Herpetology Notes, Volume 18: 389–397 (published online on 13 June 2025)

Podarcis siculus (Rafinesque, 1810) as a modern Lernaean Hydra: the emergence of a new invasive population in Crete and its implications for bridgehead invasions in the Greek Islands

Charikleia-Foteini Pantagaki[1,2,*], Vassia Spaneli[3], Robert N. Fisher[4], Giorgos Alexandrakis[1], Nikos Poulakakis[1,2,5], and Petros Lymberakis[1]

Abstract. The introduction of Invasive Alien Species (IAS) has various consequences to the native species of a region and reporting them is of major importance. The Italian Wall Lizard, *Podarcis siculus*, is an outstanding invader that constantly expands its range. We are here reporting and verifying the presence of the species on the island of Crete for the first time by using a 408 bp fragment of the cytochrome b gene from a single individual and by conducting phylogenetic analyses. Our results indicate Athens as a possible source for the new population. *Podarcis siculus* might threaten the Cretan endemic *P. cretensis*, resulting in regional extinctions. We recommend immediate measures be taken to prevent the expansion of this population.

Keywords. Mitochondrial DNA, endemism, bridgehead effect, eradication challenges, biosecurity.

Introduction

Non-native species are constantly being introduced around the world. When these species successfully establish and spread in new habitats, they are classified as invasive alien species (IAS), which may pose a significant threat to ecosystems and biodiversity (e.g., Doherty et al., 2016; Pyšek et al., 2020). IAS often adapt rapidly to new environments (Oduor et al., 2016; Adamopoulou and Pafilis, 2019; Kardum Hjort et al., 2024; Ma et al., 2024), affecting native species and causing disruption of ecosystem processes (Kraus, 2015; Bellard et al., 2021; Gentili et al., 2021; Gunn et al., 2023). Notably, island biota are more vulnerable to IAS than mainland species due to their unique adaptations developed after geographic isolation (Russell et al., 2017).

The rate of introductions has increased in the last 200 years and shows no sign of abating in the near future (Seebens et al., 2017, 2021). Human activities and climate change contribute to the rapid increase in the rate of IAS introductions (Johovic et al., 2020). Trade and transport, especially in the era of globalization, play a dominant role, as IAS are often introduced accidentally or intentionally through different pathways (Hulme, 2009; Seebens et al., 2017, 2021).

Established invasive populations can also be a source of secondary introductions (e.g., Lombaert et al., 2010; Bertelsmeier and Keller, 2018). This phenomenon, known as the bridgehead effect, has been widely observed across various species and is primarily attributed to the high densities of invasive populations and the intensity of trade and transport (Lombaert et al., 2010; Bertelsmeier and Keller, 2018; Javal et al., 2019; Blumenfeld et al., 2021). Thus, it is crucial to report IAS and track their introduction pathways to avert further introductions.

Europe hosts more than 14,000 alien species, 11% of which are considered to be invasive (Caffrey et al., 2014; Roy et al., 2018; Seebens et al., 2021). In particular the Mediterranean region is a biodiversity hotspot (Blondel et al., 2010) and one of the richest in alien and invasive species (Polce et al., 2023).

[1] Natural History Museum of Crete, University of Crete, Knossou Avenue, 71409 Herakleio, Crete, Greece.
[2] Department of Biology, School of Sciences and Engineering, University of Crete, Vassilika Vouton, 70013 Herakleio, Crete, Greece.
[3] Societas Hellenica Herpetologica, Knossou Avenue, 71409 Herakleio Crete, Greece.
[4] Western Ecological Research Center, San Diego Field Station, U.S. Geological Survey, 4165 Spruance Road, San Diego, California 92101, USA.
[5] Institute of Molecular Biology and Biotechnology, Foundation for Research and Technology - Hellas, Vassilika Vouton, 70013 Herakleio, Crete, Greece.
[*] Corresponding author. E-mail: haritini.pant@gmail.com

Crete, in Greece, is one of the larger Mediterranean islands and hosts two endemic lizard species (Lymberakis et al., 2018), the Cretan wall lizard *Podarcis cretensis* (Wettstein, 1952) and Barton's thin-toed gecko, *Mediodactylus bartoni* (Stepánek, 1934). However, two IAS also occur in the island, the Yellow-belied Slider, *Trachemys scripta* (Thunberg in Schoepff, 1792), first reported in 1998, and the American Bullfrog, *Aquarana catesbeiana* (Shaw, 1802), introduced in 1994 (Adamopoulou and Legakis, 2016).

The Italian wall lizard, *Podarcis siculus*, is a member of the family Lacertidae, native to the north Adriatic coast, the Italian Peninsula, and Sicily (Fig. 1; Isailovic et al., 2009; Bowles, 2024). According to Senczuk et al. (2017), the species consists of seven genetically divergent clades; the "Siculo-Calabrian" (S1, S2, and S3), the "Adriatic" (A1, A2, and A3), and the "Tyrrhenian" (T) clades. This species is considered to be an outstanding invader, and it is found in Europe, Asia, and America, where it is constantly expanding its range (Isailovic et al., 2009; Oskyrko et al., 2022; Bowles, 2024). This success could be attributed to the opportunistic nature of the species, characterized by the ability to thrive in a wide range of environmental conditions as an aggressive and adaptable competitor and predator (Isailovic et al., 2009; Capula and Aloise, 2012; Zuffi and Giannelli, 2013; Bowles, 2024). The first Greek invasive population of *P. siculus* was spotted in Palaio Faliro, a coastal urban area in Athens, where the species inhabited a limited sandy area along the coast approximately 7 km from the important seaport at Piraeus (Fig. 1; Silva-Rocha et al., 2014; Adamopoulou, 2015). In this study, we report on a new, invasive population of *P. siculus* on the island of Crete and trace its haplotype origin.

