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Alien reptiles on Mediterranean Islands: A model for invasion biogeography

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Abstract

Aim: The Mediterranean basin has a long history of interactions between humans and biota, with multiple ancient and recent introductions of alien species. Such a multitude of introductions makes it difficult to distinguish between alien and native species but provides an excellent opportunity to investigate factors related to introductions and long-term persistence of alien species. In this study, we combined genetic and distribution data to identify the factors promoting the presence of alien reptiles on islands, considering human-related, geographic and species features. Furthermore, we assessed whether the use of genetic evidence to identify alien species improves inference of the factors determining their distribution.

Location: Mediterranean islands.

Methods: We combined genetic data and distribution databases to obtain information on biological traits and on the native/alien status of reptiles on >900 Mediterranean islands, and we gathered data on geographic and human features of islands. We then used spatially explicit generalized additive mixed models to identify the factors associated with the establishment of alien reptiles.

Results: Alien reptile populations are more frequent on islands far from the native range and with large human population. Alien populations of reptiles that are able to feed on plants are particularly frequent. Traditional data sources underestimate the frequency of alien reptiles on Mediterranean islands, and using genetic evidence to assess the status of populations provided a more complete picture of the factors associated with the presence of alien populations.

Main conclusions: Humans are key drivers of the distribution of alien reptiles on Mediterranean islands, but the distributions are determined by a complex interplay between human activities, geographic factors and species features. Genetic data are essential for obtaining reliable biogeographic assessments of invasive species, particularly in systems with a long history of human influence.

KEYWORDS
alien reptiles, biological Invasions, genetics, human-mediated transport, Island Biogeography, Islands, Mediterranean, spatial Generalized Additive Mixed Models

1 | INTRODUCTION

Isolation and island size limit the number of terrestrial organisms that can colonize and exploit island ecosystems. As a result, islands tend to host fewer species, often with a reduced number of populations and/or smaller population sizes compared to mainland regions (MacArthur & Wilson, 1967). On islands, competition, predation and parasitism may be relaxed, making island biota particularly vulnerable to biological invasions (van Kleunen et al., 2015). The Theory of Island Biogeography states that species diversity on islands tends to approach a dynamic equilibrium, which is the result of a balance between colonization, speciation and extinction rates (MacArthur & Wilson, 1967). However, with ever-increasing global movement of species associated with human activities, a different equilibrium is expected to be established compared to natural conditions. As such, human-mediated introduction of alien species to islands might lead to increases in the distribution and numbers of the colonizing species but also to the extinction of native species, with obvious implications for conservation. As a consequence, the current distribution of island biodiversity is expected to become strongly influenced by human factors, such as economic isolation, human population size, trade and transportation (Ficetola & Padoa-Schioppa, 2009; Helmus, Mahler, & Losos, 2014; Blackburn, Delean, Pyšek, Cassey, & Field, 2016). A growing body of research is testing whether invasive species follow the same biogeographic patterns as native species, and under which circumstances human activities lead to breaking of the traditional biogeographic rules (Burns, 2015; Capinha, Essl, Seebens, Moser, & Pereira, 2015).

Assessing whether a given insular species is alien is crucial for guiding conservation priorities and management strategies. However, the distinction between alien and native species is not always easy. In some cases, alien status is accepted, either because introductions are recent and well documented, or because natural colonization is unlikely for species originating from very distant localities. However, in many cases, invasions are more difficult to disentangle from natural colonization, particularly if introductions are ancient, if species originate from nearby regions, and if invaders are well integrated into the insular ecosystems. In recent years, development of molecular genetics and phylogeographic tools has greatly improved our understanding of invasion dynamics and the demography of biological invasions, allowing a more objective determination of alien status (Le Roux & Wieczorek, 2009). Nevertheless, only a small subset of putatively alien populations has been investigated in depth using genetics and it will not be feasible to assess the alien status of insular populations over broad taxonomic and geographic scales using the same approach. Moreover, some patterns of low genetic diversity and shallow divergence can be explained either by human introductions or by recent natural colonization by very small propagules (e.g., Silva-Rocha, Salvi, & Carretero, 2012; Salvi et al., 2011; Salvi, Schembri, Sciberras, & Harris, 2014). Integrating genetic data and human factors within eco-geographic analyses (Avise, 2000) may be an effective approach for identifying the drivers of island invasions and unravelling the status of cryptic invasions. Yet to date, this approach has rarely been implemented.

