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Research Article

Origin of introduced Italian wall lizards, *Podarcis siculus* (Rafinesque-Schmaltz, 1810) (Squamata: Lacertidae), in North America

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Citation: Oskyrko O, Sreelatha LB, Hanke GF; Deichsel G, Carretero MA (2022) Origin of introduced Italian wall lizards, *Podarcis siculus* (Rafinesque-Schmaltz, 1810) (Squamata: Lacertidae), in North America. *BioInvasions Records* 11 (in press)

Received: 8 February 2022

Accepted: 15 July 2022

Published: 30 September 2022

Handling editor: Alejandro Zaldívar-Riverón

Thematic editor: Tim Adriaens

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Abstract

Invasive species are one of the main causes of biodiversity loss worldwide. As introduced, populations may increase in abundance and expand geographical range, so does the potential for negative impacts on native communities. As such, it is necessary to understand the processes driving range expansion, before a species becomes established in new areas. Through an investigation into capacity for population growth and range expansion of introduced populations of a non-native lizard, we aimed to demonstrate how multi-scale factors influence spatial spread, population growth, and invasion potential in introduced species. The Italian Wall Lizard (*Podarcis siculus*) was introduced multiple times to the United States with extant populations in California, Kansas, New Jersey, and New York. Recently, a single specimen was discovered in British Columbia, Canada, and unstudied populations are on Orcas Island and Missouri (USA). We used phylogenetic analysis of mtDNA sequences (*cytb* gene) of individuals sampled from these introduced populations and across the native range to identify potential source populations. Our phylogenetic analysis result with documentation of the introductions revealed that the Canadian individual is derived from the Tuscany clade (together with samples from Kansas and New York). The New Jersey population is likely from the Adriatic clade and the Californian one from Sicily. The Orcas Island and Missouri populations still require study. Consequently, humans are key drivers of the distribution of alien reptiles in North America, but the distributions are determined by a complex interplay between human activities, geographic factors and species features. Genetic evidence is essential for reliable biogeographic assessment of invasive species, particularly in systems with a long history of human influence.

Key words: alien species, invasion pathways, range expansion, phylogenetic, Canada, USA

Introduction

Global rise in the number of species introduced to regions beyond their native range via human-mediated translocation shows no sign of reaching a saturation point (Seebens et al. 2017). While most species fail to establish or have little negative effect following introduction, a subset of these do

spread and eventually have significant impact on economies, human health, native biodiversity, and ecosystem services (Keller et al. 2011; Kolar and Lodge 2001; Vila et al. 2010). For non-native species to become widespread and potentially damaging following introduction to new regions, introduced populations must negotiate the three stages of an introduction–establishment–invasion continuum (Blackburn et al. 2011). Evaluation of the likelihood of a species to be transported, established, and to spread, as well as the potential for having ecological, economical, and health impacts, forms the basis of “invasive” risk assessment for alien species (Bacher et al. 2018; Roy et al. 2019). As such, there is great interest in understanding the patterns of colonization, rates of expansion, as well as environmental factors which limit distributions of the introduced species (Gallien et al. 2010; Roy et al. 2019). Following introduction and successful establishment beyond native ranges, species can further expand their range through local dispersal processes and/or by jump dispersal events that may be human-mediated (i.e., deliberate or accidental movement of individuals between habitats). Human assistance was certainly behind the rapid dispersal of *Podarcis muralis* (Laurenti, 1768) in British Columbia (Engelstoff et al. 2020). Furthermore, our ability to assess and predict the temporal dynamics of invasions is often complicated by the phenomenon of lag phases; wherein, an introduced species remains at low population levels in the early stages of establishment for a protracted period of time before the sudden onset of rapid range expansion (see Crooks 2005). The key point is that rigorous tests of hypotheses for invasion success must reconstruct the invasion history, whether it is an introduction from a single native-range source or a more complicated scenario with multiple sources and admixture within introduced populations.

In recent years, development of molecular genetics tools has greatly improved our inference of invasion dynamics and the demography of biological invasions, allowing a more objective determination of alien status (Le Roux and Wicczorek 2009). Nevertheless, only a small subset of putatively alien populations has been investigated in depth using genetics. Moreover, some patterns of low genetic diversity and shallow divergence can be explained either by human introductions or by recent natural colonization by only a few individuals (e.g. Silva-Rocha et al. 2012; Salvi et al. 2011, 2014). Integrating genetic data and human factors within eco-geographic analyses (Avice 2000) constitutes an effective approach for identifying the drivers of invasions and unraveling the status of cryptic invasions. In most instances, however, the specific source of an introduced population is not known, multiple undocumented introductions are always possible, and putative routes of introduction and transport vectors may not be reliable. In these cases, molecular markers can help to reconstruct the history of an invasion, identifying the number of native-range source populations, their geographic location and extent, and the distribution of

variation from these sources in the non-native range (e.g., Wares et al. 2005; Fitzpatrick et al. 2012). Then comparisons can be made between these native-range sources and introduced populations to detect ecological and evolutionary changes.

Most reptiles tend to have poor dispersal abilities (Steinitz et al. 2006; Qian 2009). However, many species are increasingly transported by humans, which promotes both short- and long-distance range expansion (Kraus 2009). Lizards are the most abundant and wide-spread reptiles (Novosolov et al. 2016) and many species live close to humans or in highly disturbed habitats. Moreover, they can withstand long periods of starvation and desiccation and many use small cavities as refuge, increasing their chances of passive transport (McCue 2010; Silva-Rocha et al. 2019). It is, hence, not surprising that many lizard species have been introduced around the world. In some cases, repeated introductions of the same species increase the probability of admixture, which may enhance the invasive potential of introduced species (Kolbe et al. 2007; Michaelides et al. 2013) or increase the risk of hybridization with native species or lineages (Santos et al. 2019).

