



Bioclimatic and local drivers modulating the expansion of an introduced temperate reptile in a subtropical island

Iolanda Silva-Rocha^{a,b,1}, José Maurício Santos^{c,d,1}, Ricardo Rocha^{a,b,e},
Catarina Rato^{a,b,*}

^a CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Campus de Vairão, Universidade do Porto, 4485-661 Vairão, Portugal

^b BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Campus de Vairão, 4485-661 Vairão, Portugal

^c Centre for Geographical Studies, Institute of Geography and Spatial Planning, University of Lisbon, Cidade Universitária, 1600-276 Lisboa, Portugal

^d Associated Laboratory TERRA, Portugal

^e CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Instituto Superior de Agronomia, Universidade de Lisboa, 1349-017 Lisboa, Portugal

ARTICLE INFO

Keywords:

Non-native species
Species Distribution Models
Macaronesia
Biological Invasions
Tarentola mauritanica
Madeira Island

ABSTRACT

Extensive human-mediated translocation of species from their native ranges to alien environments is a trademark of the Anthropocene. Particularly in island ecosystems, established non-native species often have highly detrimental impacts on native taxa and thus the study of the drivers mediating the establishment and expansion of introduced species in areas outside their native range is crucial to delineate timely and effective mitigation measures. Species distribution models (SDMs) are widely used in invasion biology and offer great potential for the assessment of invasion risk and the identification of areas likely to be colonized by expanding alien species. Within reptiles, Gekkonidae is the second family with most introductions globally, a reflection of the group's capacity to survive long distance dispersal events. The temperate Moorish gecko (*Tarentola mauritanica*) is native to the Mediterranean basin but has established alien populations in multiple localities throughout the world. It was first reported in the subtropical island of Madeira in 1993 and over the last three decades has colonized a substantial section of the island's south coast. Here, we use Madeira Island as a case study to investigate the interplay between bioclimatic and local scale variables on the occurrence of *T. mauritanica* in areas outside its native range. We found that the species favors areas with high temperatures during the coldest month, low mean temperatures during the wettest quarter, low annual values of precipitation, and high precipitation during the driest quarter. This translates to an obvious preference for areas with more Mediterranean-like climates which in Madeira are primarily located in the south and south-eastern sections of the island. Additionally, our models predicted that some areas of the northern coast of Madeira offer suitable conditions for the gecko, although no observations have yet been recorded. *Tarentola mauritanica* is expanding its range in Madeira and has already colonized the nearby island of Porto Santo. It is paramount that more research is devoted to understanding the impact of this alien gecko on the island's native species and ecosystems, and in particular on its endemic-rich arthropod communities.

* Correspondence to: CIBIO, Campus de Vairão, 4485-661 Vairão, Portugal.

E-mail address: catarina.rato@cibio.up.pt (C. Rato).

¹ These authors contributed equally to the work.

1. Introduction

The movement of species has historically depended on the availability of suitable habitat and on the interaction between geographical constraints (e.g. marine currents, orogenic barriers) and the species' natural dispersal abilities. Yet, human action has reshaped the world's biota by translocating species to areas outside their natural ranges (Lockwood et al., 2009), often with pervasive consequences for local biodiversity (Blackburn et al., 2011; Dueñas et al., 2021; Richardson, 2011).

When non-native species are acknowledged to have negative consequences on the economy, environment or health are labelled as non-native invasive species (IUCN, 2021). These can cause severe and unpredictable impacts, including biotic homogenization, community structure disruption and social losses (Richardson, 2011). Furthermore, they can act synergistically with other human-induced stressors further contributing for the global biodiversity crisis (Didham et al., 2005; Macdougall and Turkington, 2005).

More information regarding the transport pathways and drivers of establishment and expansion of non-native species is paramount to delineate timely and effective mitigation measures to limit the impacts of biological invasions (Ricciardi et al., 2017). Over the last decade, the availability and accessibility of global data on non-native species and their geographic ranges has improved considerably (Pyšek et al., 2020), allowing a better understanding of the global and local determinants of distribution of non-native species. Species distribution models (SDMs) - also known as environmental or ecological niche models - are widely used in invasion biology (Srivastava et al., 2019), especially to predict invasion risk (e.g., Bradley et al., 2009; Jiménez-Valverde et al., 2011; Kramer et al., 2017; Lecocq et al., 2016; Tingley et al., 2018) and optimize control strategies (e.g., Giljohann et al., 2011; Tulloch et al., 2014). SDMs are also commonly used in other areas of conservation science, such as predicting the potential effects of climate change on genetic (e.g., Alsos et al., 2012; Pauls et al., 2013), taxonomic (e.g., Domisch et al., 2013; Garcia et al., 2012; Maiorano et al., 2011; Srinivasulu et al., 2021) and functional diversity (e.g., Barbet-Massin and Jetz, 2015; Thuiller et al., 2015; Weterings et al., 2019), or in the selection of protected areas (e.g., Guisan et al., 2013; Hannah et al., 2007; Marini et al., 2009).