The Mediterranean region is a world biodiversity hotspot (Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000) with one of the longest histories of interaction between humans and biodiversity, and multiple introductions of alien species occurring over millennia (Blondel, Aronson, Bodiou, & Boeuf, 2010). As a striking example, the Balearic Islands once harboured substantial levels of endemicity, as witnessed by the rich fossil record, but now host more alien than native reptile and amphibian species (Pinya & Carretero, 2011; Silva-Rocha, Salvi, Sillero, Mateo, & Carretero, 2015). This is due to the historical role of the archipelago as the crossroad of several civilizations since the Neolithic, resulting in drastic shifts in land use patterns, resource management and biota composition. Most studies of invasive species focus on short-term patterns and do not explore the long-term consequences of species introductions (Strayer, 2012). The Mediterranean is thus an excellent place to study human-driven introductions at large spatial and temporal scales.

Despite being terrestrial and largely sedentary, reptiles are among the most abundant vertebrates on small islands (Novosolov et al., 2016) and are often introduced by humans during the transport of building material, soil or cultivated plants. Thus, islands often host a large number of alien reptiles (Pitt, Vice, & Pitzler, 2005). In areas with long histories of human settlement and trade, ascertaining the native status of species may be challenging, and many reptiles, traditionally assumed to be native to Mediterranean islands, are now known to be the result of ancient introductions (i.e., cryptic introduced species). Mediterranean reptiles have been the target of multiple phylogeographic studies that provide a rich dataset for addressing several unresolved questions on biological invasions and determining the currently unclear status of certain species.

In this paper, we address the following questions: (a) what factors are associated with the distributions of alien reptiles in the Mediterranean region in the long-term; (b) what is the relative importance of geographic and human-driven factors; (c) which reptile groups are most frequently introduced and what are their specific traits; and (d) is it possible to integrate genetic, biogeographic and life history information to infer the status of island reptiles for which accurate information is available? To address these questions, we constructed a broad-scale, multispecies database with the verified status (native/alien) of island reptiles, with status ascertained via genetic and phylogeographic studies. We then assessed the relationships between status and (a) island, (b) human and (c) species characteristics, to identify the eco-geographic and human factors that increase the probability that a reptile species is alien on islands. If, in the long-term, geographic factors exert the same effects on native and alien species (Whittaker & Fernandez-Palacios, 2007; Whittaker, Fernández-Palacios, Matthews, Borregaard, & Triantis, 2017), we would expect geographic factors of islands to be the dominant drivers of alien species distribution (e.g., alien species would be