In this study, we determine the potential for range expansion of the non-native Italian wall lizard (*Podarcis siculus* (Rafinesque-Schmaltz, 1810)) in Canada. The native range of *P. siculus* is Italian Peninsula, Sicily and east coast of Adriatic and not covers most of Western and Southern Europe (Podnar et al. 2005; Kraus 2009; Senczuk et al. 2017). Many of these introductions continue to extend the species' range throughout continental Europe (Schulte and Gebhart 2011; Silva-Rocha et al. 2012; 2014; Garin-Barrío et al. 2020), but the species also has several populations established in the United States (Deichsel et al. 2010; Kolbe et al. 2013). Today we have good evidence of expansion and negative effects for *P. siculus* in Europe but much less is known for North America. In Europe, the Italian wall lizard has already been demonstrated to be harmful to native species, for example it can have competitive exclusion (Downes and Bauwens 2002) and hybridize with native *Podarcis* sp. (Capula 1993, 2002). We also have evidence of potential behavioral advantage and even resistance to parasites (Damas-Moreira et al. 2019; Nikolić et al. 2019; Tomé et al. 2021). In the United States, evidence on invasiveness of *P. siculus* is weak (Burke 2010; Deichsel et al. 2010; Goldfarb et al. 2016; Hollingsworth and Thompson 2016; Lambert et al. 2016). Some studies showed that the species may suffer local thermal acclimation and that parasitisation is very low in the USA (Burke et al. 2007, 2011; Liwanag et al. 2018). However, we know that it has been introduced in areas with contrasting climates (California, Missouri, Kansas, New England) and that such nuclei have independent origins (Sicily, Tuscany, Adriatic; Kolbe et al. 2013). Although pet trade is the most likely way of introduction, the increasing records (northwards) in California and New England suggest range expansion also occurs (Donihue et al. 2014, 2015; Briggler et al. 2015). Three of the four extant Italian wall lizard

populations in the USA originated in the pet trade with two (perhaps three) of these introductions being intentional releases (Kolbe et al. 2013). The species has most recently been reported recently from British Columbia (Canada) near an isolated population on Orcas Island, Washington state in the USA (Hanke and Deichsel 2020). In this context, we took advantage of the deep phylogenetic structure of the mtDNA of the species in its native range (Senczuk et al. 2017) to produce phylogenetic inference on the origin of the Canadian specimen, which is needed to determine if it constitutes an independent introduction from the native range or could have resulted from secondary introduction within North America. This information will provide the baseline for properly interpreting the colonization and phenotypic evolution of the species in the continent (Burke and Ner 2005; Burke et al. 2007) and eventually for managing these populations of *P. siculus*.

Materials and methods

In 2019, one female specimen (RBCM 2187) identified as *P. siculus* was collected from an industrial region of Vancouver, British Columbia, Canada (49.208641°N; 123.094219°W; Hanke and Deichsel 2020). Following the current provincial regulations on alien species, the animal was sacrificed humanely and a liver sample was preserved in 96% ethanol. Genomic DNA was extracted using a standard high-salt protocol (Sambrook et al. 1989). Amplification of the mitochondrial (mt) marker *cytochrome b* (*cytb*) gene fragment was conducted by Polymerase Chain Reaction (PCR), using the primers GluDG-L (5' TGA CTT GAA RAA CCA YCG TTG 3') and CB3H (5' GGC AAA TAG GAA RTA TCA TTC 3') from Palumbi (1991). Amplification of genomic DNA began with an initial denaturation for 15 minutes at 94 °C followed by 94 °C for 30 s, annealing at 52 °C for 60 s with 34 cycles, and extension at 72 °C for 60 s. Products were visualized with 1.5% agarose gel electrophoresis. The PCR products were purified and sequenced by an external service (Beckman Coulter Genomics). The amplified fragments were sequenced in a Sanger sequencer and deposited to the GenBank database with accession number OM287580.

Sequences from the samples from the native range in the Italian Peninsula plus Corsica and Sardinia were downloaded from GenBank (accession numbers: KY064841–KY065117, JX186516–JX186568; Kolbe et al. 2013; Senczuk et al. 2017). Additionally, ten published sequences from other introduced populations in United States: JX186567, JX186525–JX186529, JX186516–JX186518 (Kolbe et al. 2013) and one sequence from California (accession number: HQ154646; Deichsel et al. 2010) were also downloaded. To build this genealogy, a distinct GenBank sequence from *Podarcis melisellensis* (Braun, 1877) was integrated as outgroups taxa, accession number AY185057), following Silva-Rocha et al. (2014). The final alignment included 331 sequences. Sequences were edited using Geneious Prime

v.2020.1 (<https://www.geneious.com>). The alignment was performed with MAFFT v.7 (Kato and Standley 2013) which were imported into the software to MrBayes v3.2 (Huelsenbeck and Ronquist 2001). To determine the best model for phylogenetic analysis, the software PartitionFinder v.2.1.1 was used (Lanfear et al. 2012). BI was using HKY+G+I as a model of substitution and run for 10 million generations, sampled every 1000 generations, with a standard 25% burn-in. Convergence of the MCMC runs was checked with Tracer v1.7.1 (Rambaut et al. 2018). The tree was visualized using FigTree v.1.4.4 (Rambaut 2009). Map was created in QGIS 3.10.8 (QGIS Development Team 2020).