Materials and Methods

Sampling. We conducted opportunistic visual encounter surveys (VES) at Kladisos Beach and the adjacent riverbank, located west of Chania, in Crete (35.5110°N, 23.9987°E; elevation 2 m; Fig. 2A, C), on five occasions between 26 May 2023 and 11 April 2024. Survey effort varied between visits (range: 20–60 min), as did the number of observers (one or two).

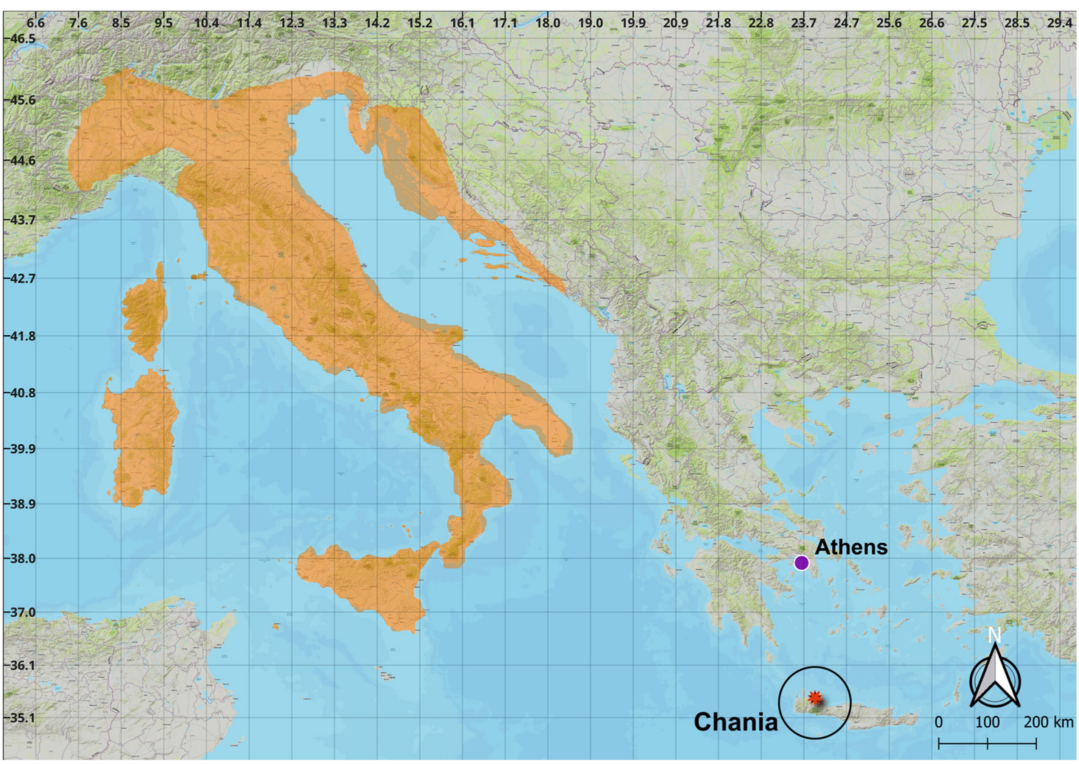

Figure 1. Native range of *Podarcis siculus* (orange) with two alien Greek populations indicated. The Athenian population is shown with a purple circle and the Cretan population in Chania with a red star in a black circle.

All lizards were photographed and identified based on morphological characteristics. In particular, lizards showed heavy reticulation on the flanks and the dorsum, in some cases exhibiting an ocellated pattern, and lack of, or very faded, white lines along the edge of the dorsum, which constitute typical characteristics of *P. siculus* but not of *P. cretensis* (Speybroeck et al., 2016).

To confirm species identification, a tail tip from one individual was collected and stored in 100% ethanol for molecular analysis. We recorded the coordinates of all the observations using a handheld GPS (WGS84) and computed a Minimum Convex Polygon (MCP) to estimate the extent of the range in hectares using the package adehabitatHR (Callenge, 2006) in R (R Core Team, 2022).

Molecular protocol. We extracted total genomic DNA from the sample using a standard ammonium acetate protocol (Bruford et al., 1998).