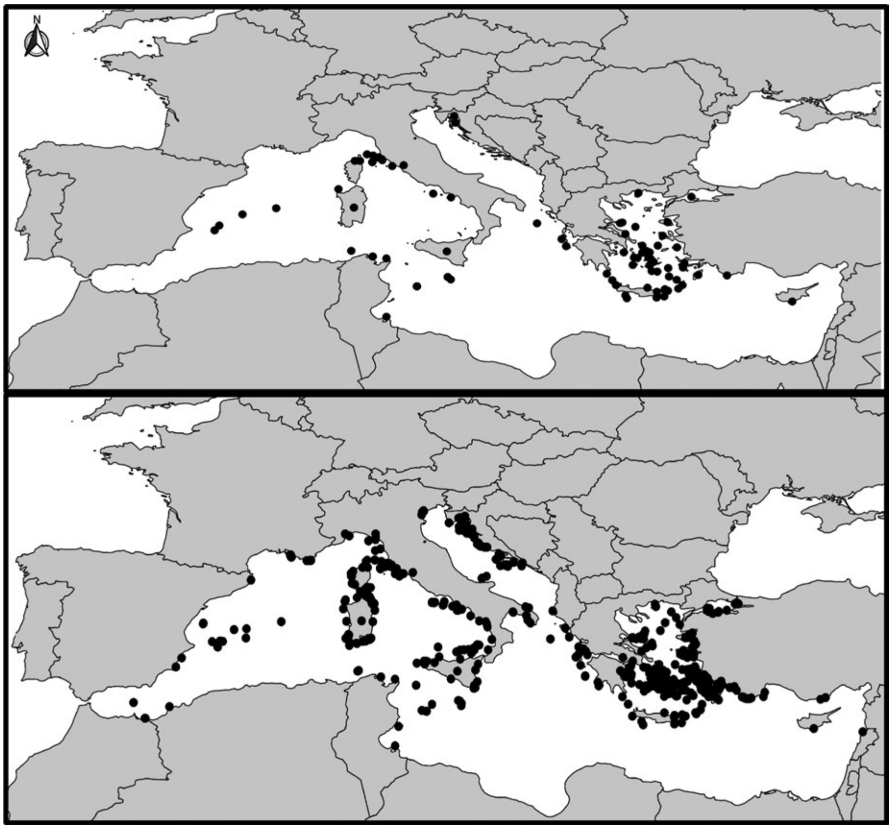

FIGURE 1 Distribution of islands used in this study. Top: islands from the confirmed dataset, for which there is genetic confirmation of alien/native status. Bottom: islands from the putative dataset, for which there is no confirmation regarding the alien status in the existing literature

more frequent on large islands, as these can support a higher number of species). On the other hand, if the effects of human activities remain the strongest even in the long term, we would expect the distributions of alien species to be dominated by human factors (e.g., alien species would be more frequent on islands with larger human populations). Finally, we integrated this information in a model to predict the status (native/alien) of Mediterranean reptiles for which no genetic information exists, to infer their alien status and to identify those islands where more alien reptile species might be present. Our analyses provide a baseline model for understanding the real dimensions of reptile invasions in the islands of the Mediterranean and elsewhere.

2 | METHODS

2.1 | Species and island data

We focused on the islands and species in the Mediterranean Basin (Figure 1). Information on species distributions on islands was obtained from Ficetola et al. (2014). For each island, we considered eleven variables representing geographic features, factors associated with human impact on the island and features of a species' life history, morphology and diet (Table 1).

The study focused on species native to the Mediterranean region. Island endemic species were not included in the analysis because they cannot be alien by definition. Likewise, species that clearly originated far away from the Mediterranean region (e.g., the American turtle *Trachemys scripta*) were also excluded. This is because most introductions have been from within the Mediterranean and species from other regions could have very different features that would have made them outliers affecting the outcome of the analyses without adding information pertinent to our objectives of identifying long-term patterns and cryptic introductions. We calculated the distance of each island to the native mainland range of each species using the *maptools* (Bivand & Lewin-Koh, 2017), *rgeos* (Bivand & Rundel, 2017) and *geosphere* (Hijmans, (2017)) packages in R. We obtained the native mainland range of each species from the IUCN Red List (IUCN, 2018) and from Sindaco, Jeremčenko, Venchi, and Grieco (2008), Sindaco, Venchi, and Grieco (2013) for species not in the Red List (i.e., *Anguis fragilis*, *Chalcides ocellatus*, *Coronella austriaca*, *Dolichophis caspius*, *Eryx jaculus*, *Hemorrhois nummifer*, *Malpolon insignitus*, *Mauremys rivulata*, *Ophiomorus punctatissimus*, *Pseudopus apodus*, *Testudo graeca*, *Testudo hermanni*, *Testudo marginata* and *Xerotyphlops vermicularis*). Species names follow the Reptile Database (Uetz, Freed, & Hosek, 2018).

Total species richness can also affect the establishment of introduced species (Kennedy et al., 2002). Therefore, an additional analysis was performed to understand its relevance to our study. A Poisson regression was performed to infer the relationship among total species richness and island area/human population. Furthermore, to confirm that excluding species richness did not alter the results, we repeated analyses excluding the human population and island area variables and including species richness.