A recent global analysis by Capinha et al. (2017) revealed that nearly 200 reptile species became established in at least one of the 359 world regions considered in their study, and that reptile invasions were accelerating, especially on islands. In fact, islands and coastal mainland regions are hotspots for the establishment of non-native species (Blackburn et al., 2016; Dawson et al., 2017) and often host a large number of non-native reptiles (Pitt et al., 2005), which are among the most successful and abundant vertebrates in small islands (Novosolov et al., 2016). Because insular ecosystems are usually unbalanced (often harboring empty niches), and many insular native species have evolved without predators, competitors or parasites, islands seem to be more amenable to herpetofaunal invasion (Whittaker and Fernandez-Palacios, 2007). For instance, the Mediterranean region has one of the longest histories of human settlements and trade, as well as of interaction between humans and biodiversity, leading to a multitude of biological introductions over millennia (Blondel et al., 2010a). Here, humans have facilitated the dispersal of a wide-array of non-native reptiles, whose current distributions are dependent on a complex interplay between human activities, geographic location, land use and bioclimatic factors and species traits (Silva-Rocha et al., 2019).

Geckos, and in particular members of the genus *Tarentola*, are among the most successful terrestrial vertebrates in undertaking successful - natural and anthropogenic - long distance dispersal events to areas outside of their native ranges (Macát et al., 2014; Ortiz-Medina et al., 2019; Perella and Behm, 2020). In fact, human translocation and posterior colonization of new areas are so common that some invasive geckos now have an almost cosmopolitan distribution in tropical and temperate regions (Baldo et al., 2008). The Moorish gecko *Tarentola mauritanica* (Linnaeus, 1758), a complex of species encompassing six putative distinct taxa (Rato et al., 2016), is widespread throughout North Africa, most of the Iberian and Italian peninsulas and multiple other Mediterranean coastal regions (Vogrin et al., 2017). However, due to its frequent association to human settlements and capacity for long-distance dispersals, it has been introduced in multiple mainland and island regions across the Mediterranean basin, Macaronesia, Caribbean as well as North and South America (Carranza et al., 2000; Harris et al., 2004a, 2004b). In the Macaronesian island of Madeira it was first reported in Garajau, a small locality ca. 8 km east of Funchal, the island's capital (Báez and Bischoito, 1993). Although the species' distribution in Madeira is poorly documented, it has been observed in several other places, as far as 20 km from the location where it was initially reported (Rato et al., 2021b), as well as in the nearby island of Porto Santo (Jesus et al., 2008). Of the multiple lineages of *Tarentola mauritanica* only one (the European lineage) is known for Madeira (Harris et al., 2004a).

The potential environmental impacts of *T. mauritanica* in Madeira are largely unknown. In general, the genus *Tarentola* seems to be less prone to become invasive than the genus *Hemidactylus*, which has several invasive species worldwide (Cole et al., 2005; Weterings and Vetter, 2018; Yang et al., 2012), one of them also introduced in Madeira (*H. mabouia*; Rato et al., 2021b). In Croatia, *T. mauritanica* is reported to compete with *Hemidactylus turcicus* through spatial displacement (Lisicic et al., 2012). In the absence of native geckos in Madeira, competition can be happening with the introduced *H. mabouia*, namely for refuge and feeding resources. Therefore, the two introduced species can be limiting each other's distribution, probably with *T. mauritanica* being more successful and aggressive in establishing its territory, as observed in the Croatian populations (Lisicic et al., 2012). On the other hand, *T. mauritanica* may be having some impact on the island's arthropod communities. A recent dietary study of *T. mauritanica* in Madeira revealed that 6% of the gecko's diet is composed of endemic arthropods, 18% of native arthropod species and 47% of introduced arthropods (Martins, 2021). Insecta was the most represented prey group, with multiple prey species classified as crop pests or vectors of diseases (e.g. salmonella) (Martins, 2021). The geographic range of the non-native vertebrates in Madeira is largely unknown (but see e.g., Rocha et al., 2020) and, thus far, no prediction was made to assess their potential distributions. Therefore, we set out to i) investigate how bioclimatic and local drivers might be modulating the expansion of *T. mauritanica* in Madeira and ii) identify the suitable geographic distribution of *T. mauritanica* across the island, based on the projection of the native and introduced range climatic conditions on the invaded insular

region, as well as on the island's local-scale land use variables.