Results

We obtained an aligned dataset of the *cytb* gene for *P. siculus* and recovered seven well-supported clades (T, A1, A2, A3, S1, S2 and S3) following Senczuk et al. 2017 results, which are previously published sequences including also sequences from the native range in Italy and nine from introduced populations in the USA reported in Kolbe et al. (2013). The three clades (S1, S2 and S3) within the Siculo-Calabrian lineage. The central-northern lineage split approximately into two main groups that for simplicity we refer to as “Adriatic” and “Tyrrhenian”. The Adriatic group also included two clades with a separation of the clades A1, A2 and A3. The Tyrrhenian clade T was also clearly separated from the others. The phylogenetic relationships inferred from the tree showed well-supported clades (BP \geq 90) with a geographic coherence. Clades were separated from each other with high support values (1.00–0.98). According to the obtained genealogy the single *P. siculus* from Canada is more closely related to individuals from Tuscany (clade T; Figure 1). Similarly, the specimens from Kansas and New York also belonged to this clade. These samples are closely related to samples from native range that were sampled in the localities of Borgo, San Lorenzo, Florence and Pistoia (Italian Peninsula). In contrast to the close association between haplotypes from Canada, Kansas and New York, samples from New Jersey and California are neither closely related to these nor to each other. Three samples from New Jersey were phylogenetically related to the Adriatic clade (clade A2) and are closely related to the native samples from Rosa Marina and Foresta Umbra (southeastern part of the Italian Peninsula). Finally, all specimens from California clustered with the clade containing individuals from Sicily (clade S3) in a large haplogroup. Overall, samples from introduced populations in North America fell in three well-supported clades: T (Tuscany), A2 (Adriatic) and S3 (Sicily). Despite introductions from multiple native-range sources, we did not detect population level admixture of haplotypes from distinct mtDNA lineages within introduced populations.

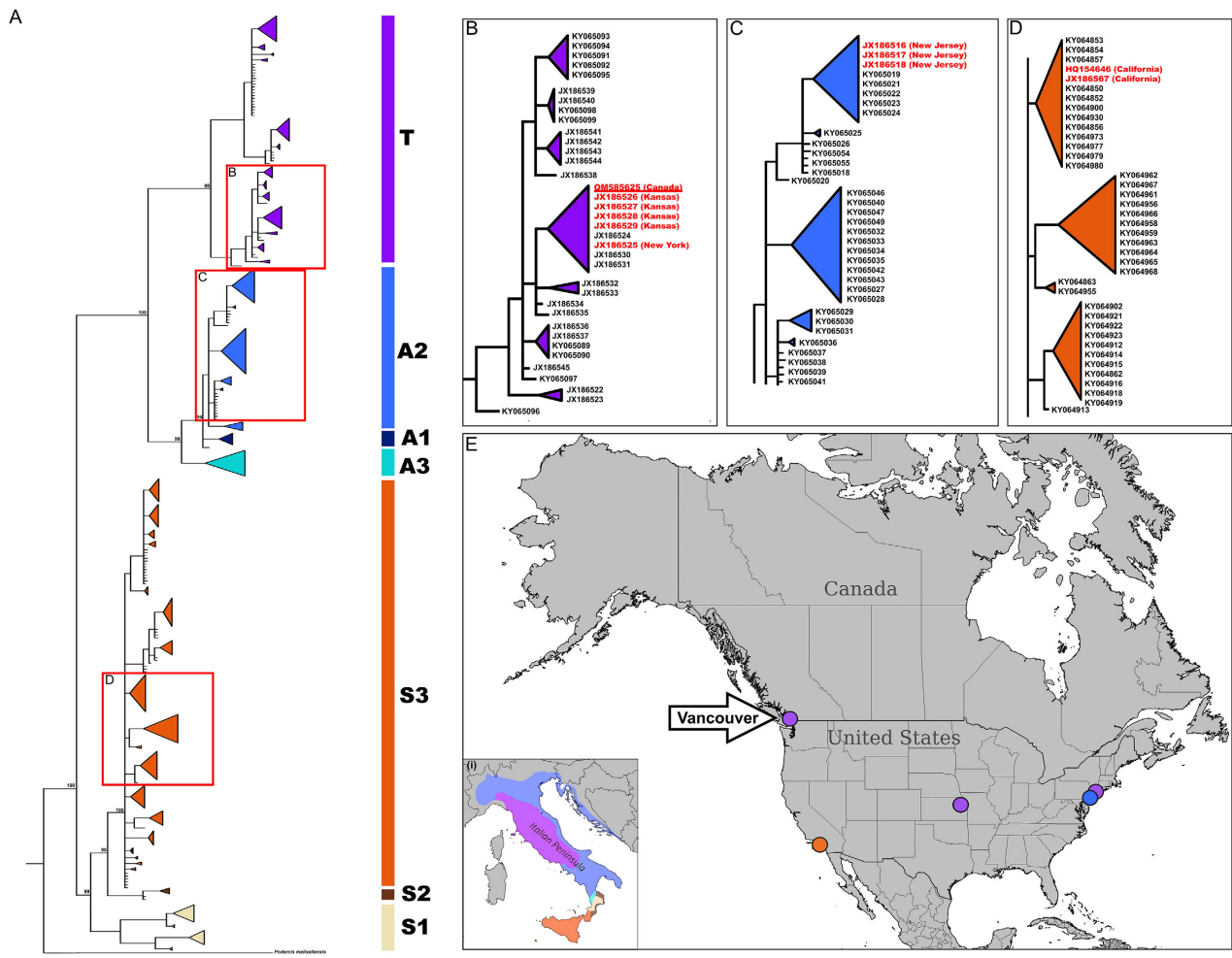


Figure 1. Phylogenetic analysis results (Bayesian inference) from native *Podarcis siculus* populations (Senczuk et al. 2017; Kolbe et al. 2013) and those from introduced populations from USA (Kolbe et al. 2013; Deichsel et al. 2010) and Canada. A. Complete phylogenetic tree with all clades. The clades are named according to Senczuk et al. (2017): A2, A3 and T clades. *P. melisellensis* were used as outgroups; B. The part of phylogenetic tree with introduced samples from Canada, New York and Kansas; C. The part of phylogenetic tree with introduced samples from New Jersey; D. The part of phylogenetic tree with introduced samples from California; E. Geographic distribution of the mtDNA clades of *P. siculus* in North America. All introduced populations are highlighted in red. The Canadian sample is highlighted by a red line. On the map, the location of the individual from Vancouver (Canada) is indicated by an arrow; (i) Geographic distribution of the mtDNA haplotypes in *P. siculus* and are colored according to the main haplogroups identified by Senczuk et al. (2017).