TABLE 1 Composition of the dataset with a brief description of variables and their importance

	Variables	Description and source:	Rationale
Islands features	Area (km^2)	Arnold (2008)	Island biogeography theory predicts higher species richness on larger islands
	Link to mainland (yes/no)	An island was considered linked if there was a land bridge connection with the mainland during the Last Glacial Maximum—LGM (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005)	The link to the mainland and/or to a big island during the LGM is important for distinguishing a natural colonization from a human-mediated introduction in the case of old introductions
	Link to main island (yes/no)	A small island was considered linked if there was a land bridge connection with a main island (Sicily, Sardinia or Corsica) during the Last Glacial Maximum—LGM (Hijmans et al., 2005)	
	Distance to native continental range (km)	Distance between the island and the nearest continental area where the species is native.	Species that are far from the native range are more likely to be alien
Human factors	Ferry available (yes/no)	Arnold (2008), Ficetola et al. (2014)	Human transport and intensity of human activities are the main correlates of introductions
	Airport present (yes/no)	Arnold (2008), Ficetola et al. (2014)	
	Human population size	Arnold (2008), Ficetola et al. (2014)	
Species features	Body length (cm)	Thuiller et al. (2015)	Body size can influence introduction rate and establishment both positively and negatively (Kolar & Lodge, 2001; Tingley et al., 2010)
	Fecundity (number of offspring)	Thuiller et al. (2015)	Invasion success is often greater in species with higher fecundity (Tingley et al., 2010)
	Minimum litter or clutch size	Arnold (2008), Ficetola et al. (2014)	
	Diet (vertebrates, invertebrates, plants mostly, plants occasionally)	Thuiller et al. (2015) 0—species does not feed on the resource; 1—species feeds on the resource.	Diet reflects adaptability in the new environment and contributes to likelihood of establishment

2.2 | Assessment of alien status

We performed an extensive literature review for each species (see Appendix S1 in Supporting Information) to assess its alien/native status on an island. This status was determined based exclusively on those phylogeographic studies that provided genetic or fossil lines of evidence for either a recent introduction or the native status of a certain species on an island. These genetic studies elucidate phylogeographic and genetic diversity patterns of mainland and island populations of a given species, allowing inferences on processes underlying island colonization and discrimination between natural and human-mediated colonization. For example, some studies estimated divergence time between mainland and island populations far exceeding a few thousand years, which allowed human introduction of a species on an island to be ruled out (e.g., Bellati et al., 2011; Poulakakis et al., 2013). In other cases, island populations were genetically similar to mainland populations but separated from them by hundreds or thousands of kilometres, indicating human-mediated colonization as the most likely process (e.g., Carretero, Perera, Cascio, Corti, & Harris, 2009; Barbanera et al., 2009). In a few cases, genetic data were inconclusive and the status of the population was considered uncertain. For our study, we relied on the conclusions stated by the papers reviewed. Studies that did not objectively confirm the alien status of a population but, relied on information from other authors' expertise or suppositions, were not considered to have ascertained the alien or native status of a population.

We built two complementary datasets. The first was of cases for which status was confirmed by genetic and/or fossils data (confirmed dataset), while the second was of cases for which the status was not confirmed (putative dataset). The confirmed dataset allows identification of predictors that explain the distribution of alien reptiles on the Mediterranean islands, which in turn were used to predict the species status of each case in the putative dataset.

2.3 | Statistical analyses

We used spatially explicit Generalized Additive Mixed Models (GAMM) to assess the factors explaining the alien status of species (Wood & Scheipl, 2016). Generalized Additive Mixed Models are an extension of generalized additive models that allow taking into account over-dispersion and non-independence of data (Lin & Zhang, 1999). The status of each species on each island was the dependent variable, while the geographic features of the island, human factors associated with the island and the species features were independent variables. This approach allowed simultaneously assessing the role of island and species features in determining the distribution and identity of alien species.