2. Material and methods

2.1. Study area

Madeira is an autonomous region of Portugal and part of the Macaronesia, a collection of five volcanic archipelagos (Madeira, Selvagens, Canary Islands, Cape Verde and Azores) in the North Atlantic, off the coasts of Africa and Europe (Fig. 1). Due to the high number of endemic species, Macaronesia is currently classified as a biodiversity hotspot (Mittermeier et al., 2005). The Madeira archipelago, which includes the islands of Madeira, Porto Santo and Desertas, was an important center for commerce, representing a stepping-stone between Europe and the New World, and due to this multiple taxa were introduced (Wetterer et al., 2007). Currently, at least 14 non-native vertebrate species and over 600 species of non-native invertebrates are known to the archipelago (Silva-Rocha et al., 2018). In addition to *T. mauritanica*, Madeira is home to one native lizard (*Teira dugesii*) and hosts two other non-native reptiles, namely *Hemidactylus mabouia* and *Indotyphlops braminus* (Silva-Rocha et al., 2018).

The subtropical Island of Madeira has a total area of 742 km², with 58 km in its longitudinal section and 23 km in its latitudinal section. The island's orography is very rough, with the highest altitudes at Pico Ruivo (1862 m), Pico das Torres (1851 m) and Pico do Areeiro (1818 m), and an average altitude of 646 m above sea level (Santos, 2018). The human population density is relatively high (305.9 inhabitants/km²; Silva et al., 2008), with the south coast, and in particular the island's capital, Funchal, harbouring most of the population.

The climate is influenced by the intensity and location of the Azores anticyclone (Figueira et al., 2006), and in conjunction with the slope, orientation and configuration of the island, contributes to the diverse micro-climates it harbours. The average annual precipitation varies between ca. 500 and 2000 mm and increases with altitude, being higher in the north coast when compared - within the same altitudinal band - to the south (Figueira et al., 2006; Santos, 2018). The climate is mild with an annual temperature average of 18.7°C and an amplitude of 6.4 degrees Celsius, being August the hottest month (average temperature of 22°C) and February the