Discussion

Biological invasion is a multi-step process, encompassing (a) introduction of species to a new environment; (b) establishment; and (c) dispersal across the new area (Simberloff et al. 2013). Our phylogenetic analysis, combined with the published evidence, suggests that the allochthonous distribution of the Italian wall lizard in North America resulted in several independent transcontinental introductions followed by successful establishment and in some cases dispersal across shorter distances in favorable environments, all likely human mediated. More importantly, our findings indicate that such an invasion process continues nowadays.

Invasion dynamics depends mostly on both the processes promoting colonization events and on traits favoring success in the new environments. Several macroecological studies have analysed biogeographic and human

factors related to the distribution of alien species around the world (Burns 2015; Capinha et al. 2015). Thus the integration of multiple sources of information, and the validation of records using unambiguous evidence is essential for a more accurate understanding of patterns of alien species distribution. Mitochondrial DNA haplotypes sampled from introduced populations in Canada and USA are derived from three genetically distinct and well-supported native range clades that are largely geographically distinct from each other. The combination of this molecular data with historical context clarifies the geographic extent of the sources in the native range, namely, that at least three independent introductions occurred in North America. This pattern of introductions from multiple native-range sources is common (Dlugosch and Parker 2008), particularly in lizards (Chapple et al. 2012; Schulte et al. 2012).

Haplotypes from the Tuscany clade T are widely distributed within the native range, making it difficult to narrow the geographic extent of the source population for the three largely separated populations. Their geographic location and temporal discovery may suggest an initial importation through New York harbor (well communicated with Europe) and then successive dispersal events westwards in a stepping-stone fashion. In fact, Kolbe et al. (2013) already put forward a similar hypothesis about a Kansas population that could have been brought from New York indirectly by humans. Also, Briggler et al. (2015) confirmed that *P. siculus* was released by humans in Joplin, Missouri. However, it cannot be discarded another colonization order or even that these separate ranges could have originated independently from the native range. These alternative hypotheses could only be disentangled with a population level sampling and fast evolving molecular markers (e.g. microsatellites; for *Podarcis* sp. see Michaelides et al. 2013; Beninde et al. 2018; Yang et al. 2021).

The first *P. siculus* on the loose in Canada was collected at the office of Honeycomb Direct in Vancouver in 2019, about 65 km north of the *P. siculus* population on Orcas Island, Washington (Hanke and Deichsel 2020). The authors suggested that it was a lone stow-away and it is possible that this Canadian specimen stowed away in camping gear used on Orcas Island, or arrived in a mail shipment from elsewhere. Unfortunately, samples from Orcas Island have not been studied. Therefore, we cannot confirm the origin of this Canadian specimen from Orcas Island. Remarkably, as of 2020, a congeneric species, *Podarcis muralis* is firmly established as an invasive species on several islands and the southern mainland of British Columbia, with evidence of demographic and geographic expansion and negative effects on native lizards (Engelstoft et al. 2020). Thus, the addition of a second *Podarcis* species would intensify the impact on the native fauna of this region.

Earlier studies point to pet trade pathway for *P. siculus* introductions to the USA (Deichsel et al. 2010; Kolbe et al. 2013; Briggler et al. 2015) resulting

in established populations that span the phylogenetic diversity and geographic extent of this species in its native range. In addition to *P. siculus*, other introduced populations of *P. muralis* and *Lacerta bilineata* have been found in the United States through animal trafficking (Burke and Deichsel 2008; Collins and Gubanyi 2010). The desire for variety in the pet trade – new species, uncommon varieties can have led to sampling of genetically diverse source populations with subsequent release and establishment in non-native areas. Whether the pet trade leads to the establishment of non-native populations with greater diversity compared to other pathways (e.g., biocontrol, cargo, tree nursery trade) remains to be tested. The numerous other new introductions of *P. siculus* (Tuniyev et al. 2020; Garin-Barrio et al. 2020; Iskenderov et al. 2021), as well as reptiles in general (Lever 2003), may serve as good subjects for tests of this hypothesis given their popularity in the pet trade.

Molecular data are still lacking for some introduced populations of *P. siculus* (Hanke and Deichsel 2020; Tuniyev et al. 2020). Obtaining exhaustive genetic data for species combinations is far from complete, yet the integration of genetic data in biogeographical analyses can be used to improve our understanding of present-day biodiversity. The human-related factors stand out as key drivers of the current distribution of alien reptiles in the world, in combination with species traits, such as diet and environmental tolerance, that are important for the success of invasion and persistence of alien species (Case 1996; Kolar and Lodge 2001; Blackburn and Duncan 2001; Cassey 2002). The integration of distribution, genetic data allowed identification of cryptic introduced species, some of which may threaten native biota (Hendrix et al. 2008; Kenis et al. 2009). The same framework could then be applied to other groups with poor natural dispersal in human-dominated regions, providing a baseline for delineating more realistic conservation strategies and detecting putative alien species.

Acknowledgements

We thank the reviewers for important comments that improved the manuscript.

Funding declaration

The project was supported by the Portuguese Foundation for Science and Technology (FCT) project 28014 02/SAICT/2017.