Four variables (area, human population size, body length and distance to native continental range) were log-transformed to reduce skewness and ensure normality. We used a multi-model inference approach to select the most important variables. Unlike stepwise model selection, multi-model inference is based on all possible sub-models developed from a set of explanatory variables, which limits model selection bias and provides a relative measure of each predictor's importance (weight of evidence). All possible models were then ranked according to their Akaike's information criterion (AIC) (Burnham & Anderson, 2002). To avoid collinearity, models that included variables with strong pairwise correlation ($|r| > 0.7$) were excluded from the set of candidate models (Dormann et al., 2013). Island identity and taxonomy (family/genus/species) were included as random nested factors in all models, in order to take into account potential non-independence. Generalized Additive Mixed Models were fitted using a binomial error using the gamm four package (Wood & Scheipl, 2016). The independent variables were fitted as linear terms. Spatial autocorrelation might also bias the outcome of regressions in spatial data analyses. Therefore, we incorporated the island coordinates in GAMM as tensor product smooth terms, using thin plate regression splines (Beale, Lennon, Yearsley, Brewer, & Elston, 2010). Simulations showed that this implementation of GAMM is able to estimate regression coefficients correctly in spatially structured datasets, with relatively good performance in the presence of violations of model assumptions, such as non-stationarity of autocorrelation (Beale et al., 2010). The importance of predictor variables was assessed by summing the AIC weights across all models in the set of models in which the variable occurs (Burnham & Anderson, 2004; Giam & Olden, 2016). The predictor variable with the largest predictor weight is estimated to be the most important, while the variable with the smallest weight is considered the least important. To confirm that our results are not biased by phylogenetic relationships, we used Pagel's lambda (Pagel, 1999) to assess whether the model residuals show significant phylogenetic signal. Phylogenetic analyses were performed using *cape* (Tyler, Lu, Hendrick, Philip, & Carter, 2013) based on the Pyron, Burbrink, and Wiens (2013) phylogeny.

We tested the quality of the model by calculating the true skill statistics (TSS; Allouche, Tsoar, & Kadmon, 2006) on the confirmed dataset. A cross-validation approach was used to confirm the robustness of predictions, by randomly splitting the confirmed dataset into three sub-datasets (33% of data each) and then calculating TSS for each sub-dataset in which 75% of data was used to build the model and 25% to predict species status. We used the threshold maximizing TSS to predict that status (native or alien) of species in the putative dataset. Finally, we used the best AIC model for predicting the most likely status (native/alien) of each species record of the putative dataset.

3 | RESULTS

The final confirmed dataset contained 186 island-by-species combinations, representing 41 species and 78 islands covering the entire Mediterranean (Figure 1). Fifty-three cases were occurrences of alien species (lizards and geckos: 45%; snakes: 34%; and turtles: 21%), which were particularly frequent in Western Mediterranean Islands. A total of 133 cases were occurrences of native species (lizards and geckos: 56%; snakes: 38%; turtles: 6%).

The final putative dataset had 2045 island-by-species combinations, corresponding to 69 species and 598 islands (Figure 1b). In total, 82 cases were putatively considered to be alien and 1963 to be native based on non-genetic information from the literature. Geckos and snakes were the groups with most (putative) alien cases.

3.1 | Variables related to the alien status

We found a strong correlation between island area and human population size, ferry presence and airport ($r = 0.95$, $r = 0.70$ and $r = 0.73$, respectively) and between human population size and both ferry presence and airport presence ($r = 0.80$ and $r = 0.78$, respectively). The models with only one of these variables were retained, while the models with more than one were removed to avoid collinearity (Dormann et al., 2013). The best AIC model suggested that alien species are particularly frequent in islands with larger human population ($B = 5.23 \pm 0.364$; Z-value = 14.37; $p < 0.0001$). Alien species were also more frequent in species-by-island combinations that were further from the continental range of the species ($B = 24.83 \pm 0.741$; Z-value = 33.53; $p < 0.0001$). Species that can occasionally feed on plants ($B = 56.35 \pm 1.058$; Z-value = 53.27; $p < 0.0001$) but not depend on vertebrates ($B = -39.58 \pm 1.059$; Z-value = −37.36; $p < 0.0001$) were more frequently alien (Table 2). No phylogenetic signal was detected on model residuals (Pagel's lambda = 0.452, not significantly different from 0; $p = 0.29$). The cross-validation approach indicated an excellent predictive power of this model, as the average TSS was 0.98 ± 0.03.

Some uncertainty in model selection existed, as several alternative models showed $\Delta\text{AIC} < 5$, and included variables such as body length, island area, presence of airports and presence of ferry (Table 2). However, all the alternative models showed limited AIC weight. Overall, distance to the native range and the capacity of feeding on plants were the variables with the greatest weight (AIC weight ≥ 0.95). Vertebrate diet and human population size showed a medium importance, while the importance of all the remaining variables was very low (Figure 2).

Total species richness was strongly related to island area (Poisson regression with total species richness as dependent variable and island area as independent: $R^2 = 0.59$, $p < 0.001$) and to human population ($R^2 = 0.58$, $p < 0.001$); therefore, these variables could not be included together in the same model. Models including species richness showed higher AIC values than models with human population and island size (for all models with species richness, $\Delta\text{AIC} \geq 6.86$ compared to the best models in Table 2), suggesting that species richness was not a major predictor of status of reptile populations.