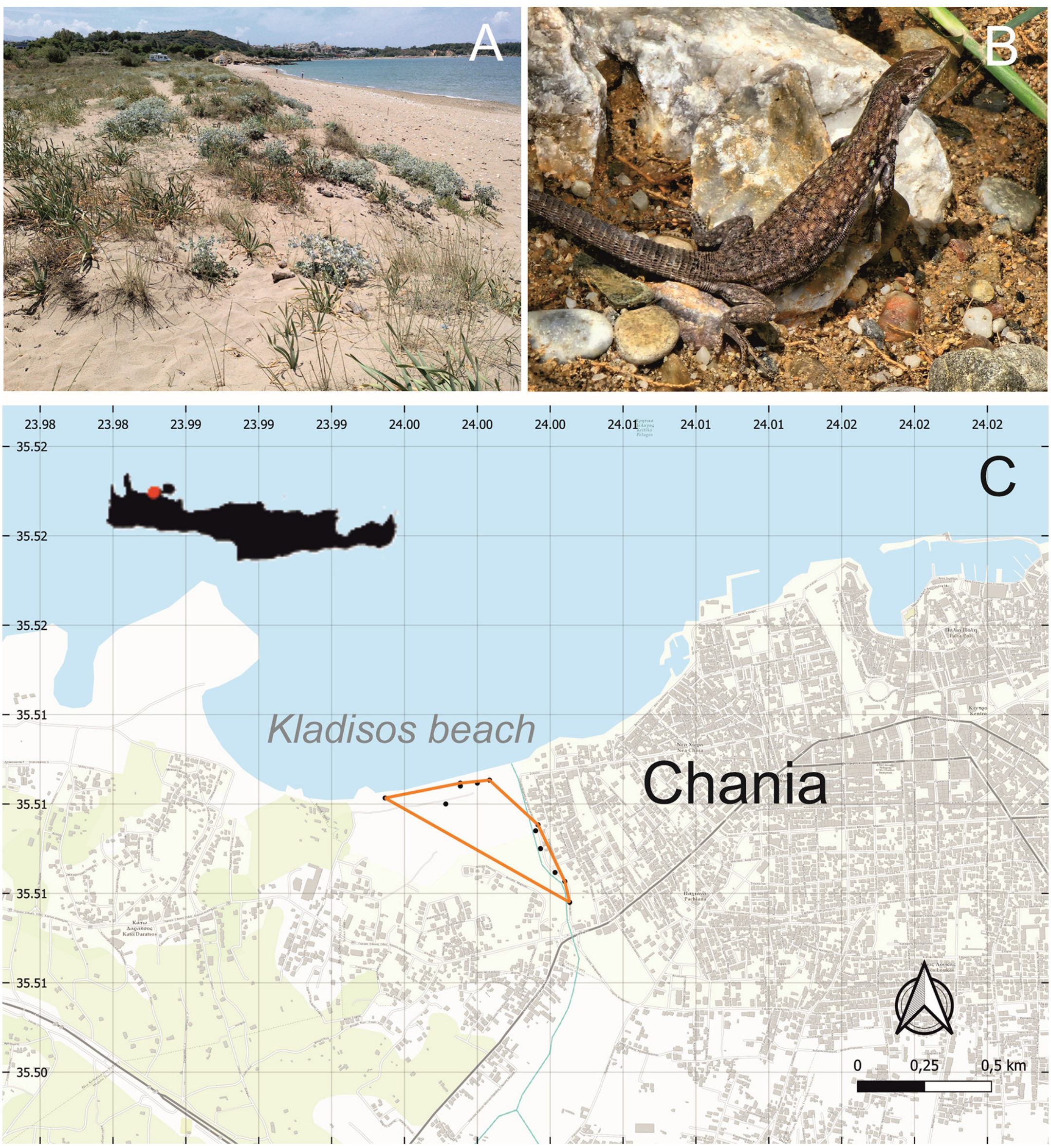

Figure 2. *Podarcis siculus* in Crete. (A) The location on Kladisos Beach in Chania where the species was first spotted. (B) An individual of *P. siculus*. (C) Minimum Convex Polygon for *P. siculus* in Crete. Photos by Vassia Spaneli (A) and Robert Fisher (B).

We then amplified a fragment of ca. 430 base pairs (bp) of the cytochrome *b* (cyt *b*) mitochondrial gene via PCR, with the primers GLUDG and CB2 (Palumbi, 1996) and the conditions described in Psonis et al. (2017). The PCR product was sequenced using the Big-Dye Terminator Cycle Sequencing Kit v3.1 on an ABI3730 automated sequencer (CEMIA, Larissa, Greece) according to the manufacturer's protocol. The sequence was edited using CodonCode Aligner v9.0.1 (CodonCode Corporation). Then, we evaluated the identity and authenticity of this sequence by conducting a BLAST search in the NCBI genetic database (https://blast.ncbi.nlm.nih.gov/Blast.cgi).

Phylogenetic analysis. We conducted a phylogenetic analysis and reconstructed the haplotype network, to confirm species identification and reconstruct the origin of the individual. We built a dataset of cyt *b* sequences with representatives of the seven *P. siculus* clades (Senczuk et al., 2017), including all the available sequences from the population in Athens. As outgroups, we used sequences of *P. muralis* (GenBank numbers: DQ001031, DQ001026) and *P. waglerianus* (MK035075, MK035073). Alignment was performed using the algorithm MUSCLE, which is embedded in MEGAX v10.2.2 (Kumar et al., 2018). We also used MEGAX to estimate the pairwise distances (p-distances). The best model of nucleotide substitution was chosen using PartitionFinder (PF) v2.1 (Guindon et al., 2010; Lanfer et al., 2017).

