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What makes an island a suitable refuge for an endemic lizard?

Daniel Escoriza [ID]

GRECO, Institute of Aquatic Ecology,
University of Girona, Girona, Spain

Correspondence
Daniel Escoriza, GRECO, Institute of Aquatic
Ecology, University of Girona, Campus de
Montillivi, 17071 Girona, Spain.
Email: daniel_escoriza@hotmail.com

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Abstract

Aim: To identify and evaluate the environmental properties of the Mediterranean islands that make them a suitable habitat for their endemic lizards. This would represent an important improvement in our knowledge and would assist the conservation of these lizards, which are threatened by both the expansion of mainland species and the increasing intensity of human disturbance on these islands.

Location: Mediterranean Basin.

Methods: I assessed the environmental associations of 50 species of lizard (19 endemic) across 552 Mediterranean islands using outlying mean index analysis. The strength of the species responses was assessed using binomial generalized linear models.

Results: The presence of endemic species is positively correlated with the distance of the island from the mainland. Island connectivity is also positively correlated with an increased presence of endemic lizards, but not with an increased presence of mainland species (i.e. those with exclusive or mainly continental natural distribution). In addition, island size, temperature and vegetation productivity are positively correlated with the presence of mainland species. Outlying mean index (OMI) analysis showed that the endemic species occupy niche positions that are similar to the average environmental conditions in the archipelago, but frequently without using the entire range of niches. The mainland species usually occur in more peripheral positions in the environmental space, except for some highly expansive species.

Conclusions: Lizards that are endemic to the Mediterranean islands were found to be present on a large number of islands within an archipelago, but they quickly disappear as the conditions change, largely because of human activity. Large islands act as population reservoirs for mainland species, facilitating secondary colonization of peripheral islets.

KEYWORDS
invasions, island assemblages, Mediterranean, niche breadth, reptiles

1 | INTRODUCTION

Islands are seen as a paradigm for vulnerable ecosystems because of the rapid loss of diversity that usually occurs after human arrival

(Loehle & Eschenbach, 2012). Islands that have been isolated for a long time contain endemic faunas that are highly sensitive to newly introduced predators or competitors (Poulakakis et al., 2008; Wikelski et al., 2004). Species extinctions are faster on small islands,

as populations are also smaller (Schoener & Schoener, 1983). Extinctions are also common on larger islands, but in some situations, endemic populations may remain depending on their interactions with the introduced mainland species or the existence of refuge habitats (Fox & Fox, 2000; Olson et al., 2006).

The Mediterranean Basin provides an interesting setting that can be used to evaluate patterns of coexistence among mainland and endemic island faunas. This basin comprises more than 3,000 islands that show great geophysical disparity and are spread over an area of 2,500,000 km^2 (Coll et al., 2010). The groups of islands include some that can be classified as "near-oceanic," such as the Balearic Islands or Crete, which have experienced long periods of isolation and endemic evolutionary radiation initiated after the Messinian salinity crisis (Brown et al., 2008; Lalueza-Fox et al., 2005). However, most are continental islands, which remained connected to the mainland during glacial-eustatic regressions (Palombo, 2009). The isolation of all of these archipelagos ended with the first human settlers, who arrived during the Upper Epipalaeolithic (Cherry & Leppard, 2018). The arrival of humans was synchronous with significant changes in the fauna and botanical composition across the Mediterranean islands, which suggests that human activity led to significant environmental impacts (Gippoliti & Amori, 2006; Jalut et al., 2009). The changes involved the introduction of numerous continental species, a process that has been maintained until the present (Barun et al., 2011).

Despite the long history of disturbance, reptile extinctions in the Mediterranean islands have been scarce, at least when compared with other groups of vertebrates (Bover et al., 2008). These extinctions affected large species, such as giant tortoises, turtles and lizards on Malta, and isolated populations of extant species, such as *Testudo marginata* on Crete and *Podarcis lilfordi* on Mallorca and Menorca (Bachmayer et al., 1976; Böhme & Zammit-Maempel, 1982; Terrasa et al., 2009). The extinction of reptiles on the larger islands occurred in prehistoric times, possibly as a result of overharvesting by the first human settlers and the introduction of saurophagic snakes (Kotsakis, 1977; Mencía et al., 2017). On the smaller islands, extinctions followed the accidental translocation of congeneric lizards, such as *P. siculus* during the 20th century (Corti et al., 2014; D'Amico et al., 2018).

In this study, I evaluate the factors that influence the occurrence of endemic and mainland lizards on the Mediterranean islands. I expected greater habitat heterogeneity (e.g. island size, topography and vegetation) to be correlated with higher species richness within both groups of lizards. However, larger islands can also harbour more predators, which shifts the species balance in favour of the mainland lizards (Van Moorleghem et al., 2020). I also expected that distance from the continent would be correlated with a greater presence of endemic species (Kougioumoutzis & Tiniakou, 2015). Marine channels, even if they are relatively shallow, can constitute an almost impassable barrier for some small lizards (Hurston et al., 2009), although there are also opposite examples (Phillips et al., 2019; Raia et al., 2017). Consequently, I hypothesized that isolation relative to other islands in an archipelago would be negatively associated with both groups of lizards.

2 | MATERIALS AND METHODS

2.1 | Study area

This study focuses on those archipelagos of the Mediterranean Basin where endemic lizard species occur. The term lizards includes limbed squamates (i.e. agamids, geckoes, skinks and lacertids) and anguids. In total, 19 species of endemic lizards are known to occur across the Mediterranean islands (Kornilios et al., 2020; Kotsakiozi et al., 2018; Senczuk et al., 2019; Speybroeck et al., 2016) (Figure 1). A total of 31 species of mainland lizards also occur in the same archipelagos, most of which are confined to the larger islands (Kotsakiozi et al., 2018; Speybroeck et al., 2016) (Figure 2). Data related to the presence or absence of lizards on 552 islands were obtained from biogeographic atlases (Delaugerre & Cheylan, 1992; Mayol, 1997; Sindaco et al., 2006; Valakos et al., 2008; Appendix S1). The environmental responses of the species were evaluated by biogeographic subregions as proposed by Coll et al. (2010) and Kougioumoutzis et al. (2017).