TABLE 2 Models explaining the invasion status of reptiles on Mediterranean Islands, with ΔAIC < 5. Models are ranked on the basis of Akaike's information criterion (AIC). K is the degree of freedom of the model of the *Z*-distribution. *w* is the Akaike weight of each model which reflects the relative likelihood of that model being the best within a set of N models

Ranking	Model	*K*	AIC	ΔAIC	*w*
1	Distance to Native Range + Human Population Size + Plants Occasionally – Vertebrates	15	72.24	0	0.46
2	Distance to Native Range + Human Population Size + Plants Occasionally	14	75.20	2.96	0.10
3	Distance to Native Range + Plants Occasionally – Invertebrates – Body Length	15	75.36	3.12	0.10
4	Airport + Distance to Native Range + Plants Occasionally - Vertebrates	15	76.45	4.21	0.06
5	Area + Distance to Native Range + Plants Occasionally	14	76.62	4.38	0.05
6	- Body Length + Distance to Native Range + Vertebrates	14	76.63	4.39	0.05
7	Ferry Presence + Distance to Native Range + Plants Mostly + Plants Occasionally	15	76.72	4.48	0.05
8	- Invertebrates – Link to Mainland – Body Length + Distance to Native Range + Plants Occasionally	16	76.96	4.72	0.04
9	Airport – Link to Big Islands + Distance to Native Range + Plants Occasionally – Vertebrates	16	77.07	4.83	0.04
10	Minimum Litter Clutch Size + Distance to Native Range + Plants Occasionally – Vertebrates	16	77.14	4.9	0.04

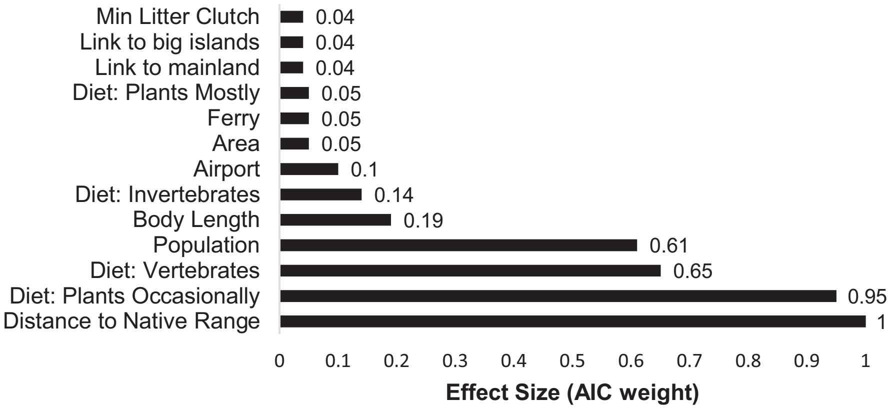

FIGURE 2 AIC weight of variables included in candidate models

3.2 | Assessing the putative status of insular populations

The best model, obtained analysing the confirmed dataset (Table 2, Model 1), was then projected on the island-by-species combinations of the putative dataset. When we projected the best model, 81% of occurrences in the putative dataset were predicted to be native and 19% to be alien. Model projections generally matched the status proposed in the literature (likelihood ratio test: $\chi^2_1 = 62.9$, $p < 0.0001$). However, in some cases model projections suggested a different status. Of the 1942 species records taken as native in the literature, 328 (16.9%) were projected as alien. Among lizards, geckos were the group with most cases projected to be alien, particularly with *Hemidactylus turcicus* (63 islands) and *Tarentola mauritanica* (69 islands), followed by skinks such as *C ocellatus* (56 islands) whereas, among lacertids, wall lizards of the genus *Podarcis* represented the majority of projected alien cases on islands (222 islands), especially *Podarcis sicula* (38 islands). We also detected several projected alien occurrences for snakes, such as *Hierophis viridiflavus* (42 islands) and *Natrix maura* (7 islands). Of the 82 species records taken as alien in the literature, 54 (66%) were projected as alien, while 28 (34%) were projected as native. When we combined both putatively native species predicted to be alien, and putatively alien species predicted to be native, the frequency of alien records increased from 4% to 19%. Overall, if we used the predicted status instead of the status in the bibliography (putative dataset), the average richness of native species on Mediterranean islands decreased by ~ 17%.