Phylogenetic reconstruction was accomplished using Bayesian Inference (BI) in MrBayes v3.2.7 (Ronquist et al., 2012). The analysis included four runs and eight chains (107 generations each, sampling every 103 generations) for each run. Several MCMC convergence diagnostics were used to check for convergence and stationary, following the manual's instructions, and the first 25% of the trees were discarded as burn-in, as a measure to sample from the stationary distribution and avoid the possibility of including random, sub-optimal trees. A majority rule consensus tree was then produced from the posterior distribution of trees, and the posterior probabilities were calculated as the percentage of samples recovering any particular clade. Posterior probabilities $\geq$ 0.95 were considered to indicate statistically significant support (Huelsenbeck and Ronquist, 2001).

Population network. A population network was constructed using PopART v1.7 (Leigh and Bryant, 2015) based on a median joining network (Bandelt et al., 1999).

Results and Discussion

The first observations of *P. siculus* on Crete were made on 26 May 2023 by one of the authors (RF) at Kladisos Beach (Fig. 2B). On 13 June 2023, two observers (VS, AC) surveyed a wider area (Fig. 2A), and detected and collected a single individual. Finally, GA observed ten individuals from 9–11 April 2024. The invasive population of *P. siculus* was recorded in an area of 11.8 hectares, as estimated by MCP. This area includes Kladisos Beach, in the transition zone between the sandy habitat and the beach vegetation, as well as the adjacent Kladisos riverbank (Fig. 2C).

We obtained 408 bp of cyt *b* sequences from the sampled individual (OR636396). The BLAST search revealed that the cyt *b* sequence we produced was highly similar (identity 90–100%) to the available cyt *b* sequences of *P. siculus* (including samples from the terra typica of the species). The alignment had 58 variable and 49 parsimony-informative sites (75 and 70 when the outgroups were included, respectively). The p-distances between the individual from Chania and *P. siculus* ranged from 0.3–9.6%. The best nucleotide substitution model and partitioning scheme was K80 + I for the first and second codon positions and HKY for the third. In the BI analysis (harmonic mean $-lnL$ = -1364.05), the MCMC diagnostics indicated stationarity and provided clues of convergence. The examined specimen from Chania forms a statistically highly supported clade with *P. siculus* at a posterior probability (*p.p.*) of 1.00. More specifically, the individual forms a clade (*p.p.* = 1.00) with samples from the A1, A2, A3, and T clades, including also the specimens from Athens (Fig. 3). As for the population network, the sample from Chania is joined with the Athenian samples and the clades A1, A2, and A3 (Fig. 4).

According to our results, Athens is the most likely source of the Cretan population, also considering the geographical position and the constant ship connections between the two localities. However, we cannot exclude the possibility that the species was introduced via private vessels coming from the Adriatic coast. *Podarcis siculus* was probably introduced to Crete accidentally, and we cannot exclude a multiple-origin scenario for this population. Further studies with a larger sample size will allow testing this hypothesis.

The Italian wall lizard is a problematic invasive species that has successfully invaded several regions across the world including areas in France, Spain, Latvia, Turkey, the United States, and Balkan countries, like Montenegro and Greece (Silva-Rocha et al., 2014;

