the mitochondrial signature (Bisconti *et al.*, 2011; While *et al.*, 2015; Senczuk *et al.*, 2018c), a number of case studies has shown that nuclear information based on sequence data is difficult to interpret, in particular at population level. For example, the mito-nuclear discordance represents a tangled pattern that has been widely observed in animals (Toews & Brelsford, 2012) and extensively discussed for this species (Salvi *et al.*, 2017). Microsatellite loci would be useful because of their fast evolving nature. However, on some of the sampled islets the density of lizards was so low that it was impossible to collect the number of samples needed to obtain reliable inference when using microsatellites or other nuclear markers.

Considering that island ecosystems are particularly vulnerable to disturbance (Corti *et al.*, 1999; Foufopoulos & Ives, 1999; Senczuk *et al.*, 2018a), we would suggest conservation priority for each insular genetic lineage. Another important issue is raised concerning future conservation policies addressed to “island groups”. We would like to stress the importance of some physiographic features related to island

**Figure 2** Statistical parsimony networks for the main four *Podarcis tiliguerta* lineages of Corsica and Sardinia with haplotypes' geographic distribution. Haplotype frequencies are represented in the networks by circles with size proportional to frequency; single branches represent one inferred mutational step while slashes indicate additional mutations. [Colour figure can be viewed at [zslpublications.onlinelibrary.wiley.com](https://zslpublications.onlinelibrary.wiley.com)]





**Figure 3** Scatter plots comparing *Podarcis tiliguerta* nucleotide diversity and (a) number of islands and (b) maximum altitude for each archipelago/island group (a = Northern Islands; b = Îles Cerbicale; c = Lavezzi Islands; d = La Maddalena Archipelago). [Colour figure can be viewed at [zslpublications.onlinelibrary.wiley.com](http://zslpublications.onlinelibrary.wiley.com)].

systems such as “complexity” in terms of number of islands and elevation, in order to identify those “archipelagos” that deserve special attention and conservation priority.

### The complex biogeography of Corsica and Sardinia

Since the last decades, Corsica and Sardinia have been the scene of intensive phylogeographic studies that provided a number of interesting insights into the processes driving genetic diversity on islands. In many studies, complex patterns similar to those observed for other continental species, characterized by wider ranges, occur (Gentile *et al.*, 2010; Salvi *et al.*, 2010, 2016; Bisconti *et al.*, 2013a, 2013b). The evolutionary history of the Tyrrhenian wall lizard, *Podarcis tiliguerta*, is among these examples. The high genetic diversity reported here, along with that observed in other phylogeographic studies, places the Tyrrhenian wall lizard among those species characterized by high genetic diversity regardless of its relatively small distribution (Ketmaier & Caccone, 2013 and references therein; Salvi *et al.*, 2016). Within *Podarcis*, such a high intraspecific differentiation is only comparable to some continental species such as *P. siculus*, *P. muralis* and *P. tauricus* (Salvi *et al.*, 2013; Psonis *et al.*, 2017, 2018; Senczuk *et al.*, 2017). Although Corsica and Sardinia are geographically less complex than mainland Europe, most of the examined species showed complex responses to the Pleistocene climate oscillations. Indeed, evidences show that ice sheet formations occurred during the glacial phases, were conspicuous in the central mountain ranges of both Corsica and Sardinia, promoting allopatric fragmentation in several temperate species (Kuhlemann *et al.*, 2005, 2008).

Corsica and Sardinia have offered an attractive setting that also gave rise to a new concept of the classical expansion-contraction (EC) paradigm (Provan & Bennet, 2008). Indeed, the bathymetric profile surrounding Corsica and Sardinia (Fig. 1) clearly suggests that the current shallow waters separating the two main islands were lowlands during the glacial peaks (Ulzega, 1996), condition that favours populations' expansion across different landmasses. Such a scenario has been suggested for the Tyrrhenian tree frog, *Hyla sarda* that underwent glacial expansion rather than

contraction due to the increasing favourable conditions occurring along coasts (Bisconti *et al.*, 2011). Even if not formally explained, other cases would conform to this dynamic of population expansion over glacial land bridges, as for the land snail *Solatopupa guidoni*, and the Bedriaga rock lizard *Archaeolacerta bedriagae* (Ketmaier *et al.*, 2010; Salvi *et al.*, 2010). Considering the bathymetry of the Bonifacio Strait (never exceeding 100 m), we would have expected a certain degree of genetic admixture at least between the Lavezzi Islands and La Maddalena Archipelago as the result of the glacial connections occurred between Corsica and Sardinia. However, only one haplotype, belonging to the southern Corsican lineage, was found in one individual of La Presa Island (La Maddalena Arc.), but a recent accidental introduction could not be excluded.