2.2 | Environmental data

Several ensembles of variables were selected based on their influence on the composition of the island biotic communities (Ding et al., 2006). The variables describe the geophysical, climatic and biotic characteristics of the islands, as well as their isolation relative to the mainland (i.e. continental territories) and surrounding islands (Table 1). The geophysical characteristics of the islands include the surface area (km^2) and elevation (which can be used as a proxy for habitat heterogeneity; Kougioumoutzis & Tiniakou, 2015), obtained from published data (Koster, 2005) and Google Earth Pro 7.3.2.5776 (Google LLC).

The isolation of the islands was assessed by calculating the shortest distance to the mainland and the average elevation around the 10 km perimeter of the island (Kreft et al., 2008). These data were generated from a raster-based geographical information system (Figure 1) showing negative or positive elevational values relative to sea level (Becker et al., 2009). The island isolation relative to other islands within an archipelago was evaluated after constructing a connection network (Kougioumoutzis et al., 2017). This network was based on simple proximity relationships, linking the islands with their closest neighbour, the largest islands with each other and these in turn with the mainland. Network properties were used to estimate the connectivity, using simulated annealing (Carstensen et al., 2012). The connectivity indicates the relative importance of the nodes (islands) within the entire network, based on the estimation of the Z_i parameter (Guimerà & Amaral, 2005). I also calculated the island radiality (i.e. the ease with which a node can reach other network nodes, which is determined using the geographical distance) (Borgatti & Everett, 2006). If the islands are close to each other, radiality values are expected to be high, whereas islands far from the main clusters will show lower values. Connectivity and
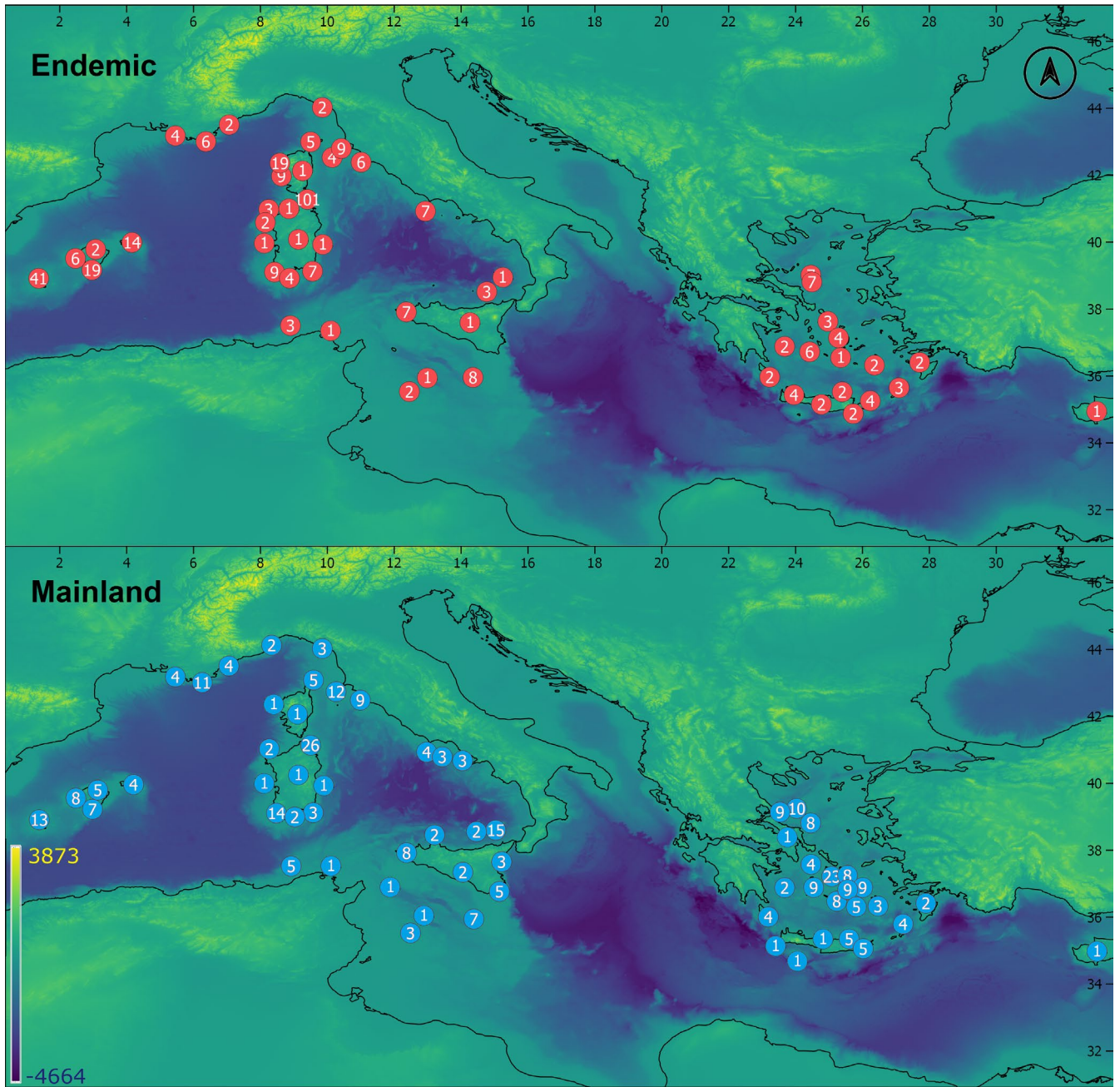
FIGURE 1 Map of the study region, where the terrain elevation has been superimposed. Upper panel, Number of islands populated by endemic species, grouped within a radius of 50 km (red circles); lower panel, number of islands populated by species of mainland origin, grouped within a radius of 50 km (blue circles)

radiality parameters were calculated with the rnetcarto (Doulcier & Stouffer, 2015) and igraph (Csardi & Nepusz, 2006) packages for the R environment (R Development Core Team, 2020).