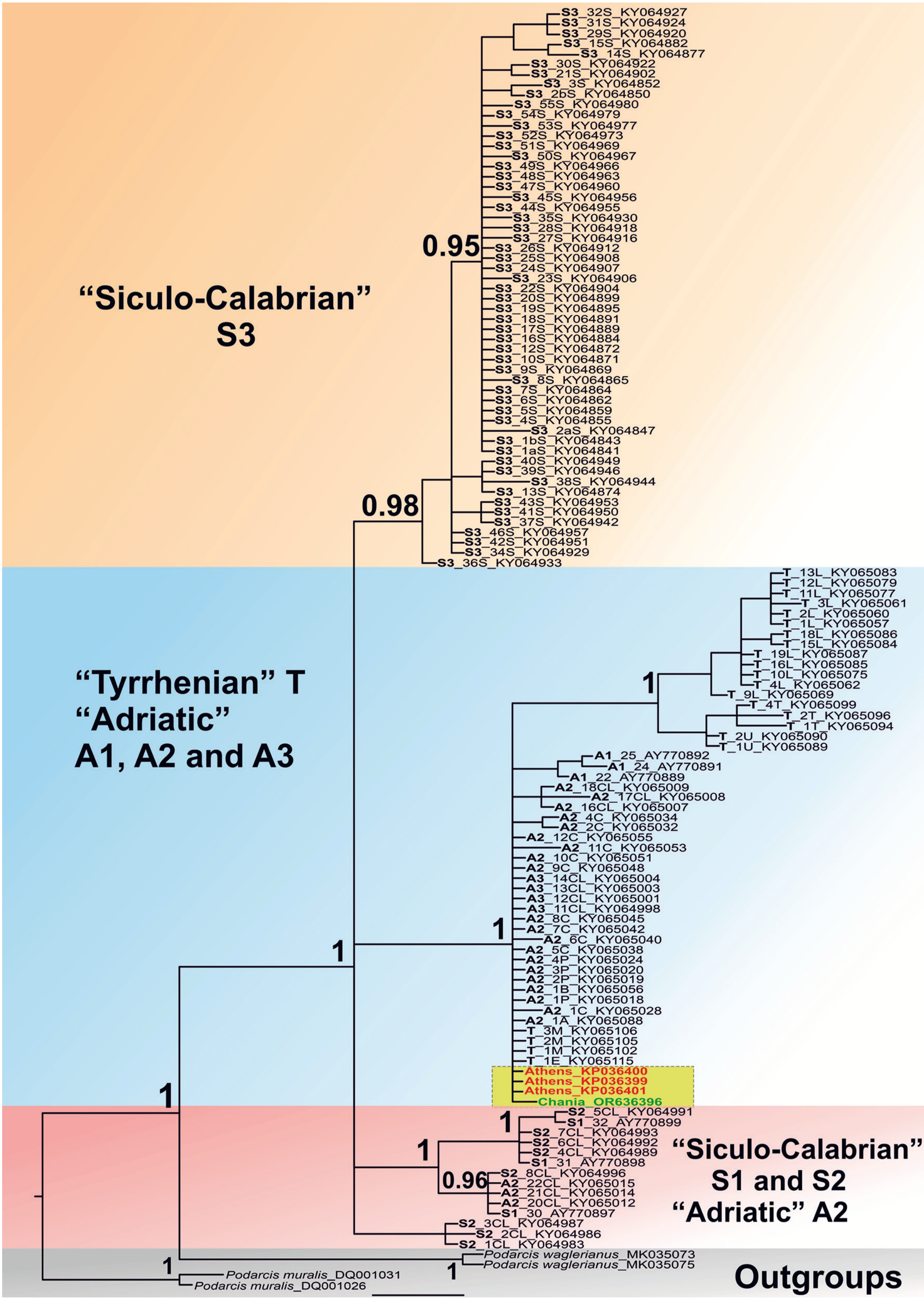

Figure 3. Bayesian Inference tree for *Podarcis siculus*, based on cyt *b* sequences with posterior probabilities shown near the branches. The major clades of *P. siculus* are shown and the Greek populations are highlighted in orange.

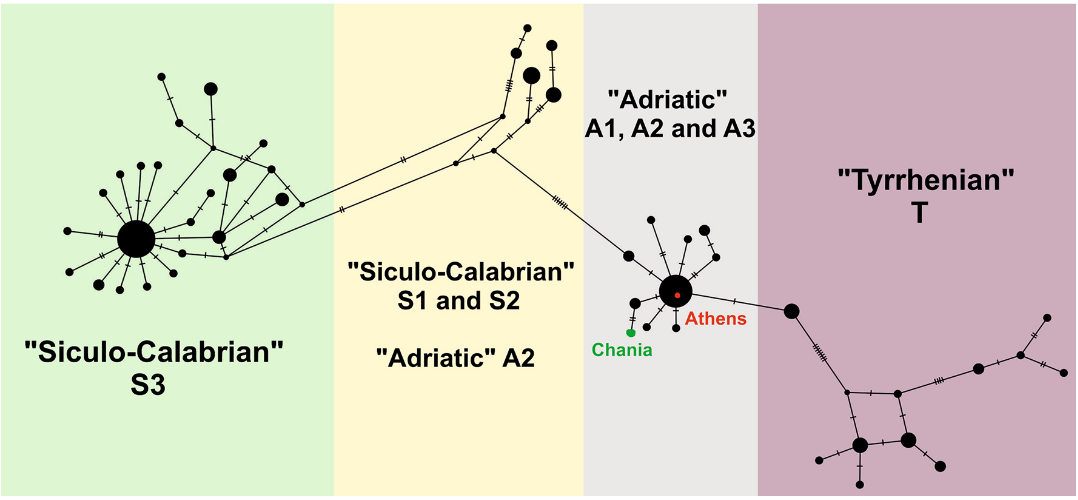

Figure 4. Population network of *Podarcis siculus* based on cyt *b* sequences showing the major clades of the species. The populations from Athens (red) and Chania (green) are shown within the Adriatic clades (A1, A2 and A3).

Pupins et al., 2023; Bowles, 2024). There are several reports of competition with other species, leading to the extirpation of the native competitor (Capula et al., 2002; Damas-Moreira et al., 2020; Limnios et al., 2022) or hybridization with native *Podarcis* species (Gorman et al., 1975; Capula, 1993, 2002; Capula et al., 2002). For instance, the Aeolian wall lizard *P. raffonei* Mertens, 1952, which inhabits only the Aeolian Islands, is facing extinction due to competitive exclusion and hybridization with *P. siculus* (Capula et al., 2002; D'Amico et al., 2018; Ficetola et al., 2021).

Climate conditions and habitats in Crete are largely similar to those found in the native range of *P. siculus* (Isailovic et al., 2009) and the invasive population is therefore expected to thrive. This raises concerns for the native fauna, especially for *P. cretensis*, which is syntopic with the invasive *P. siculus* population (VS, AC, pers. comm.). *Podarcis cretensis* has a limited range (western Crete and satellite islets) and inhabits mainly shrublands, rocky areas and dry riverbeds. It is threatened by human activities, such as tourism, which cause habitat degradation and loss (Lymberakis, 2009). The presence of *P. siculus* in the core of the *P. cretensis* range raises concerns about the potential for local extinction due to hybridization or competitive exclusion if complete niche overlap exists between the two species. This scenario is plausible, as *P. cretensis* evolved on Crete without the presence of other *Podarcis* species (Lymberakis et al., 2018; Spilani et al., 2019). The risk is higher on smaller islets, where populations are more vulnerable and may face a fate similar to that of *P. raffonei* in the Aeolian Archipelago.