Further studies should be addressed to some of the pending questions related to the observed phylogeographic discontinuities: are these the result of historical processes or other selective pressures intervened? In this regard, additional molecular tools, including the genomic approach, would be essential to better understand the mechanisms underlying the observed differentiation.

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### References

- Arevalo, E., Davis, S.K. & Sites, J.W. Jr (1994). Mitochondrial DNA sequence divergence and phylogenetic relationships among eight chromosome races of the *Sceloporus grammicus*

- complex (Phrynosomatidae) in central Mexico. *Syst. Biol.* **43**, 387–418.
- Biaggini, M., Corti, C. (2019). Disclosing the herpetofauna of large and tiny islands: a revision and updates on La Maddalena Archipelago. *Atti del XXII Congresso della Societas Herpetologica Italica*, Università della Calabria, Rende (CS).
- Bisconti, R., Canestrelli, D., Colangelo, P. & Nascetti, G. (2011). Multiple lines of evidence for demographic and range expansion of a temperate species (*Hyla sarda*) during the last glaciation. *Mol. Ecol.* **20**, 5313–5327.
- Bisconti, R., Canestrelli, D. & Nascetti, G. (2013a). Has living on islands been so simple? Insights from the insular endemic frog *Discoglossus montalentii*. *PLoS One* **8**, e55735.
- Bisconti, R., Canestrelli, D., Salvi, D. & Nascetti, G. (2013b). A geographic mosaic of evolutionary lineages within the insular endemic newt *Euproctus montanus*. *Mol. Ecol.* **22**, 143–156.
- Blondel, J., Aronson, J., Bodiou, J.Y. & Boeuf, G. (2010). *The Mediterranean region: biological diversity in space and time*. Oxford University Press.
- Brown, R.P., Terrasa, B., Pérez-Mellado, V., Castro, J.A., Hoskisson, P.A., Picornell, A. & Ramon, M.M. (2008). Bayesian estimation of post-Messinian divergence times in Balearic Island lizards. *Mol. Phylogenet. Evol.* **48**, 350–358.
- Bruschi, S., Corti, C., Carretero, M.A., Harris, J.D., Lanza, B. & Leviton, A. (2006). Comments on the Status of the Sardinian-Corsican Lacertid Lizard *Podarcis tiliguerta*. *Proc. Calif. Acad. Sci.* **57**, 191–211.
- Bruschi, S., Corti, C. and Capula, M. (2010). *Podarcis tiliguerta* (Gmelin, 1789). In *Fauna d'Italia. Reptilia. Edizioni Calderini de Il Sole 24*: 417–427. In: Corti, C., Capula, M., Luiselli, L., Razzetti, E. and Sindaco, R. (Eds). Bologna: Ore Editoria Specializzata S.r.l.». ISBN 9788850653621.
- Carmignani, L., Decandia, F.A., Disperati, L., Fantozzi, P.L., Lazzarotto, A., Liotta, D. & Oggiano, G. (1995). Relationships between the Tertiary structural evolution of the Sardinia-Corsica-Provençal Domain and the Northern Apennines. *Terra Nova* **7**, 128–137.
- Carrara, C., Cremaschi, M. & Dai Pra, G. (1994). Oscillazioni del livello marino, depositi e morfogenesi continentali nelle isole pontine (Italia Centrale). *Geogr. Fis. Din. Quat.* **17**, 139–153.
- Clement, M., Posada, D.C.K.A. & Crandall, K.A. (2000). TCS: a computer program to estimate gene genealogies. *Mol. Ecol.* **9**, 1657–1659.
- Cody, M.L. (2006). *Plants on islands: diversity and dynamics on a continental archipelago*. London: University of California Press.