The island environment was also characterized based on climate and vegetation. I used two variables to describe the climate, that is mean annual temperature and mean annual precipitation, which were obtained from the WorldClim 2 database (Fick & Hijmans, 2017). Vegetation was characterized using the enhanced vegetation index (EVI), a proxy for primary productivity and food resource availability (Huete et al., 2002; Wei et al., 2019); EVI data were obtained for the mid-spring (April–May) period from the high-resolution

Landsat 8 Collection Tier 1 32-Day EVI composite images (Chander et al., 2009). Ten islets had a surface area that fell below the raster resolution (250 m/pixel; Chander et al., 2009). Given that the EVI value approaches zero for those islets with a surface area of less than 500 m^2 (mean EVI = 0.016, n = 15), a zero value was assigned to these ten islets smaller than the pixel area. Human population density and snake presence were also included in the models. Human density because it is associated with the alteration of island ecosystems and greater penetration of mainland species (Escoriza, 2020a; Silva-Rocha et al., 2019) and snake presence because these reptiles are thought to play a role in moulding island lizard assemblages

Species percentage chart
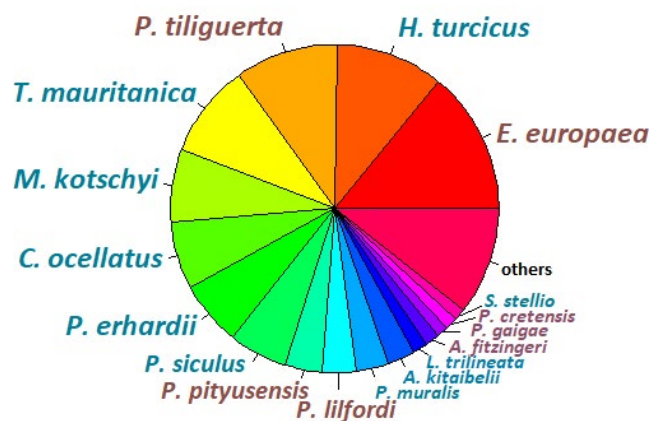
FIGURE 2 Relative frequency of occurrences of island lizard species. Red, island endemics; blue, species of mainland origin that occur on islands

information criterion (BIC; Schwarz, 1978). BIC was recommended over the Akaike information criterion when models are optimized for explanatory purposes (Aho et al., 2014). The importance of each variable was determined according to its model-averaged weighting based on the 100 best models. These analyses were conducted using the package glmulti (Calcagno & de Mazancourt, 2010) in R.

Species associations with the island environment were assessed using outlying mean index (OMI) analysis (Dolédec et al., 2000). This method describes the species responses by quantifying their ecological marginality, that is the distance between the species centroid and the average environmental conditions (OMI; Dolédec et al., 2000). An OMI value approaching zero indicates a higher resemblance between the species position and the environmental average. The OMI analysis also provides an estimate of the niche width of the species (tolerance index). In this study, I used an extension of this OMI analysis, the within outlying mean index (WitOMI) approach, which was developed to evaluate the responses of species within spatial subsets (Karasiewicz et al., 2017). Following arcsine transfor-

TABLE 1 Environmental factors used for binomial generalized linear models and outlying mean index analyses

Variable	Category	Description	Median	Range
Island surface	Geophysical	Area (km^2)	0.048	0.0001–25,832
Elevation	Geophysical	Island maximum elevation (masl)	23	1–3,329
Mainland distance	Isolation	Shortest distance to the mainland (m)	146,596	52–322,000
Sea depth	Isolation	Perimeter mean elevation (m)	–79	–1,845 to 339
Connectivity	Isolation	Island role in local connectivity	–0.22	–1 to 9.23
Radiality	Isolation	Island reachability	0.91	0.0003–1.0
Temperature	Climate effect	Mean annual temperature (°C)	17.2	13.3–19.4
Precipitation	Climate effect	Annual precipitation (mm/y)	493	274–945
EVI	Habitat effect	Enhanced vegetation index (April–May)	0.21	0.0–0.64
Mainland lizard richness	Biotic effect	Number of species	1	0–9
Snake presence	Biotic effect	Presence–absence	0	0–1
Human density	Biotic effect	Individuals per km^2	0	0.0–2,449.3

(Brock et al., 2015; Pérez-Mellado et al., 2008). Human population density data were obtained from open-access censuses.

2.3 | Data analysis

Prior to analysis, variables with values of skew and kurtosis that suggested that they followed a non-normal distribution were logarithmically transformed (Lewis, 1977), generating a new distribution with skewness and kurtosis values near zero. All of the continuous variables were normalized. The response of the species was evaluated using binomial generalized linear models (BGLMs). The models were built using two dependent variables: the presence of endemic and mainland lizards. The relative contribution of the pooled variables to the models was evaluated using an automated procedure (Calcagno & de Mazancourt, 2010), ranking the models with the Bayesian

mation, the distributions of the OMI indices were compared using a *t* test. These analyses have been carried out using the packages ade-4 (Dray & Dufour, 2007) and subniche (Karasiewicz et al., 2017) for the R environment.
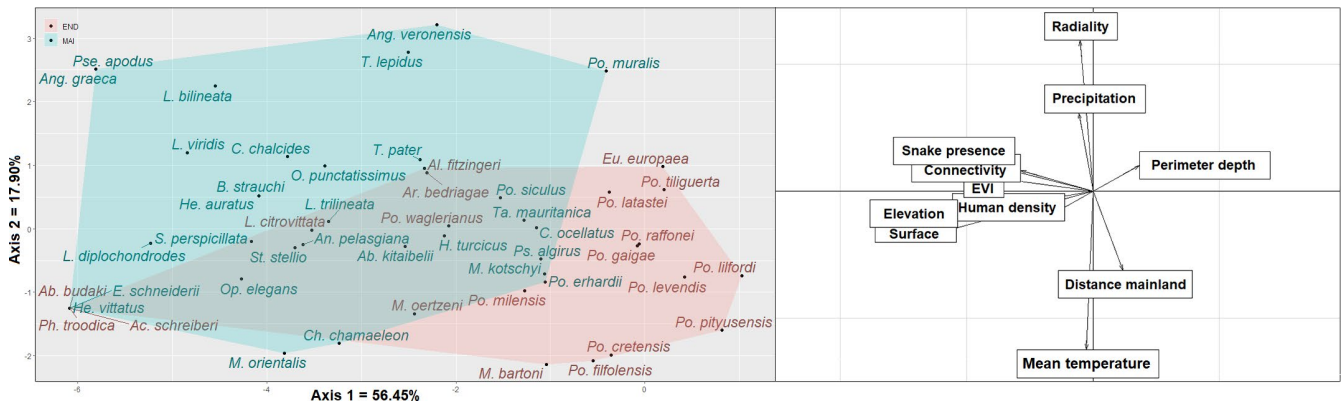
3 | RESULTS