The complete eradication of invasive populations is a very challenging process (Zavaleta et al., 2001; Adams and Pearl, 2007; Green and Grosholz, 2021). Complete removal of individuals requires significant resources and time, and success depends on the size of the population, the characteristics of the area, and the challenges of detecting and removing individuals (Green and Grosholz, 2021). In 2015, the Hellenic Herpetological Society initiated an eradication program to remove the invasive *P. siculus* population from Athens but did not achieve complete eradication (Adamopoulou and Pafilis, 2019).

In conclusion, like the Lernaean Hydra – a mythological Greek creature that grows new heads each time one is cut off – *P. siculus* has established yet another invasive population in Greece, potentially representing the first case of a bridgehead invasion by this species in the country. This finding raises more concern about future invasions of *P. siculus* on other Greek islands. The Cretan population should be monitored closely to estimate its dynamics and possible impacts in the recipient environment. This should also be applied to the Athenian population, whose dynamics need to be reevaluated. The frequency of bridgehead invasions can be linked to the structure and configuration of human transport networks (Bertelsmeier and Keller, 2018). Greece's coastal transport network is highly complex, with over 120 ports (Pallis, 2006) and daily connections between the mainland and islands. In conclusion, the findings of this study highlight the need for proactive measures, such as strengthening biosecurity protocols for trade and transport, to prevent future invasions on other Greek islands. Additionally, this study also provides valuable information in supporting future assessments of alien species flows in the Mediterranean Basin.

References

Adamopoulou, C. (2015): First record of *Podarcis siculus* (Rafinesque-Schmaltz, 1810) from Greece. Herpetozoa **27**: 187–188.

Adamopoulou, C., Legakis, A. (2016): First account on the occurrence of selected invasive alien vertebrates in Greece. BioInvasions Records **5**: 189–196.

Adamopoulou, C., Pafilis, P. (2019): Eaten or beaten? Severe population decline of the invasive lizard *Podarcis siculus* (Rafinesque-Schmaltz, 1810) after an eradication project in Athens, Greece. Herpetozoa **32**: 165–169.

Adams, M.J., Pearl, C.A. (2007): Problems and opportunities managing invasive bullfrogs: is there any hope? In: Biological Invaders in Inland Waters: Profiles, Distribution, and Threats, p. 679–693. Gherardi, F., Ed., Dordrecht, The Netherlands, Springer.

Arnold, E.N., Ovenden, D. (2002): A Field Guide to the Reptiles and Amphibians of Britain and Europe. London, UK, Harper Collins. 320 pp.

Bandelt, H.J., Forster, P., Röhl, A. (1999): Median-joining networks for inferring intraspecific phylogenies. Molecular Biology and Evolution **16**: 37–48.

Bellard, C., Bernery, C., Leclerc, C. (2021): Looming extinctions due to invasive species: Irreversible loss of ecological strategy and evolutionary history. Global Change Biology **27**: 4967–4979.

Bertelsmeier, C., Keller, L. (2018): Bridgehead effects and role of adaptive evolution in invasive populations. Trends in Ecology & Evolution **33**: 527–534.

Blondel, J., Aronson, J., Bodiou, J.-Y., Boeuf, G. (2010): The Mediterranean Region: Biological Diversity in Space and Time. Oxford, UK, Oxford University Press.

Blumenfeld, A.J., Eyer, P.A., Husseneder, C., Mo, J., Johnson, L.N.L., Wang, C., et al. (2021): Bridgehead effect and multiple introductions shape the global invasion history of a termite. Communications Biology **4**: 196.

Bowles, P. (2024): *Podarcis siculus*. The IUCN Red List of Threatened Species 2024: e.T222915874A217280511.

Bruford, M.W., Hanotte, O., Brookfield, J.F.Y., Burke, T. (1998): Multilocus and single-locus DNA fingerprinting. In: Molecular Genetic Analysis of Populations: a Practical Approach, p. 287–336. Hoelzel, A.R., Ed., Oxford, UK, IRL Press.

Caffrey, J., Baars, J., Barbour, J.H., Boets, P., Boon, P.J., Davenport, K., et al. (2014): Tackling invasive alien species in Europe: the top 20 issues. Management of Biological Invasions **5**: 1–20.

Calenge, C. (2011): Exploratory Analysis of the Habitat Selection by the Wildlife in R: the adehabitatHS Package. Available at: https://cran.r-project.org/web/packages/adehabitatHS/vignettes/adehabitatHS.pdf. Accessed on 1 June 2025.

Capula, M. (1993): Natural hybridization in *Podarcis sicula* and *P. wagleriana* (Reptilia: Lacertidae). Biochemical Systematics and Ecology **21**: 373–380.

Capula, M. (2002): Genetic evidence of natural hybridization between *Podarcis sicula* and *Podarcis tiliguerta* (Reptilia: Lacertidae). Amphibia-Reptilia **23**: 313–321.

Capula, M., Luiselli, L., Bologna, M.A., Ceccarelli, A. (2002): The decline of the Aeolian wall lizard, *Podarcis raffonei*: causes and conservation proposals. Oryx **36**: 66–72.