- Corti, C. (2006). *Podarcis tiliguerta*. In *Atlante degli Anfibi e Rettili d'Italia/Atlas of Italian Amphibians and Reptiles*: 490–493. Sindaco, R., Doria, G., Razzetti, E. and Bernini, F. (Eds). Polistampa, Firenze: Societas Herpetologica Italica/Polistampa Firenze.
- Corti, C., Masseti, M., Delfino, M. & Pérez-Mellado, V. (1999). Man and herpetofauna of the Mediterranean islands. *Rev. Esp. Herp.* **13**, 83–100.
- Corti, C., Biaggini, M., Delauger, M. and Lo Cascio, P. (2014). New data on the herpetofauna of the National Park “Arcipelago di La Maddalena” (NE Sardinia, Italy). In *Scripta Herpetologica, Studies on Amphibians and Reptiles in honour of Benedetto Lanza*: 200. Capula, M. and Corti, C. (Eds). Latina, Italy: Edizioni Belvedere.
- Darriba, D., Taboada, G.L., Doallo, R. & Posada, D. (2012). jModelTest 2: more models, new heuristics and parallel computing. *Nat. Methods* **9**, 772–772.
- Drummond, A.J., Suchard, M.A., Xie, D. & Rambaut, A. (2012). Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Mol. Biol. Evol.* **29**, 1969–1973.
- Duggen, S., Hoerle, K., Van Den Bogaard, P., Rüpke, L. & Morgan, J.P. (2003). Deep roots of the Messinian salinity crisis. *Nature* **422**, 602.
- Foufopoulos, J. & Ives, A.R. (1999). Reptile extinctions on land-bridge islands: life-history attributes and vulnerability to extinction. *Am. Nat.* **153**, 1–25.
- Gentile, G., Campanaro, A., Carosi, M., Sbordoni, V. & Argano, R. (2010). Phylogeography of *Helleria brevicornis* Ebner 1868 (Crustacea, Oniscidea): old and recent differentiations of an ancient lineage. *Mol. Phylogenet. Evol.* **54**, 640–646.
- Grill, A., Casula, P., Lecis, R. & Menken, S. (2007). *Endemism in Sardinia. In Phylogeography of southern European refugia*: 273–296. Dordrecht: Springer.
- Hall, T.A. (1999). BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. In *Nucleic acids symposium series* (Vol. 41, No. 41): 95–98. Oxford University Press (Ed). London: Information Retrieval Ltd., c1979-c2000.
- Harris, D.J., Pinho, C., Carretero, M.A., Corti, C. & Böhme, W. (2005). Determination of genetic diversity within the insular lizard *Podarcis tiliguerta* using mtDNA sequence data, with a reassessment of the phylogeny of *Podarcis*. *Amphibia-Reptilia* **26**, 401–407.
- Hewitt, G.M. (2011). Quaternary phylogeography: the roots of hybrid zones. *Genetica* **139**, 617–638.
- Hipsley, C.A. & Müller, J. (2014). Beyond fossil calibrations: realities of molecular clock practices in evolutionary biology. *Front. Genet.* **5**, 138.
- Kalmar, A. & Currie, D.J. (2006). A global model of island biogeography. *Glob. Ecol. Biogeogr.* **15**, 72–81.
- Ketmaier, V. & Caccione, A. (2013). *Twenty years of molecular biogeography in the West Mediterranean islands of Corsica and Sardinia: lessons learnt and future prospects*: 71–93. Croatia: Current Progress in Biological Research. InTech.
- Ketmaier, V., Manganelli, G., Tiedemann, R. & Giusti, F. (2010). Peri-Tyrrhenian phylogeography in the land snail *Solatopupa guidoni* (Pulmonata). *Malacologia* **52**, 81–96.
- Kodandaramaiah, U. (2011). Tectonic calibrations in molecular dating. *Curr. Zool.* **57**, 116–124.
- Kreft, H., Jetz, W., Mutke, J., Kier, G. & Barthlott, W. (2008). Global diversity of island floras from a macroecological perspective. *Ecol. Lett.* **11**, 116–127.