The results obtained from the BGLMs show that the parameters that best explain the variations in the occurrence of the endemic lizards are mainland distance, annual temperature and mainland lizard species richness (Table 2). This association was positive and statistically significant with mainland distance ($\beta = 0.673$, $p = 1.27e^{-8}$) and connectivity ($\beta = 0.467$, $p = .0019$), but negative and statistically significant with annual mean temperature ($\beta = -0.578$, $p = 7.27e^{-7}$) and mainland lizard species richness ($\beta = -0.384$, $p = 1.05e^{-6}$; Table 2).

Subregion	Group	*n*	WitOMI	Tolerance
Balearic	Endemic	2	15.3 ± 2.8	4.1 ± 3.2
	Mainland	5	65.8 ± 42.9	20.7 ± 26.9
Continental islands	Endemic	1	4.2	21.4
	Mainland	11	66.7 ± 35.8	7.9 ± 10.6
Corsica–Sardinia	Endemic	4	18.7 ± 17.8	35.1 ± 6.8
	Mainland	5	31.8 ± 11.6	30.3 ± 9.5
Pontine	Endemic	1	77.4	0.8
	Mainland	3	23.7 ± 18.6	39.1 ± 27.5
Sicily–Aeolian	Endemic	2	41.4 ± 17.6	18.4 ± 10.7
	Mainland	6	40.1 ± 47.4	19.3 ± 19.9
Strait of Sicily	Endemic	1	1.6	23.4
	Mainland	6	38.3 ± 39.8	17.4 ± 10.9
Crete–Pori	Endemic	3	25.8 ± 38.5	17.5 ± 25.1
	Mainland	9	62.6 ± 32.9	23.3 ± 21.9
Central Aegean	Endemic	4	52.9 ± 39.8	6.0 ± 5.5
	Mainland	11	53.2 ± 36.8	14.9 ± 12.9
Southern Aegean	Endemic	1	2.8	29.9
	Mainland	10	50.9 ± 32.3	9.9 ± 10.9

Note: Endemic: species with exclusive or mainly insular natural distribution; mainland: species with exclusive or mainly continental natural distribution. *n*, number of species. WitOMI, distance between the species' environmental centroid and the subregion environmental centroid. Tolerance, breadth of the species' niche.
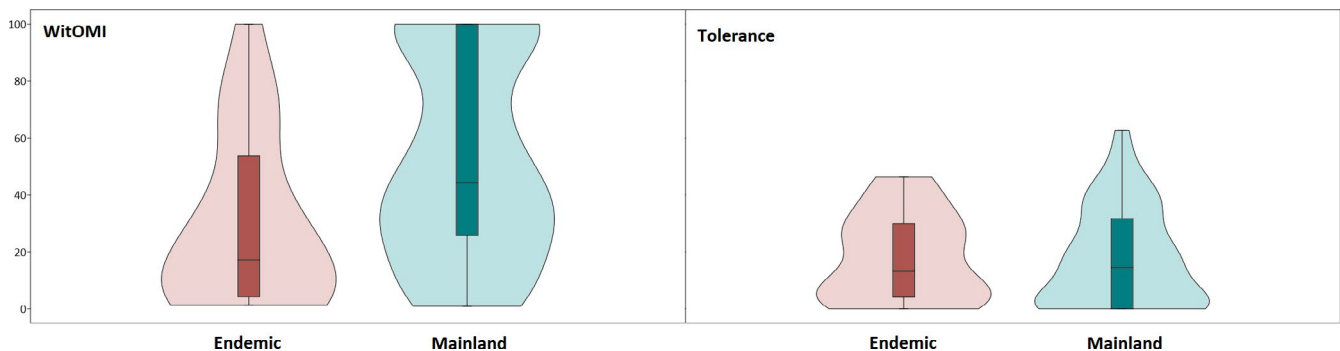
FIGURE 4 Violin–box plots for the niche indices, generated by WitOMI analysis. Red: endemics; blue: species of mainland origin that occur on islands

lizards: (i) endemic species tend to occur on islands distant from the mainland, but well-connected within an archipelago, and (ii) the size of the island is more relevant to the presence of the mainland species than for the endemics. These findings imply that large islands are more easily colonized by mainland species than smaller islands (MacArthur & Wilson, 1967) and that island inter-connectivity is relevant only for those species that have been established in an archipelago for long periods of time. An alternative interpretation of these results would be that island endemic lizards have a greater capacity for transmarine dispersal, but this hypothesis is not supported by the colonization times estimated for peripheral islets (Rodríguez et al., 2013, 2014; Terrasa et al., 2009). The larger islands are more easily colonized by mainland species for two reasons: first, the greater probability of being reached (due to the effect of the surface and also favoured by human transportation), and second, the greater capacity to support stable populations (Whittaker et al., 2008).

Most of the endemic species are well represented on the satellite islets, and in some cases, these islands constitute their last sanctuaries (Pérez-Mellado et al., 2008). With the possible exception of the larger species (Čerňanský et al., 2016), the low occurrence of mainland species on the islets is more likely to be a reflection of the difficulty of reaching these smaller islands in the first place, rather than of their inherent habitat limitations. The observation that accidentally translocated species become quickly established on the islets supports this hypothesis (Corti et al., 2014; Koren et al., 2011). Mainland species are usually superior competitors and display

aggressive behaviour and more efficient antipredatory responses (Corti et al., 2009; Nikolic et al., 2019). Therefore, the absence of mainland species in small islets is possibly a consequence of the lack of human activity (Corti et al., 2014; Grbac & Brnin, 2006).