Capula, M., Aloise, G. (2012): Extreme feeding behaviours in the Italian wall lizard, *Podarcis siculus*. Acta Herpetologica **6**: 11–14.

Damas-Moreira, I., Riley, J.L., Carretero, M.A., Harris, D.J., Whiting, M.J. (2020): Getting ahead: exploitative competition by an invasive lizard. Behavioral Ecology and Sociobiology **74**: 1–12.

D'Amico, M., Bastianelli, G., Faraone, F.P. (2018): The spreading of the invasive Italian wall lizard on Vulcano, the last island inhabited by the critically endangered Aeolian wall lizard. Herpetological Conservation & Biology **13**: 146–157.

Doherty, T.S., Glen, A.S., Nimmo, D.G., Ritchie, E.G., Dickman, C.R. (2016): Invasive predators and global biodiversity loss. Proceedings of the National Academy of Sciences USA **113**: 11261–11265.

Gentili, R., Schaffner, U., Martinoli, A., Citterio, S. (2021): Invasive alien species and biodiversity: impacts and management. Biodiversity **22**: 1–3.

Gorman, G.C., Soule, M., Yang, Y., Nevo, E. (1975): Evolutionary genetics of insular Adriatic lizards. Evolution **29**: 52–71.

Green, S.J., Grosholz, E.D. (2021): Functional eradication as a framework for invasive species control. Frontiers in Ecology and the Environment **19**: 98–107.

Guindon, S., Dufayard, J.F., Lefort, V., Anisimova, M., Hordijk, W., Gascuel, O. (2010): New algorithms and methods to estimate maximum-likelihood phylogenies: assessing the performance of PhyML 3.0. Systematic Biology **59**: 307–321.

Gunn, R.L., Benkwitt, C.E., Graham, N.A., Hartley, I.R., Algar, A.C., Keith, S.A. (2023): Terrestrial invasive species alter marine vertebrate behaviour. Nature Ecology & Evolution **7**: 82–91.

Ficetola, G.F., Silva-Rocha, I., Carretero, M.A., Vignoli, L., Sacchi, R., Melotto, A., Scali, S., Salvi, D. (2021): Status of the largest extant population of the critically endangered Aeolian lizard *Podarcis raffonei* (Capo Grosso, Vulcano Island). PloS ONE **16**: e0253631.

Huelsenbeck, J.P., Ronquist, F. (2001): MRBAYES: Bayesian inference of phylogenetic trees. Bioinformatics **17**: 754–755.

Hulme, P.E. (2009): Trade, transport and trouble: managing invasive species pathways in an era of globalization. Journal of Applied Ecology **46**: 10–18.

Isailovic, J.C., Vogrin, M., Corti, C., Mellado, V.P., Sa-Sousa, P., Cheylan, M., et al. (2009): *Podarcis siculus*. The IUCN Red List of Threatened Species 2009: e.T61553A221687194.

Javal, M., Lombaert, E., Tsykun, T., Courtin, C., Kerdelhué, C., Prospero, S., et al. (2019): Deciphering the worldwide invasion of the Asian long-horned beetle: a recurrent invasion process from the native area together with a bridgehead effect. Molecular Ecology **28**: 951–967.

Johovic, I., Gama, M., Banha, F., Tricarico, E., Anastácio, P. M. (2020): A potential threat to amphibians in the European Natura 2000 network: forecasting the distribution of the American bullfrog *Lithobates catesbeianus*. Biological Conservation **245**: 108551.

Kardum Hjort, C., Paris, J.R., Smith, H.G., Dudaniec, R.Y. (2024): Selection despite low genetic diversity and high gene flow in a rapid island invasion of the bumblebee, *Bombus terrestris*. Molecular Ecology **33**: e17212.

Kraus, F. (2015): Impacts from invasive reptiles and amphibians. Annual Review of Ecology, Evolution and Systematics **46**: 75–97.

Kumar, S., Stecher, G., Li, M., Knyaz, C., Tamura, K. (2018): MEGA X: molecular evolutionary genetics analysis across computing platforms. Molecular Biology and Evolution **35**: 1547–1549.

Lanfear, R., Frandsen, P.B., Wright, A.M., Senfeld, T., Calcott, B. (2017): Partitionfinder 2: new methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. Molecular Biology and Evolution **34**: 772–773.

Leigh, J.W., Bryant, D. (2015): POPART: full-feature software for haplotype network construction. Methods in Ecology and Evolution **6**: 1110–1116.

Limnios, A., Adamopoulou, C., Carretero, M.A., Pafilis, P. (2022): Invasive Italian wall lizards outcompete native congeneric species in finding food in a Y-maze. Acta Ethologica **25**: 43–55.

Lombaert, E., Guillemaud, T., Cornuet, J.M., Malausa, T., Facon, B., Estoup, A. (2010): Bridgehead effect in the worldwide invasion of the biocontrol harlequin ladybird. PLoS ONE **5**: e9743.

Lymberakis, P. (2009): *Podarcis cretensis*. The IUCN Red List of Threatened Species 2009: e.T157252A5060934.

Lymberakis, P., Pafilis, P., Poulakakis, N., Sotiropoulos, K., Valakos, E. (2018): The amphibians and reptiles of the Aegean Sea. In: Biogeography and Biodiversity of the Aegean, p. 169–189. Sfenthourakis, S., Pafilis, P., Parmakelis A., Poulakakis, N., Triantis, K.A., Eds., Nicosia, Cyprus, Broken Hill.