4 | DISCUSSION

Biological invasion is a multi-step process, characterized by (a) introduction of species to a new environment; (b) establishment; and (c) dispersal across the new area (Simberloff et al., 2013). Our study suggests that the distribution of alien reptiles on Mediterranean islands depends mostly on the processes determining introductions (stage 1) and on traits favouring success in the new environments (stage 2).

Several studies have analysed biogeographic and human factors related to the distribution of alien species both in the Mediterranean and in other areas of the world (Burns, 2015; Capinha et al., 2015), but most of them have relied on expertise and general knowledge to define the alien/native status of island populations, and few have used genetics to confirm this putative status. However, the complex history of human introductions in the Mediterranean basin makes the identification of species as alien challenging and the traditional approach prone to underestimating the occurrences of aliens. Our study shows that molecular data allow identification of a higher number of alien species than expected based on traditional evidence, 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.

MacArthur and Wilson's (1967) theory states that in an ecological time-frame, the diversity of species on islands is driven by two major factors determining the equilibrium between extinction and colonization rates: island size and distance from a mainland source of immigrants. Immediately after introduction, the distribution of alien species is rarely at equilibrium. However, the temporal extent of human interactions in the Mediterranean has spanned millennia and many reptiles have probably been introduced on islands centuries or even thousands of years ago, thus potentially allowing the native and alien island biotas to reach a new equilibrium. Studies suggest that alien richness is related mainly to human population size and other human-related variables, in addition to island size (e.g., Roura-Pascual, Sanders, & Hui, 2016). Our findings suggest that human factors are indeed more important than geographic ones (e.g., island area), even after a long introduction history, but nonetheless that the joint effect of geographic and human factors can be important.

The probability that a reptile record is native decreased with distance from the native mainland range. This finding is not unexpected, given that human-mediated dispersal can move species over much longer distances than natural processes (Wilson, Dormontt, Prentis, Lowe, & Richardson, 2009). Although reptiles can occasionally disperse long distances over seas, in several cases it is uncertain if the presence of reptiles on offshore Mediterranean islands is a result of natural or human-mediated processes (e.g., Kyriazi et al., 2013; Poulakakis et al., 2013). Our study confirms that distance from the native mainland range interacts with human activities in determining the likelihood of island colonization, and it provides quantitative evidence (weight values of variables) of the relative importance of the two processes. However, the relationship between the frequency of aliens and distance from the mainland range could also be caused by additional processes related to interspecific interactions, such as Darwin's (1859) naturalization hypothesis and/or Elton's (1958) species-richness hypothesis. Darwin's naturalization hypothesis focuses on stage 2 of invasions—that is, the establishment and predicts that alien species phylogenetically distant from the native community are most likely to become established. Our results are potentially in agreement with these predictions, since alien species present on islands far from the native range are less likely to be closely related to the native island species and, therefore, the absence of related species could increase the likelihood of establishment. Some studies on reptiles support this hypothesis (van Wilgen & Richardson, 2011), while others provide weak evidence, and even suggest that the success of alien species might be related to the presence of congeners (i.e., pre-adaptation hypotheses—successful alien species are likely to have traits that pre-adapt them to the new environment) (Ferreira, Beard, Peterson, Poessel, & Callahan, 2012; Liu et al., 2014; Tingley, Phillips, & Shine, 2011). Elton's species-richness hypothesis states that species-rich communities are more resistant to invasions because more of the available niche space is used by the natives. This might accord with the observed pattern, given that native richness is generally lower on islands far from the mainland (Warren et al., 2015). Nevertheless, several studies found weak support for this pattern, as in many cases the richest communities have more alien species (Lockwood, Hoopes, & Marchetti, 2009; Nunez-Mir et al., 2017; Richardson, 2011; Yiming, Zhengjun, & Duncan, 2006).