Authors' contribution

OO: methodology, software, validation, formal analysis, writing – original draft, writing – review and editing; LBS: laboratory work; GFH, GD: sample collection, editing– original draft; MAC: conceptualization, writing – review and editing, project administration, funding acquisition.

Ethics and permits

All *Podarcis* are Schedule C of the British Columbia Wildlife Act and that means there are no permits required to catch and euthanize *Podarcis*. The single *P. siculus* specimen was euthanized according to Canadian Council of Animal Care standards.

References

- Avise JC (2000) Phylogeography - The history and formation of species. Harvard University Press, Cambridge, UK, 447 pp, <https://doi.org/10.2307/j.ctv1nznfj7>
- Bacher S, Blackburn TM, Essl F, Jeschke JM, Genovesi P, Heikkilä J, Jones G, Keller R, Kenis M, Kueffer C, Martinou AF, Nentwig W, Pergl J, Pyšek P, Rabitsch W, Richardson DM, Roy HE, Saul WC, Scalera R, Vilà M, Wilson JR, Kumschick S (2018) Socio-economic impact classification of alien taxa (SEICAT). *Methods in Ecology and Evolution* 9: 159–168, <https://doi.org/10.1111/2041-210X.12844>
- Beninde J, Feldmeier S, Veith M, Hochkirch A (2018) Admixture of hybrid swarms of native and introduced lizards in cities is determined by the cityscape structure and invasion history. *Proceedings of the Royal Society B: Biological Sciences* 285: 20180143, <https://doi.org/10.1098/rspb.2018.0143>
- Blackburn TM, Duncan RP (2001) Establishment patterns of exotic birds are constrained by non-random patterns in introduction. *Journal of Biogeography* 28: 927–939, <https://doi.org/10.1046/j.1365-2699.2001.00597.x>
- Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarosik V, Wilson JR, Richardson DM (2011) A proposed unified framework for biological invasions. *Trends in Ecology & Evolution* 26: 333–339, <https://doi.org/10.1016/j.tree.2011.03.023>
- Briggler JT, Rimer RL, Deichsel G (2015) First Record of the Northern Italian Wall Lizard (*Podarcis siculus campestris*) in Missouri. *IRCF Reptiles and Amphibians* 22: 43–45, <https://doi.org/10.17161/randa.v22i1.14040>
- Burke RL (2010) *Podarcis siculus campestris* (Italian Wall Lizards). USA: New Jersey. *Herpetological Review* 41: 514
- Burke RL, Ner S (2005) Seasonal and daily activity patterns of Italian Wall Lizards, *Podarcis sicula campestris*, in New York. *Northeastern Naturalist* 12: 349–360, [https://doi.org/10.1656/1092-6194\(2005\)012\[0349:SADAPO\]2.0.CO;2](https://doi.org/10.1656/1092-6194(2005)012[0349:SADAPO]2.0.CO;2)
- Burke RL, Deichsel G (2008) Lacertid lizards introduced into North America: history and future. In: Mitchell JC, Jung Brown RE, Bartholomew B (eds), *Urban herpetology*. SAAR, Salt Lake City, USA, pp 347–353
- Burke RL, Goldberg S, Bursey C, Perkins S, Andreadis P (2007) Depauperate parasite fauna in introduced populations of *Podarcis* (Squamata: Lacertidae) lizards in North America. *Journal of Herpetology* 41: 755–757, <https://doi.org/10.1670/07-023.1>
- Burke RL, Hussain AA, Storey JM, Storey KB (2011) Freeze Tolerance and Supercoiling Ability in the Italian Wall Lizard, *Podarcis sicula*, Introduced to Long Island, New York. *Copeia* 2002: 836–842, [https://doi.org/10.1643/0045-8511\(2002\)002\[0836:FTASAI\]2.0.CO;2](https://doi.org/10.1643/0045-8511(2002)002[0836:FTASAI]2.0.CO;2)
- Burns KC (2015) A theory of island biogeography for exotic species. *American Naturalist* 186: 441–451, <https://doi.org/10.1086/682934>
- Capinha C, Essl F, Seebens H, Moser D, Pereira HM (2015) The dispersal of alien species redefines biogeography in the Anthropocene. *Science* 348: 1248–1251, <https://doi.org/10.1126/science.aaa8913>
- Capula M (1993) Natural hybridization in *Podarcis sicula* and *P. wagleriana* (Reptilia: Lacertidae). *Biochemical Systematics and Ecology* 21: 373–380, [https://doi.org/10.1016/0305-1978\(93\)90028-P](https://doi.org/10.1016/0305-1978(93)90028-P)
- Capula M (2002) Genetic evidence of natural hybridization between *Podarcis sicula* and *Podarcis tiliguerta* (Reptilia). *Amphibia-Reptilia* 23: 313–321, <https://doi.org/10.1163/15685380260449199>
- Case TJ (1996) Global patterns in the establishment and distribution of exotic birds. *Biological Conservation* 78: 69–96, https://doi.org/10.1007/978-3-319-43314-1_2
- Cassey P (2002) Life history and ecology influences establishment success of introduced land birds. *Biological Journal of the Linnean Society* 76: 465–480, <https://doi.org/10.1046/j.1095-8312.2002.00086.x>
- Chapple DG, Miller KA, Kraus F, Thompson MB (2012) Divergent introduction histories among invasive populations of the delicate skink (*Lampropholis delicata*): has the importance of genetic admixture in the success of biological invasions been overemphasized? *Diversity and Distributions* 19: 134–146, <https://doi.org/10.1111/j.1472-4642.2012.00919.x>
- Collins JT, Gubanyi JE (2010) History and distribution of the western green *Lacerta*, *Lacerta bilineata* (Reptilia: Squamata: Lacertidea) in Topeka, Kansas. *Journal of Kansas Herpetology* 34: 8–9
- Crooks JA (2005) Lag times and exotic species: The ecology and management of biological invasions in slow-motion. *Ecoscience* 12: 316–329, <https://doi.org/10.2980/1195-6860-12-3-316.1>
- Damas-Moreira I, Riley JL, Harris DJ, Whiting MJ (2019) Can behaviour explain invasion success? A comparison between sympatric invasive and native lizards. *Animal Behaviour* 151: 195–202, <https://doi.org/10.1016/j.anbehav.2019.03.008>
- Deichsel G, Nafis G, Hakim J (2010) *Podarcis siculus* (Italian Wall Lizard) USA: California. *Herpetological Review* 41: 513–514