- Kuhlemann, J., Frisch, W., Székely, B., Dunkl, I., Danišik, M. & Krumrei, I. (2005). Würmian maximum glaciation in Corsica. *Austrian J. Earth Sci.* **97**, 68–81.
- Kuhlemann, J., van der Borg, K., Bons, P.D., Danišik, M. & Frisch, W. (2008). Erosion rates on subalpine paleosurfaces in the western Mediterranean by in-situ <sup>10</sup>Be concentrations in granites: implications for surface processes and long-term landscape evolution in Corsica (France). *Int. J. Earth Sci.* **97**, 549–564.
- Leigh, J.W. & Bryant, D. (2015). popart: full feature software for haplotype network construction. *Methods Ecol. Evol.* **6**, 1110–1116.
- Librado, P. & Rozas, J. (2009). DnaSP v5: a software for comprehensive analysis of DNA polymorphism data. *Bioinformatics* **25**, 1451–1452.
- Malatesta, A. & Zarlenga, F. (1988). Evidence of Middle Pleistocene marine transgressions along the Mediterranean coast. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **68**, 311–315.
- Mayr, E. (1944). Wallace's line in the light of recent zoogeographic studies. *The Q. Rev. Biol.* **19**, 1–14.
- Pérez-Mellado, V. & Corti, C. (1993). Dietary adaptations and herbivory in lacertid lizards of the genus *Podarcis* from western Mediterranean islands (Reptilia: Sauria). *Bonn. Zool. Beitr.* **44**, 193–220.
- Pinho, C., Corti, C., Carretero, M.A. and Harris, D.J. (2004). Genetic variability within *Podarcis tiliguerta*: preliminary evidence from 12s rRNA gene sequences. Fifth International Symposium on the Lacertids of the Mediterranean Basin, Lipari, Aeolian Islands, Sicily, Italy, 7–11 May 2004. Abstract Book, pp. 35. ISBN 88-8453-181-0
- Podnar, M., Mayer, W. & Tvrtković, N. (2005). Phylogeography of the Italian wall lizard, *Podarcis sicula*, as revealed by mitochondrial DNA sequences. *Mol. Ecol.* **14**, 575–588.
- Provan, J. & Bennet, K.D. (2008). Phylogeographic insights into cryptic glacial refugia. *Trend Ecol. Evol.* **23**, 564–571.
- Psonis, N., Antoniou, A., Kukushkin, O., Jablonski, D., Petrov, B., Crnobrnja-Isailović, J. & Poulakakis, N. (2017). Hidden diversity in the *Podarcis tauricus* (Sauria, Lacertidae) species subgroup in the light of multilocus phylogeny and species delimitation. *Mol. Phylogenet. Evol.* **106**, 6–17.
- Psonis, N., Antoniou, A., Karameta, E., Leaché, A.D., Kotsakiozi, P., Darriba, D., Kozlov, A., Stamatakis, A., Poursanidis, D., Kukushkin, O., Jablonski, D., Crnobrnja-Isailović, J., Gherghel, I., Lymberakis, P. and Poulakakis, N. 2018. Resolving complex phylogeographic patterns in the Balkan Peninsula using closely related wall-lizard species as a model system. *Mol. Phylogenet. Evol.* **125**: 100–115.
- Qi, X.S., Yuan, N., Comes, H.P., Sakaguchi, S. & Qiu, Y.X. (2014). A strong 'filter' effect of the East China Sea land bridge for East Asia's temperate plant species: inferences from molecular phylogeography and ecological niche modelling of *Platycrater arguta* (Hydrangeaceae). *BMC Evol. Biol.* **14**, 41.
- Raia, P., Guarino, F.M., Turano, M., Polese, G., Rippa, D., Carotenuto, F., Monti, D.M., Cardi, M. & Fulgione, D. (2010). The blue lizard spandrel and the island syndrome. *BMC Evol. Biol.* **10**, 289.
- Rambaut, A., Suchard, M., Xie, D. and Drummond, A. (2014). Tracer v1.6. <http://beast.bio.ed.ac.uk/Tracer>; (Online 2015, May 29).
- Robertson, A.H.F. & Grasso, M. (1995). Overview of the Late Tertiary-Recent tectonic and palaeo-environmental development of the Mediterranean region. *Terra Nova* **7**, 114–127.
- Rodríguez, V., Buades, J.M., Brown, R.P., Terrasa, B., Pérez-Mellado, V., Corti, C., Delaugerre, M., Castro, J.A., Picornell, A. & Ramon, C. (2017). Evolutionary history of *Podarcis tiliguerta* on Corsica and Sardinia. *BMC Evol. Biol.* **17**, 27.
- Salah, M.A. & Martínez, I. (1997). Universal and rapid salt-extraction of high quality genomic DNA for PCR-based techniques. *Nucleic Acid Res.* **25**, 4692–4693.
- Salvi, D., Harris, D.J., Bombi, P., Carretero, M.A. & Bologna, M.A. (2010). Mitochondrial phylogeography of the Bedriaga's rock lizard, *Archaeolacerta bedriagae* (Reptilia: Lacertidae) endemic to Corsica and Sardinia. *Mol. Phylogenet. Evol.* **56**, 690–697.
- Salvi, D., Harris, D.J., Kaliontzopoulou, A., Carretero, M.A. & Pinho, C. (2013). Persistence across Pleistocene ice ages in Mediterranean and extra-Mediterranean refugia: phylogeographic insights from the common wall lizard. *BMC Evol. Biol.* **13**, 147.
- Salvi, D., Schembri, P.J., Sciberras, A. & Harris, D.J. (2014). Evolutionary history of the Maltese wall lizard *Podarcis filfolensis*: insights on the 'Expansion–Contraction' model of Pleistocene biogeography. *Mol. Ecol.* **23**, 1167–1187.
- Salvi, D., Bisconti, R. & Canestrelli, D. (2016). High phylogeographical complexity within Mediterranean islands: insights from the Corsican fire salamander. *J. Biogeogr.* **43**, 192–203.
- Salvi, D., Pinho, C. & Harris, D.J. (2017). Digging up the roots of an insular hotspot of genetic diversity: decoupled mitochondrial histories in the evolution of the Corsican-Sardinian endemic lizard *Podarcis tiliguerta*. *BMC Evol. Biol.* **17**, 63.
- Senczuk, G., Colangelo, P., De Simone, E., Aloise, G. & Castiglia, R. (2017). A combination of long term fragmentation and glacial persistence drove the evolutionary history of the Italian wall lizard *Podarcis siculus*. *BMC Evol. Biol.* **17**, 6.
- Senczuk, G., Colangelo, P., Avramo, V., Castiglia, R., Böhme, W. & Corti, C. (2018a). A study in scarlet: incipient speciation, phenotypic differentiation and conservation implications of the *Podarcis* lizards of the western Pontine islands (Italy). *Biol. J. Linn. Soc.* **125**, 50–60.
- Senczuk, G., Havenstein, K., Milana, V., Ripa, C., De Simone, E., Tiedemann, R. & Castiglia, R. (2018b). Spotlight on islands: on the origin and diversification of an ancient lineage of the Italian wall lizard *Podarcis siculus* in the western Pontine Islands. *Sci. Rep.* **8**, 15111.
- Senczuk, G., Harris, D.J., Castiglia, R., Litsi Mizan, V., Colangelo, P., Canestrelli, D. & Salvi, D. (2018c).