Ma, L.-J., Cao, L.-J., Chen, J.-C., Tang, M.-Q., Song, W., Yang, F.-Y., et al. (2024): Rapid and repeated climate adaptation involving chromosome inversions following invasion of an insect. Molecular Biology and Evolution **41**: msae044.

Oduor, A.M., Leimu, R., van Kleunen, M. (2016): Invasive plant species are locally adapted just as frequently and at least as strongly as native plant species. Journal of Ecology **104**: 957–968.

Oskyrko, O., Sreelatha, L.B., Silva-Rocha, I., Sos, T., Vlad, S.E., Cogălniceanu, D., et al. (2022): Molecular analysis of recently introduced populations of the Italian wall lizard (*Podarcis siculus*). Acta Herpetologica **17**: 147–157.

Pallis, A.A. (2006). Port governance in Greece. Research in Transportation Economics **17**: 155–169.

Palumbi, S.R. (1996): Nucleic acids II: the polymerase chain reaction. In: Molecular Systematics, p. 205–248. Hillis, D.M., Moritz, C., Mable, B.K., Eds., Sunderland, Massachusetts, USA, Sinauer.

Polce, C., Cardoso, A.C., Deriu, I., Gervasini, E., Tsiamis, K., Vigiak, O., et al. (2023): Invasive alien species of policy concerns show widespread patterns of invasion and potential pressure across European ecosystems. Scientific Reports **13**: 8124.

Psonis, N., Antoniou, A., Kukushkin, O., Jablonski, D., Petrov, B., Crnobrnja-Isailović, J., et al. (2017): Hidden diversity in the *Podarcis tauricus* (Sauria, Lacertidae) species subgroup in the light of multilocus phylogeny and species delimitation. Molecular Phylogenetics and Evolution **106**: 6–17.

Pupins, M., Martinez-Silvestre, A., Arribas, O., Čeirāns, A., Kirjusina, M. (2023): First records of *Scinax ruber*, *Podarcis siculus*, *Podarcis ionicus* and their parasites in Latvia: fruit trade is an intercontinental alien herpetofauna and parasitofauna invasion vector into Europe. BioInvasions Records **12**: 321–329.

Pyšek, P., Hulme, P.E., Simberloff, D., Bacher, S., Blackburn, T.M., Carlton, J.T., et al. (2020): Scientists' warning on invasive alien species. Biological Reviews **95**: 1511–1534.

R Core Team (2022): R: a language and environment for statistical computing. Vienna, Austria, R Foundation for Statistical Computing.

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., et al. (2012): MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology **61**: 539–542.

Roy, H.E., Bacher, S., Essl, F., Adriaens, T., Aldridge, D.C., Bishop, J.D.D., et al. (2018): Developing a list of invasive alien species likely to threaten biodiversity and ecosystems in the European Union. Global Change Biology **25**: 1032–1048.

Russell, J.C., Meyer, J.Y., Holmes, N.D., Pagad, S. (2017): Invasive alien species on islands: impacts, distribution, interactions and management. Environmental Conservation **44**: 359–370.

Seebens, H., Blackburn, T.M., Dyer, E.E., Genovesi, P., Hulme, P.E., Jeschke, J.M., et al. (2017): No saturation in the accumulation of alien species worldwide. Nature Communications **8**: 14435.

Seebens, H., Bacher, S., Blackburn, T.M., Capinha, C., Dawson, W., Dullinger, S., et al. (2021): Projecting the continental accumulation of alien species through to 2050. Global Change Biology **27**: 970–982.

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 Evolutionary Biology **17**: 1–15.

Silva-Rocha, I., Salvi, D., Harris, D.J., Freitas, S., Davis, C., Foster, J., et al. (2014): Molecular assessment of *Podarcis sicula* populations in Britain, Greece and Turkey reinforces a multiple-origin invasion pattern in this species. Acta Herpetologica **9**: 253–258.

Spilani, L., Bougiouri, K., Antoniou, A., Psonis, N., Poursanidis, D., Lymberakis, P., Poulakakis, N. (2019): Multigene phylogeny, phylogeography and population structure of *Podarcis cretensis* species group in south Balkans. Molecular Phylogenetics and Evolution **138**: 193–204.

Speybroeck, J., Beukema, W., Bok, B., Van Der Voort, J. (2016). Field Guide to the Amphibians and Reptiles of Britain and Europe. London, UK, Bloomsbury.

Vogiatzakis, I.N., Mannion, A.M., Sarris, D. (2016): Mediterranean island biodiversity and climate change: the last 10,000 years and the future. Biodiversity and Conservation **25**: 2597–2627.

Zavaleta, E.S., Hobbs, R.J., Mooney, H.A. (2001): Viewing invasive species removal in a whole-ecosystem context. Trends in Ecology & Evolution **16**: 454–459.

Zuffi, M.A., Giannelli, C. (2013): Trophic niche and feeding biology of the Italian wall lizard, *Podarcis siculus campestris* (De Betta, 1857) along western Mediterranean coast. Acta Herpetologica **8**: 35–39.

Accepted by Fulvio Licata