- Dlugosch KM, Parker IM (2008) Founding events in species invasions: genetic variation, adaptive evolution, and the role of multiple introductions. *Molecular Ecology* 17: 431–449, <https://doi.org/10.1111/j.1365-294X.2007.03538.x>
- Donihue CM, Lambert MR, Watkins-Colwell GJ (2014) *Podarcis sicula* (Italian Wall Lizard). *Herpetological Review* 45: 661–662
- Donihue CM, Lambert MR, Watkins-Colwell GJ (2015) *Podarcis sicula* (Italian Wall Lizard). Habitat, invasion of suburban area of New England. *Herpetological Review* 46: 260–261
- Downes S, Bauwens D (2002) An experimental demonstration of direct behavioural interference in two Mediterranean lacertid lizard species. *Animal Behaviour* 63: 1037–1046, <https://doi.org/10.1006/anbe.2002.3022>
- Engelstoft C, Robinson J, Fraser D, Hanke G (2020) Recent rapid expansion of Common Wall Lizards (*Podarcis muralis*) in British Columbia, Canada. *Northwestern Naturalist* 101: 50–55, <https://doi.org/10.1898/1051-1733-101.1.50>
- Fitzpatrick BM, Fordyce JA, Niemiller ML, Reynolds RG (2012) What can DNA tell us about biological invasions? *Biological Invasions* 14: 245–253, <https://doi.org/10.1007/s10530-011-0064-1>
- Gallien L, Munkemüller T, Albert CH, Boulangéat I, Thuiller W (2010) Predicting potential distributions of invasive species: Where to go from here? *Diversity and Distributions* 16: 331–342, <https://doi.org/10.1111/j.1472-4642.2010.00652.x>
- Garin-Barrio I, Blanco Y, Cabido C, Carretero MA, Fernández-Arrieta A, Izagirre-Egaña A, López-Aizpuru J, Mandiola E, Oskyrko O, Silva-Rocha I (2020) Introducción reciente de *Podarcis sicula* en dos enclaves costeros del País Vasco. *Boletín de la Asociación Herpetológica Española* 31(2): 181–186
- Goldfarb BA, Lambert MR, Donihue CM, Whatkins-Colwell GJ (2016) *Podarcis siculus* (Italian Wall Lizard). *Herpetological Review* 47: 82
- Hanke GF, Deichsel G (2020) First record of an Italian Wall Lizard (*Podarcis siculus*) in British Columbia, Canada. *Canadian Field-Naturalist* 134: 60–63, <https://doi.org/10.22621/cfn.v134i1.2483>
- Hendrix PF, Callahan MA Jr., Drake JM, Huang CY, James SW, Snyder BA, Zhang W (2008) Pandora's Box Contained Bait: The global problem of introduced earthworms. *Annual Review of Ecology and Systematics* 39: 593–613, <https://doi.org/10.1146/annurev.ecolsys.39.110707.173426>
- Hollingsworth BD, Thompson A (2016) *Podarcis sicula* (Italian Wall Lizard). *Herpetological Review* 47: 424
- Huelsenbeck JP, Ronquist F (2001) MRBAYES: Bayesian inference of phylogeny. *Bioinformatics* 17: 754–755, <https://doi.org/10.1093/bioinformatics/17.8.754>
- Iskenderov TM, Doronin IV, Mustafayeva GA, Kulieva AM (2021) First record of the lizard genus *Podarcis* Wagler 1830 (Reptilia, Lacertidae) in the Caucasus. *The Biological Bulletin* 48: 1319–1322, <https://doi.org/10.31857/S0044513420120041>
- Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* 30: 772–780, <https://doi.org/10.1093/molbev/mst010>
- Keller RP, Geist J, Jeschke JM, Kühn I (2011) Invasive species in Europe: Ecology, status, and policy. *Environmental Sciences Europe* 23: 23, <https://doi.org/10.1186/2190-4715-23-23>
- Kenis M, Auger-Rozenberg MA, Roques A, Timms L, Péré C, Cock MJW, Settele J, Augustin S, Lopez-Vaamonde C (2009) Ecological effects of invasive alien insects. *Biological Invasions* 11: 21–45, https://doi.org/10.1007/978-1-4020-9680-8_3
- Kolar CS, Lodge DM (2001) Progress in invasion biology: Predicting invaders. *Trends in Ecology & Evolution* 16: 199–204, [https://doi.org/10.1016/S0169-5347\(01\)02101-2](https://doi.org/10.1016/S0169-5347(01)02101-2)
- Kolbe JJ, Glor RE, Rodríguez-Schettino L, Chamizo-Lara A, Larson A, Losos JB (2007) Multiple Sources, Admixture, and Genetic Variation in Introduced Anolis Lizard Populations. *Conservation Biology* 21: 1612–1625, <https://doi.org/10.1111/j.1523-1739.2007.00826.x>
- Kolbe JJ, Lavin BR, Burke RL, Rugiero L, Capula M, Luiselli L (2013) The desire for variety: Italian wall lizard (*Podarcis siculus*) populations introduced to the United States via the pet trade are derived from multiple native-range sources. *Biological Invasions* 15: 775–783, <https://doi.org/10.1007/s10530-012-0325-7>
- Kraus F (2009) Alien Reptiles and Amphibians: A Scientific compendium and analysis. Springer, New York, US, 569 pp, <https://doi.org/10.1007/978-1-4020-8946-6>
- Lambert MR, Goldfarb BA, Watkins-Colwell GJ, Donihue CM (2016) *Podarcis siculus* (Italian Wall Lizard). Habitat and suburban invasion. *Herpetological Review* 47: 467–468
- Lanfear R, Calcott B, Ho SYW, Guindon S (2012) PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution* 29: 1695–1701, <https://doi.org/10.1093/molbev/mss020>
- Le Roux J, Wicczorek AM (2009) Molecular systematics and population genetics of biological invasions: Towards a better understanding of invasive species management. *Annals of Applied Biology* 154: 1–17, <https://doi.org/10.1111/j.1744-7348.2008.00280.x>