Temperature is another environmental factor that is positively associated with the occurrence of mainland species. The most widespread mainland species (i.e. *Chalcides ocellatus*, *Hemidactylus turcicus* and *Tarentola mauritanica*) display thermophilous habits, as they evolved in the southern Mediterranean (Kornilios et al., 2010; Martínez Rica, 1974). These species were transported by humans in historical times and were able to colonize several Mediterranean archipelagos (Kornilios et al., 2010; Rato et al., 2011). However, their presence in the northern Mediterranean is more localized, possibly because of the effect of the lower temperatures (Delaugerre & Cheylan, 1992).

The results of the WitOMI analysis presented here demonstrate that island endemic species occupy niche positions that are similar to the environmental average, but show a relatively low niche breadth. This is to be expected if a species occupies a large number of sites, but these are environmentally homogeneous (i.e. the islets). Most of the mainland species occupy more marginal positions and also show low niche breadth. This pattern is compatible with the hypothesis of limiting similarity, where the recent colonizers exploit niches far from those preferred by the resident species (Tilman, 1982). A similar pattern has been described in many other island biotic communities, demonstrating the relevance of competitive interactions structuring island ecosystems (Karadimou et al., 2015; MacArthur, 1965).

However, some mainland species (e.g. *C. ocellatus*, *H. turcicus*, *Podarcis siculus* and *T. mauritanica*) do not fit this pattern, as they occupy positions similar to the island endemic species and broad niches. This means that these species are able to colonize many heterogeneous islands, highlighting their propensity for opportunistic implantation (Barreiros et al., 2010). In the case of at least one species, *P. siculus*, expansion has been correlated with the rapid decline of island endemic species, but adverse effects have also been postulated for the other species (D'Amico et al., 2018; Mayol-Serra, 1977). Although islets are colonized by species of alien reptiles that are quite diverse phylogenetically (Escoriza, 2020b), those evolutionarily close to endemics, as using similar resources, are frequently associated with the collapse of native populations (Nikolic et al., 2019).

5 | CONCLUSIONS

The results of this study suggest that the populations of endemic island lizards could be threatened by the expansion of mainland lizards. Most of the endemic species occupy niche positions similar to the environmental average, but without using the entire range of available niches within the archipelago, particularly large islands with the presence of competitors and/or predators. Satellite islets play a key role as refuges for endemic species, and this role is supported by their inherent isolation. Large islands are more easily colonized by mainland species, thereby acting as reservoirs for secondary colonization.

ORCID

Daniel Escoriza 🆔 https://orcid.org/0000-0002-6853-0134

REFERENCES

Aho, K., Derryberry, D., & Peterson, T. (2014). Model selection for ecologists: The worldviews of AIC and BIC. *Ecology, 95*, 631–636. https://doi.org/10.1890/13-1452.1

Bachmayer, F., Brinkerink, J. P., & Symeonidis, N. (1976). Pleistozäne Schildkröten aus Höhlen der Insel Kreta. *Annales Géologiques des Pays Helléniques, 27*, 100–120.

Barreiros, J. P., Elias, R. B., Lourenço, J., Dias, E., & Borges, P. A. (2010). First records of *Tarentola mauritanica* (Linnaeus, 1758) (Reptilia; Gekkonidae) in the Azores. *Arquipélago, 27*, 73–75.

Barun, A., Simberloff, D., Tvrtkovic, N., & Pascal, M. (2011). Impact of the introduced small Indian mongoose (*Herpestes auropunctatus*) on abundance and activity time of the introduced ship rat (*Rattus rattus*) and the small mammal community on Adriatic islands, Croatia. *NeoBiota, 11*, 51–61. https://doi.org/10.3897/neobiota.11.1819

Becker, J. J., Sandwell, D. T., Smith, W. H. F., Braud, J., Binder, B., Depner, J., Fabre, D., Factor, J., Ingalls, S., Kim, S.-H., Ladner, R., Marks, K., Nelson, S., Pharaoh, A., Trimmer, R., Von Rosenberg, J., Wallace, G., & Weatherall, P. (2009). Global bathymetry and elevation data at 30 arc seconds resolution: SRTM30_PLUS. *Marine Geodesy, 32*, 355–371. https://doi.org/10.1080/01490410903297766

Böhme, W., & Zammit-Maempel, G. (1982). *Lacerta siculimelitensis* sp. n. (Sauria: Lacertidae), a giant lizard from the late Pleistocene of Malta. *Amphibia-Reptilia, 3*, 257–268. https://doi.org/10.1163/156853882X00473

Borgatti, S. P., & Everett, M. G. (2006). A graph-theoretic perspective on centrality. *Social Networks, 28*, 466–484. https://doi.org/10.1016/j.socnet.2005.11.005

Bover, P., Quintana, J., & Alcover, J. A. (2008). Three islands, three worlds: Paleogeography and evolution of the vertebrate fauna from the Balearic Islands. *Quaternary International, 182*, 135–144. https://doi.org/10.1016/j.quaint.2007.06.039

Brock, K. M., Bednekoff, P. A., Pafilis, P., & Foufopoulos, J. (2015). Evolution of antipredator behavior in an island lizard species, *Podarcis erhardii* (Reptilia: Lacertidae): The sum of all fears? *Evolution, 69*, 216–231. https://doi.org/10.1111/evo.12555

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. *Molecular*

Phylogenetics and Evolution, *48*, 350–358. https://doi.org/10.1016/j.ympev.2008.04.013

Calcagno, V., & de Mazancourt, C. (2010). glmulti: An R package for easy automated model selection with (generalized) linear models. *Journal of Statistical Software*, *34*, 1–29.