- Evolutionary and demographic correlates of Pleistocene coastline changes in the Sicilian wall lizard *Podarcis wagneriana*. *J. Biogeogr.* **46**, 224–237.
- Sillero, N., Biaggini, M. & Corti, C. (2018). Analysing the importance of stepping-stone islands in maintaining structural connectivity and endemism. *Biol. J. Linn. Soc.* **124**, 113–125.
- Thibault, J.C., Cibois, A., Prodon, R. & Pasquet, E. (2016). Quaternary history of an endemic passerine bird on Corsica Island: Glacial refugium and impact of recent forest regression. *Quaternary Res.* **85**, 271–278.
- Thompson, J.D., Lavergne, S., Affre, L., Gaudeul, M. & Debussche, M. (2005). Ecological differentiation of Mediterranean endemic plants. *Taxon* **54**, 967–976.
- Toews, D.P. & Brelsford, A. (2012). The biogeography of mitochondrial and nuclear discordance in animals. *Mol. Ecol.* **21**, 3907–3930.
- Ulzega, A. (1996). Paleogeografia delle «piccole isole» della Sardegna alla fine dell'ultimo glaciale. *J. Integr. Biogeogr.* **18**.
- Vasconcelos, R., Harris, D.J., Carretero, M.A., Pinho, C., Corti, C., Capula, M., Bassu, L., Spano, G. and Delaunoy, M. (2006). Genetic diversity within Corsican and Sardinian specimens of the Tyrrhenian wall lizard, *Podarcis tiliguerta*, estimated using mtDNA sequences. In *Mainland and insular lizards. A Mediterranean perspective*: 199–207. Corti, C., Lo Cascio, P. and Biaggini, M. (eds). Florence, Italy: Firenze University Press.
- While, G.M., Michaelides, S., Heathcote, R.J., MacGregor, H.E., Zajac, N., Beninde, J., Carazo, P., de Lanuza, G.P., Sacchi, R., Zuffi, M., Horváthová, T., Fresnillo, B., Schulte, U., Veith, M., Hochkirch, A. & Uller, T. (2015). Sexual selection drives asymmetric introgression in wall lizards. *Ecol. Lett.* **18**, 1366–1375.
- Whittaker, R.J., Triantis, K.A. & Ladle, R.J. (2008). A general dynamic theory of oceanic island biogeography. *J. Biogeogr.* **35**, 977–994.
- Wilson, E.O. & MacArthur, R.H. (1967). *The theory of island biogeography*. Princeton NJ: Princeton University Press.
- Wright, D.H. (1983). Species-energy theory: an extension of species-area theory. *Oikos* **49**, 496–506.

## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Figure S1.** Bayesian phylogenetic reconstruction showing the mean of time of the most common ancestor (TMRCA) of both the main lineages end those including insular populations of *Podarcis tiliguerta*.

**Table S1.** Locality codes, geographic location/coordinates with their relative lineage and haplotype are reported for individual. Accession numbers used in this study (\* Accession numbers will be submitted upon acceptance).