- Lever C (2003) Naturalized reptiles and amphibians of the world. Oxford University Press, Oxford, UK, 344 pp
- Liwanag HEM, Haro D, Callejas B, Labib G, Pauly GB (2018) Thermal tolerance varies with age and sex for the nonnative Italian Wall Lizard (*Podarcis siculus*) in Southern California. *Journal of Thermal Biology* 78: 269, <https://doi.org/10.1016/j.jtherbio.2018.10.010>
- McCue MD (2010) Starvation physiology: reviewing the different strategies animals use to survive a common challenge. *Comparative Bio-chemistry and Physiology* 156: 1–18, <https://doi.org/10.1016/j.cbpa.2010.01.002>
- Michaelides S, White GM, Bell C, Uller T (2013) Human introductions create opportunities for intra-specific hybridization in an alien lizard. *Biological Invasions* 15: 1101–1112, <https://doi.org/10.1007/s10530-012-0353-3>
- Nikolić B, Josic P, Buric D, Tkalec M, Lisicic D, Blazevic SA, Hranilovic D (2019) Coexisting lacertid lizard species *Podarcis siculus* and *Podarcis melisellensis* differ in dopamine brain concentrations. *Journal of Comparative Physiology A* 205: 451–456, <https://doi.org/10.1007/s00359-019-01335-3>
- Novosolov M, Rodda GH, Feldman A, Kadison AE, Dor R, Meiri S (2016) Power in numbers. Drivers of high population density insular lizards. *Global Ecology and Biogeography* 25: 87–95, <https://doi.org/10.1111/geb.12390>
- Palumbi S, Martin A, Romano S, Millan WO, Stice L, Grabowski G (1991) The simple fool's guide to PCR (ver. 2). University of Hawaii, Honolulu, US, 47 pp
- Podnar M, Mayer W, Tvrtković N (2005) Phylogeography of the Italian wall lizard, *Podarcis sicula*, as revealed by mitochondrial DNA sequences. *Molecular Ecology* 14: 575–588, <https://doi.org/10.1111/j.1365-294X.2005.02427.x>
- QGIS Development Team (2020) QGIS geographic information system. Beaverton, OR: Open Source Geospatial Foundation
- Qian H (2009) Global comparisons of beta diversity among mammals, birds, reptiles, and amphibians across spatial scales and taxonomic ranks. *Journal of Systematics and Evolution* 47: 509–514, <https://doi.org/10.1111/j.1759-6831.2009.00043.x>
- Rambaut A (2009) Figtree. <http://tree.bio.ed.ac.uk/software/figtree/> (accessed 1 June 2021)
- Rambaut A, Drummond AJ, Xie D, Baele G, Suchard MA (2018) Posterior Summarization in Bayesian Phylogenetics Using Tracer 1.7. *Systematic Biology* 67: 901–904, <https://doi.org/10.1093/sysbio/syy032>
- Roy HE, Bacher S, Essl F, Adriaens T, Aldridge DC, Bishop JDD, Blackburn TM, Branquart E, Brodie J, Carboneras C, Cottier-Cook EJ, Copp GH, Dean HJ, Eilenberg J, Gallardo B, Garcia M, García-Berthou E, Genovesi P, Hulme PE, Kenis M, Kerckhof F, Kettunen M, Minchin D, Nentwig W, Nieto A, Pergl J, Pescott OL, Peyton M, Preda J, Roques C, Rorke A, Scalera SL, Schindler R, Schönrogge S, Sewell K, Solarz J, Stewart W, Tricarico AJA, Vanderhoeven E, Velde S, Vilà G, Wood M, Zenetos CA, Rabitsch AW (2019) Developing a list of invasive alien species likely to threaten biodiversity and ecosystems in the European Union. *Global Change Biology* 25: 1032–1048, <https://doi.org/10.1111/geb.14527>
- Salvi D, Harris DJ, Bologna MA, Perera A, Carretero MA, Bologna MA, Carretero MA (2011) Preliminary survey on genetic variation within the Pygmy Agyroides, *Agyroides fitzingeri*, across Corsica and Sardinia. *Amphibia-Reptilia* 32: 281–286, <https://doi.org/10.1163/017353711X556989>
- Salvi D, Schembri PJ, Sciberras A, Harris DJ (2014) Evolutionary history of the Maltese wall lizard *Podarcis filfolensis*: Insights on the “Expansion-Contraction” model of Pleistocene biogeography. *Molecular Ecology* 23: 1167–1187, <https://doi.org/10.1111/mec.12668>
- Sambrook J, Fritsch F, Maniatis T (1989) Molecular Cloning: a laboratory manual, 2nd. Cold Spring Harbor Laboratory, Cold Spring Harbor Laboratory Press, New York, US, 545 pp
- Santos JL, Zagar A, Drašler K, Rato C, Ayres C, Harris DJ, Carretero MA, Salvi D (2019) Phylogeographic evidence for multiple long-distance introductions of the common wall lizard associated with human trade and transport. *Amphibia-Reptilia* 40: 121–127, <https://doi.org/10.1163/15685381-20181040>
- Schulte U, Gebhart J (2011) Geographic origin of a population of the Italian Wall Lizard *Podarcis siculus* (Rafinesque-Schmaltz, 1810), introduced north of the Alps. *Herpetozoa* 24: 96–97, <https://doi.org/10.3906/zoo-1601-22>
- Schulte U, Hochkirch A, Lotters S, Rodder D, Schweiger S, Weimann T, Veith M (2012) Cryptic niche conservatism among evolutionary lineages of an invasive lizard. *Global Ecology and Biogeography* 21: 198–211, <https://doi.org/10.1111/j.1466-8238.2011.00665.x>
- Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, Jeschke JM, Pagad S, Pysek P, Winter M, Arianoutsou M, Bacher S, Blasius B, Brundu G., Capinha C, Celesti-Grapow L, Dawson W, Dullinger S, Fuentes N, Jager H, Kartesz J, Kenis M, Kühn I, Liebhold A, Mosena A, Nishino M, Pearman D, Pergl J, Rabitsch W, Rojas-Sandoval J, Roques A, Rorke S, Rossinelli S, Roy HE, Scalera R, Schindler S, Štajerová K, Tokarska-Guzik B, van Kleunen M, Walker K, Yamanaka T, Essl F (2017) Global rise in emerging alien species results from accessibility of new source pools. *Proceedings of the National Academy of Sciences of the United States of America* 115: E2264–E2273, <https://doi.org/10.1073/pnas.1719429115>