Carstensen, D. W., Dalsgaard, B., Svenning, J. C., Rahbek, C., Fjeldså, J., Sutherland, W. J., & Olesen, J. M. (2012). Biogeographical modules and island roles: A comparison of Wallacea and the West Indies. *Journal of Biogeography*, *39*, 739–749. https://doi.org/10.1111/j.1365-2699.2011.02628.x

Čerňanský, A., Klembara, J., & Smith, K. T. (2016). Fossil lizard from central Europe resolves the origin of large body size and herbivory in giant Canary Island lacertids. *Zoological Journal of the Linnean Society*, *176*, 861–877. https://doi.org/10.1111/zoj.12340

Chander, G., Markham, B. L., & Helder, D. L. (2009). Summary of current radiometric calibration coefficients for Landsat MSS, TM, ETM+, and EO-1 ALI sensors. *Remote Sensing of Environment*, *113*, 893–903. https://doi.org/10.1016/j.rse.2009.01.007

Cherry, J. F., & Leppard, T. P. (2018). Patterning and its causation in the pre-Neolithic colonization of the Mediterranean islands (Late Pleistocene to Early Holocene). *The Journal of Island and Coastal Archaeology*, *13*, 191–205. https://doi.org/10.1080/15564894.2016.1276489

Coll, M., Piroddi, C., Steenbeek, J., Kaschner, K., Ben Rais Lasram, F., Aguzzi, J., Ballesteros, E., Bianchi, C. N., Corbera, J., Dailianis, T., Danovaro, R., Estrada, M., Froglia, C., Galil, B. S., Gasol, J. M., Gertwagen, R., Gil, J., Guilhaumon, F., Kesner-Reyes, K., … Voultsiadou, E. (2010). The biodiversity of the Mediterranean Sea: Estimates, patterns, and threats. *PLoS One*, *5*, e11842. https://doi.org/10.1371/journal.pone.0011842

Corti, C., Biaggini, M., & Berti, R. (2009). Different habitats, different pressures? Analysis of escape behaviour and ectoparasite load in *Podarcis sicula* (Lacertidae) populations in different agricultural habitats. *Amphibia-Reptilia*, *30*, 453–461. https://doi.org/10.1163/156853809789647068

Corti, C., Biaggini, M., Delaugerre, M., & Lo Cascio, P. (2014). New data on the herpetofauna of the National Park "Arcipelago di La Maddalena" (NE Sardinia, Italy). In M. Capula, & C. Corti (Eds.), *Scripta herpetologica, studies on amphibians and reptiles in honour of Benedetto Lanza* (pp. 55–62). Societas Herpetologica Italica-Edizioni Belvedere.

Csardi, G., & Nepusz, T. (2006). The igraph software package for complex network research. *Complex Systems*, *1695*, 1–9.

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 and Biology*, *13*, 146–157.

Delaugerre, M., & Cheylan, M. (1992). *Atlas de Repartition des Batraciens et Reptiles de Corse*. Parc Naturel Regional de Corse-Ecole Pratique des Hautes Etudes.

Ding, T. S., Yuan, H. W., Geng, S., Koh, C. N., & Lee, P. F. (2006). Macro-scale bird species richness patterns of the East Asian mainland and islands: Energy, area and isolation. *Journal of Biogeography*, *33*, 683–693. https://doi.org/10.1111/j.1365-2699.2006.01419.x

Dolédec, S., Chessel, D., & Gimaret-Carpentier, C. (2000). Niche separation in community analysis: A new method. *Ecology*, *81*, 2914–2927. 10.1890/0012-9658(2000)081[2914:NSICAA]2.0.CO;2

Doulcier, G., & Stouffer, D. (2015). *Rnetcarto: Fast network modularity and roles computation by simulated annealing*. R package version 0.2.4.

Dray, S., & Dufour, A. B. (2007). The ade4 package: Implementing the duality diagram for ecologists. *Journal of Statistical Software*, *22*, 1–20.

Escoriza, D. (2020a). Ship rats and island reptiles: Patterns of co-existence in the Mediterranean. *PeerJ*, *8*, e8821. https://doi.org/10.7717/peerj.8821

Escoriza, D. (2020b). Organization of Squamata (Reptilia) assemblages in Mediterranean archipelagos. *Ecology and Evolution*, *10*, 1592–1601. https://doi.org/10.1002/ece3.6013

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, *37*, 4302–4315. https://doi.org/10.1002/joc.5086

Fox, B. J., & Fox, M. D. (2000). Factors determining mammal species richness on habitat islands and isolates: Habitat diversity, disturbance, species interactions and guild assembly rules. *Global Ecology and Biogeography*, *9*, 19–37. https://doi.org/10.1046/j.1365-2699.2000.00184.x

Gippoliti, S., & Amori, G. (2006). Ancient introductions of mammals in the Mediterranean Basin and their implications for conservation. *Mammal Review*, *36*, 37–48. https://doi.org/10.1111/j.1365-2907.2006.00081.x

Grbac, I., & Brnin, K. (2006). Habitat use of sympatric populations of *Podarcis sicula* and *P. melisellensis* on a small Adriatic island. *Periodicum Biologorum*, *108*, 177–182.

Guimerà, R., & Amaral, L. A. (2005). Functional cartography of complex metabolic networks. *Nature*, *43*, 895–900. https://doi.org/10.1038/nature03288

Huete, A., Didan, K., Miura, T., Rodriguez, E. P., Gao, X., & Ferreira, L. G. (2002). Overview of the radiometric and biophysical performance of the MODIS vegetation indices. *Remote Sensing of Environment*, *83*, 195–213. https://doi.org/10.1016/S0034-4257(02)00096-2

Hurston, H., Voith, L., Bonanno, J., Foufopoulos, J., Pafilis, P., Valakos, E., & Anthony, N. (2009). Effects of fragmentation on genetic diversity in island populations of the Aegean wall lizard *Podarcis erhardii* (Lacertidae, Reptilia). *Molecular Phylogenetics and Evolution*, *52*, 395–405. https://doi.org/10.1016/j.ympev.2009.03.028

Jalut, G., Dedoubat, J. J., Fontugne, M., & Otto, T. (2009). Holocene circum-Mediterranean vegetation changes: Climate forcing and human impact. *Quaternary International*, *200*, 4–18. https://doi.org/10.1016/j.quaint.2008.03.012

Karadimou, E., Tsiripidis, I., Kallimanis, A. S., Raus, T., & Dimopoulos, P. (2015). Functional diversity reveals complex assembly processes on sea-born volcanic islands. *Journal of Vegetation Science*, *26*, 501–512. https://doi.org/10.1111/jvs.12255

Karasiewicz, S., Dolédec, S., & Lefebvre, S. (2017). Within outlying mean indexes: Refining the OMI analysis for the realized niche decomposition. *PeerJ*, *5*, e3364. https://doi.org/10.7717/peerj.3364

Koren, T., Laus, B., Buric, I., & Kuljeric, M. (2011). Contribution to the herpetofauna (amphibians & reptiles) of the Kornati achipelago, Croatia. *Natura Croatica*, *20*, 387–396.