On the other hand, in our study the presence of alien reptiles was highest on islands with large human populations, confirming the keystone importance of human activities on reptile invasions. A strong human signal has also been found in many other studies in the Mediterranean and elsewhere. Some of these studies considered human population size or human presence as overall proxies of human impact (e.g., Ficetola & Padoa-Schioppa, 2009; Roura-Pascual et al., 2016; Spatz et al., 2017); however, other parameters may better target the key drivers, such as the frequency of tourist visitation (Phillips, 2010) or economic isolation (Helmus et al., 2014). Overall, although the human influence on the islands could be mediated by different pressures, humans have a deep impact on islands biotas and their distributions, which reinforces the importance of integrating human-related variables into biogeographic analyses.

Since our study area involves ancient introductions, we could not discriminate between two separate steps of the invasion process: (a) frequency of introductions and (b) establishment success. All the alien species had been introduced and successfully established over the course of many years. Diet was the only species trait included in highly supported models, with alien species often able to use plants as a significant part of their diet, generally not depending on vertebrates as a main resource. These traits are clearly not associated with colonization but with success of establishment and persistence.

Most reptiles are generalist predators, but some are able to shift trophic level and incorporate plant items into their diets. Islands may be resource-poor environments, and a wide dietary spectrum (i.e., the ability to eat both plants and animals) is important for survival in habitats with limited food availability, especially during the dry season in Mediterranean climates. On small islands, alien lizards often eat more plants than conspecifics on the mainland, and species feeding on plants can reach higher densities than those feeding mostly on arthropods (Herrel et al., 2008; Sagonas et al., 2014). For example, in a few decades, wall lizards introduced to a small island developed strategies for consuming and digesting plant matter, survived better and increased their abundance in these resource-poor environments (Carretero, 2004; Herrel et al., 2008; Pérez-Mellado & Corti, 1993; Sagonas et al., 2014). Our study shows that these processes, acting at the population level, may also be evident at the biogeographic scale, as diet spectrum of species emerged among the most important factors (Figure 2). It is also possible that herbivorous lizards survive better during transit to a new island, for instance because of their lower basal metabolic rate, or because they can more easily find food. Nevertheless, there are cases in which consuming fibres may require higher body temperatures for digestion and therefore higher metabolic rates (Tracy, Flack, Zimmerman, Espinoza, & Tracy, 2005; Clarke & O'Connor, 2014). More data are needed to understand relationships between diet and survival during transit.

Molecular data are still lacking for most species on islands. The Mediterranean is among the most studied areas of the world, yet genetic data were available for fewer than 10% of the species-by-island combinations. However, genetic data substantially changed our vision of alien reptiles in the Mediterranean. Thus, 28% of the confirmed dataset records were of alien species, while just 14% of them would have been considered alien if genetic information had been lacking. Moreover, when we analysed the same dataset ignoring the genetic information, we obtained a different picture of the factors related to the distribution of alien species and did not identify some of the most important variables (see Appendix S2 in Supporting Information). This sends a word of caution regarding conclusions extracted from meta-analyses not incorporating genetic evidence (e.g., Capinha et al., 2017).

Obtaining exhaustive genetic data for all species-by-islands 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. When projecting the model built using genetic data to a dataset of records lacking genetic data, we identified many species-by-island combinations that might actually be alien records. Model extrapolation certainly incurs a degree of error and cannot be used as the sole source of information on the status of species on islands. Nevertheless, projecting the model to the putative dataset provides preliminary information on the frequency of cryptic invaders in this system and highlights species and islands that warrant targeted research. Geckos, for example, have been extensively studied, yet, their origin and the human role in their distributions remain widely discussed (Delaugerre, Ouni, & Nouira, 2011; Rato, Carranza, & Harris, 2011, 2012). Our predictions suggest that geckos are indeed alien on the islands where they are present. Integration of various tools and methodologies could clarify these kinds of issues.

In conclusion, human-related factors stand out as key drivers of the current distribution of alien reptiles in the Mediterranean, in combination with species traits, such as diet, that are important for the success of invasion and persistence of alien species on islands. The integration of distribution, genetic and fossil data allowed identification of cryptic introduced species, some of which (e.g., snakes) may threaten native biota. 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.

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BIOSKETCH

IS-R is a recently finished PhD interested in biological invasions, using different tools to investigate these processes and set up guidelines for conservation management plans. This work was performed by an international team aiming at understanding the underlying processes of Mediterranean reptile's biodiversity at both broad and local scale.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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