- 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: 6, <https://doi.org/10.1186/s12862-016-0847-1>
- Silva-Rocha I, Salvi D, Carretero MA (2012) Genetic data reveal a multiple origin for the populations of the Italian Wall lizard *Podarcis sicula* (Squamata: Lacertidae) introduced in the Iberian Peninsula and Balearic Islands. *Italian Journal of Zoology* 79: 502–510, <https://doi.org/10.1080/11250003.2012.680983>
- Silva-Rocha I, Salvi D, Harris DJ, Freitas S, Davis C, Foster J, Deichsel G, Adamopoulou C, Carretero MA (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, https://doi.org/10.13128/Acta_Herpetol-14968
- Silva-Rocha I, Salvi D, Carretero MA, Ficetola GF (2019) Alien reptiles on Mediterranean islands: a model for invasion biogeography. *Diversity and Distributions* 25: 995–1005, <https://doi.org/10.1111/ddi.12911>
- Simberloff D, Martin JL, Genovesi P, Maris V, Wardle DA, Aronson J, Courchamp F, Galil B, Garcia-Berthou E, Pascal M, Pysek P, Sousa R, Tabacchi E, Vila M (2013) Impacts of biological invasions: What’s what and the way forward. *Trends in Ecology & Evolution* 28: 58–66, <https://doi.org/10.1016/j.tree.2012.07.013>
- Steinitz O, Heller J, Tsoar A, Rotem D, Kadmon R (2006) Environment, dispersal and patterns of species similarity. *Journal of Biogeography* 33: 1044–1054, <https://doi.org/10.1111/j.1365-2699.2006.01473.x>
- Tuniyev BS, Shagarov LM, Arribas OJ (2020) *Podarcis siculus* (Reptilia: Sauria: Lacertidae), a new alien species for Russian fauna. *Proceedings of the Zoological Institute RAS* 324: 364–370, <https://doi.org/10.31610/trudyzin/2020.324.3.364>
- Tomé B, Harris DJ, Perera A, Damas-Moreira I (2021) Invasive lizard has fewer parasites than native congener. *Parasitology Research* 120: 2953–2957, <https://doi.org/10.1007/s00436-021-07233-5>
- Vila M, Basnou C, Pysek P, Josefsson M, Genovesi P, Gollasch S, Nentwig W, Olenin S, Roques A, Roy D, Hulme PE, Andriopoulos P, Arianoutsou M, Augustin S, Bacher S, Bazos I, Bretagnolle F, Chiron F, Clergeau P, Cochard PO, Cocquempot C, Coeur d’Acier A, David M, Delipetrou P, Desprez-Loustau ML, Didžiulis V, Dorkeld F, Essl F, Galil BS, Gasquez J, Georghiou K, Hejda M, Jarošík V, Kark S, Kokkoris I, Kühn I, Lambdon PW, Lopez-Vaamonde C, Marcer A, Migeon A, McLoughlin M, Minchin D, Navajas M, Panov VE, Pascal M, Pergl J, Perglová I, Pino J, Pobljšaj K, Rabitsch W, Rasplus JY, Sauvard D, Scalera R, Sedláček O, Shirley S, Winter M, Yannitsaros A, Yart A, Zagatti P, Zikos A, Partners D (2010) How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. *Frontiers in Ecology and the Environment* 8: 135–144, <https://doi.org/10.1890/080083>
- Wares JP, Hughes AR, Grosberg RK (2005) Mechanisms that drive evolutionary change: insights from species introductions and invasions. In: Sax DF, Stachowicz JJ, Gaines SD (eds), *Species invasions: insights into ecology, evolution, and biogeography*. Sinauer, Sunderland, pp 229–257
- Yang W, Feiner N, Pinho C, While GM, Kaliontzopoulou A, Harris DJ, Salvi D, Uller T (2021) Extensive introgression and mosaic genomes of Mediterranean endemic lizards. *Nature Communications* 12: 2762–2768, <https://doi.org/10.1038/s41467-021-22949-9>