Kornilios, P., Kyriazi, P., Poulakakis, N., Kumlutaş, Y., Ilgaz, Ç., Mylonas, M., & Lymberakis, P. (2010). Phylogeography of the ocellated skink *Chalcides ocellatus* (Squamata, Scincidae), with the use of mtDNA sequences: A hitch-hiker's guide to the Mediterranean. *Molecular Phylogenetics and Evolution*, *54*, 445–456. https://doi.org/10.1016/j.ympev.2009.09.015

Kornilios, P., Thanou, E., Lymberakis, P., Ilgaz, Ç., Kumlutaş, Y., & Leaché, A. (2020). A phylogenomic resolution for the taxonomy of Aegean green lizards. *Zoologica Scripta*, *49*, 14–27. https://doi.org/10.1111/zsc.12385

Koster, E. A. (2005). *The physical geography of Western Europe*. Oxford University Press.

Kotsakiozi, P., Jablonski, D., Ilgaz, Ç., Kumlutaş, Y., Avcı, A., Meiri, S., Itescu, Y., Kukushkin, O., Gvoždík, V., Scillitani, G., Roussos, S. A., Jandzik, D., Kasapidis, P., Lymberakis, P., & Poulakakis, N. (2018). Multilocus phylogeny and coalescent species delimitation in Kotschy's gecko, *Mediodactylus kotschyi*: Hidden diversity and cryptic species. *Molecular Phylogenetics and Evolution*, *125*, 177–187. https://doi.org/10.1016/j.ympev.2018.03.022

Kotsakis, T. (1977). I resti di anfibi e rettili pleistocenici della grotta «Bate» (Rethymnon, Creta). *Atti Della Accademia Nazionale Dei*

Lincei. Classe Di Scienze Fisiche, Matematiche E Naturali. Rendiconti, 63, 571–582.

Kougioumoutzis, K., & Tiniakou, A. (2015). Ecological factors driving plant species diversity in the South Aegean Volcanic Arc and other central Aegean islands. *Plant Ecology & Diversity, 8*, 173–186. https://doi.org/10.1080/17550874.2013.866989

Kougioumoutzis, K., Valli, A. T., Georgopoulou, E., Simaiakis, S. M., Triantis, K. A., & Trigas, P. (2017). Network biogeography of a complex island system: The Aegean Archipelago revisited. *Journal of Biogeography, 44*, 651–660. https://doi.org/10.1111/jbi.12920

Kreft, H., Jetz, W., Mutke, J., Kier, G., & Barthlott, W. (2008). Global diversity of island floras from a macroecological perspective. *Ecology Letters, 11*, 116–127. https://doi.org/10.1111/j.1461-0248.2007.01129.x

Lalueza-Fox, C., Castresana, J., Sampietro, L., Marquès-Bonet, T., Alcover, J. A., & Bertranpetit, J. (2005). Molecular dating of caprines using ancient DNA sequences of *Myotragus balearicus*, an extinct endemic Balearic mammal. *BMC Evolutionary Biology, 5*, 70. https://doi.org/10.1186/1471-2148-5-70

Lewis, W. M. Jr (1977). Ecological significance of the shapes of abundance-frequency distributions for coexisting phytoplankton species. *Ecology, 58*, 850–859. https://doi.org/10.2307/1936220

Loehle, C., & Eschenbach, W. (2012). Historical bird and terrestrial mammal extinction rates and causes. *Diversity and Distributions, 18*, 84–91. https://doi.org/10.1111/j.1472-4642.2011.00856.x

MacArthur, R. H. (1965). Patterns of species diversity. *Biological Reviews, 40*, 510–533. https://doi.org/10.1111/j.1469-185X.1965.tb00815.x

MacArthur, R. H., & Wilson, E. O. (1967). *The theory of island biogeography.* Princeton University Press.

Martínez Rica, J. P. (1974). *Contribución al estudio de la biología de los gecónidos ibéricos (Rept. Sauria).* Publicaciones del Centro Pirenaico de Biología Experimental.

Mayol, J. (1997). Biogeografía de los anfibios y reptiles de las islas baleares. In J. M. Pleguezuelos (Ed.), *Distribución y biogeografía de los anfibios y reptiles en españa y Portugal* (pp. 371–379). Monografías de Herpetología 3. : Asociación Herpetológica Española-Universidad de Granada.

Mayol-Serra, J. (1977). Presència de Gecònids (Rept. Sauria) als illots balears. *Mayurqa, 17*, 167–174.

Mencía, A., Ortega, Z., & Pérez-Mellado, V. (2017). From tameness to wariness: Chemical recognition of snake predators by lizards in a Mediterranean island. *PeerJ, 5*, e2828. https://doi.org/10.7717/peerj.2828

Nikolic, B., Josic, P., Buric, D., Tkalec, M., Lisicic, D., Blazevic, S. A., & 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

Olson, D., Farley, L., Naisilisili, W., Raikabula, A., Prasad, O. M., Atherton, J., & Morley, C. (2006). Remote forest refugia for Fijian wildlife. *Conservation Biology, 20*, 568–572. https://doi.org/10.1111/j.1523-1739.2006.00412.x

Palombo, M. R. (2009). Biochronology, paleobiogeography and faunal turnover in western Mediterranean Cenozoic mammals. *Integrative Zoology, 4*, 367–386. https://doi.org/10.1111/j.1749-4877.2009.00174.x

Pérez-Mellado, V., Martín-Vallejo, J., Brown, R., Picornell, A., Castro, J., Ramón, M. M., Terrassa, B., García-Díez, T., & Hernández-Estévez, J. Á. (2008). Population density in *Podarcis lilfordi* (Squamata, Lacertidae), a lizard species endemic to small islets in the Balearic Islands (Spain). *Amphibia-Reptilia, 29*, 49–60. https://doi.org/10.1163/156853808783431587

Phillips, J. G., Burton, S. E., Womack, M. M., Pulver, E., & Nicholson, K. E. (2019). Biogeography, systematics, and ecomorphology of Pacific island anoles. *Diversity, 11*(9), 141. https://doi.org/10.3390/d11090141

Poulakakis, N., Glaberman, S., Russello, M., Beheregaray, L. B., Ciofi, C., Powell, J. R., & Caccone, A. (2008). Historical DNA analysis reveals living descendants of an extinct species of Galápagos tortoise.

Proceedings of the National Academy of Sciences, 105, 15464–15469. https://doi.org/10.1073/pnas.0805340105

R Development Core Team (2020). *R: A language and environment for statistical computing.* R version 4.0.0.

Raia, P., Ferranti, L., Castiglione, S., Melchionna, M., Saggese, F., Raimondi, R., Serio, C., Carotenuto, F., Passaro, F., & Antonioli, F. (2017). Predicted sea-level changes and evolutionary estimates for age of isolation in Central Mediterranean insular lizards. *The Holocene, 27*, 418–426. https://doi.org/10.1177/0959683616660169

Rato, C., Carranza, S., & Harris, D. J. (2011). When selection deceives phylogeographic interpretation: The case of the Mediterranean house gecko, *Hemidactylus turcicus* (Linnaeus, 1758). *Molecular Phylogenetics and Evolution, 58*, 365–373. https://doi.org/10.1016/j.ympev.2010.12.004

Rodríguez, V., Brown, R. P., Terrasa, B., Pérez-Mellado, V., Castro, J. A., Picornell, A., & Ramon, M. M. (2013). Multilocus genetic diversity and historical biogeography of the endemic wall lizard from Ibiza and Formentera, *Podarcis pityusensis* (Squamata: Lacertidae). *Molecular Ecology, 22*, 4829–4841. https://doi.org/10.1111/mec.12443

Rodríguez, V., Brown, R. P., Terrasa, B., Pérez-Mellado, V., Picornell, A., Castro, J. A., & Ramon, C. (2014). Genetic diversity and historical biogeography of the Maltese wall lizard, *Podarcis filfolensis* (Squamata: Lacertidae). *Conservation Genetics, 15*, 295–304. https://doi.org/10.1007/s10592-013-0538-z

Schoener, T. W., & Schoener, A. (1983). The time to extinction of a colonizing propagule of lizards increases with island area. *Nature, 302*, 332–334. https://doi.org/10.1038/302332a0

Schwarz, G. (1978). Estimating the dimension of a model. *The Annals of Statistics, 6*, 461–464. https://doi.org/10.1214/aos/1176344136

Senczuk, G., Castiglia, R., & Böhme, W. (2019). *Podarcis siculus latastei* (Bedriaga, 1879) of the Western Pontine Islands (Italy) raised to the species rank, and a brief taxonomic overview of *Podarcis* lizards. *Acta Herpetologica, 14*, 71–80. https://doi.org/10.13128/a_h-7744

Silva-Rocha, I. R., Salvi, D., Carretero, M. A., & Ficetola, G. F. (2019). Alien reptiles on Mediterranean Islands: A model for invasion biogeography. *Diversity and Distributions, 25*, 995–1005. https://doi.org/10.1111/ddi.12911

Sindaco, R., Doria, G., Razzetti, E., & Bernini, F. (2006). *Atlante degli Anfibi e dei Rettili d'Italia.* Calderini.

Speybroeck, J., Beukema, W., Bok, B., & Van Der Voort, J. (2016). *Field guide to the amphibians and reptiles of Britain and Europe.* Bloomsbury.

Terrasa, B., Pérez-Mellado, V., Brown, R. P., Picornell, A., Castro, J. A., & Ramon, M. M. (2009). Foundations for conservation of intraspecific genetic diversity revealed by analysis of phylogeographical structure in the endangered endemic lizard *Podarcis lilfordi*. *Diversity and Distributions, 15*, 207–221. https://doi.org/10.1111/j.1472-4642.2008.00520.x

Tilman, D. (1982). *Resource competition and community structure.* Princeton University Press.

Valakos, V., Pafilis, P., Sotiropoulos, K., Lymberakis, P., Maragou, P., & Foufopoulos, J. (2008). *The Amphibians and reptiles of Greece.* Chimaira.

Van Moorleghem, C., Huyghe, K., & Van Damme, R. (2020). Chemosensory deficiency may render island-dwelling lizards more vulnerable to invasive predators. *Biological Journal of the Linnean Society, 129*, 128–142. https://doi.org/10.1093/biolinnean/blz142

Wei, J., Xin, Q., Ji, L., Gong, P., & Si, Y. (2019). A new satellite-based indicator to identify spatiotemporal foraging areas for herbivorous waterfowl. *Ecological Indicators, 99*, 83–90. https://doi.org/10.1016/j.ecolind.2018.12.016

Whittaker, R. J., Triantis, K. A., & Ladle, R. J. (2008). A general dynamic theory of oceanic island biogeography. *Journal of Biogeography, 35*(6), 977–994. https://doi.org/10.1111/j.1365-2699.2008.01892.x

Wikelski, M., Foufopoulos, J., Vargas, H., & Snell, H. (2004). Galápagos birds and diseases: Invasive pathogens as threats for island species. *Ecology and Society, 9*, 5.

BIOSKETCH

Daniel Escoriza is a researcher from the Institute of Aquatic Ecology (University of Girona), Spain. He has a Ph.D. on amphibian ecology (2015) from the University of Girona. Daniel Escoriza studies the factors that shape the diversity of reptile assemblages across the western Palaearctic ecoregion. The research team focuses on the ecology and management of alien amphibians and reptiles .

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.