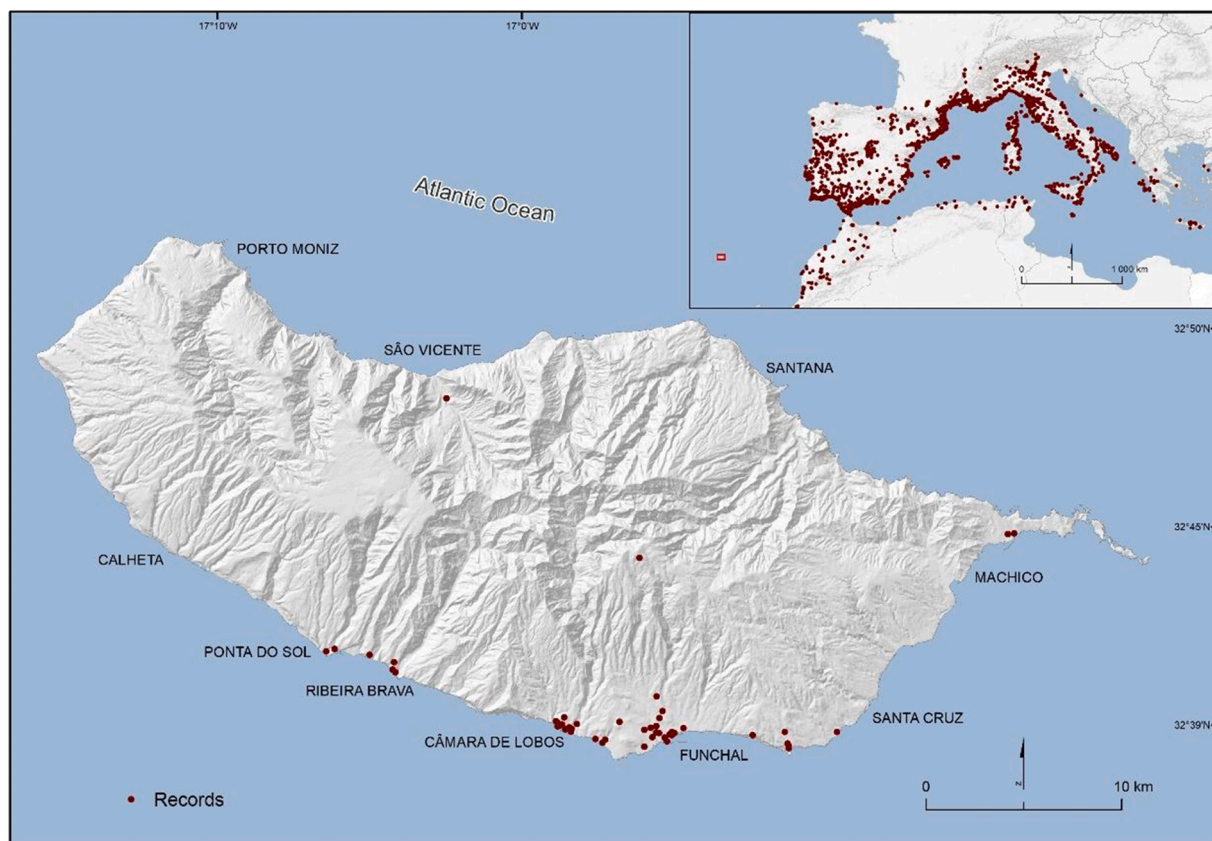


Fig. 1. Known distribution records of the Moorish gecko *Tarentola mauritanica* in Madeira Island and inset map representing the species' native range. The geographic location of Madeira Island is indicated by a red square in the insert map. Occurrence points used for the bioclimatic and local land use models are represented as red circles. (For interpretation of the references to colour in this figure, the reader is referred to the web version of this article.)

coldest month (average temperature of 15°C) (Quintal, 2007). Madeira presents a wide diversity of land use covers – e.g., urban areas, agricultural fields, exotic tree plantations and native forest – converging within relative short distances (Fig. A.1) (Santos, 2018), thus providing a diverse array of habitats to the island's biodiversity.

2.2. Species occurrence

In order to assess the habitat suitability of *T. mauritanica* in Madeira, we collected occurrence data for the species' native and non-native global range, including all known records from Madeira Island.

We compiled a total of 2897 records for the species' native and introduced distributions from the personal database of Rato, C. (166 records), as well as from the Global Biodiversity Information Facility (GBIF) database (2682 records from November 2020, www.gbif.org), which contains species records from a wide array of museum collections, online platforms (e.g., iNaturalist), and other published (Fig. 1; Fig. B.1). From GBIF, we examined only records containing animal pictures. Therefore, we considered that the integration of personal sampling and the GBIF database was enough to cover the entire distribution (i.e., native and introduced) of *T. mauritanica*. The occurrence records in Madeira Island were collected by Rocha, R. (49 records) over the last 15 years, complemented with fieldwork conducted by some of the authors in September 2020 (Fig. 1). All records were cleaned and filtered for double records (i.e., records from the same location), and erroneous geo-referenced records which were removed from the final dataset. Furthermore, to avoid over-representation of environmental conditions in densely sampled areas, we kept only one observation record per grid cell (Mammola et al., 2018). There are two points, one in the center of the island and another in the north coast (São Vicente), which represent odd records considering the remaining known distribution of *T. mauritanica* throughout the island. However, retaining or excluding these points did not significantly alter the results. We thus decided to include them in the analyses. All records used in this study are publicly available on <https://doi.org/10.6084/m9.figshare.19674306.v1>.

2.3. Bioclimatic and local data

Bioclimatic variables containing environmental data from native and introduced ranges were downloaded from CHELSEA v.1.2 (Karger et al., 2017) at a resolution of 30 arc-seconds (1 km²) and used to calculate the realized niche of the species on the introduced range. Using only a species' native range for model fitting usually leads to poor model performance, resulting in the observation of climatic niche shifts for non-native herpetofauna (Li et al., 2014).

Bioclimatic variables are a set of 19 derived variables developed for species distribution modelling and related ecological applications, and represent annual trends, seasonality and extreme or limiting environmental factors (Table C.1; Karger et al., 2017). Following Brun et al. (2020), we conducted a multicollinearity analysis to exclude redundant variables and reduce model complexity, thus allowing for easier model interpretation. Two well-supported methods were used to perform this analysis: Pearson correlation and Variance Inflation Factors (VIF). Only variables presenting simultaneously values below 0.7 and 5, respectively, were retained (Brun et al., 2020; James et al., 2021). Furthermore, the ecology and biology of the species was also considered in the selection of these variables (Rato et al., 2015a; Rato and Carretero, 2015). Thus, from the initial 19 variables, the following four variables were selected to perform the *climatic model*: Minimum Temperature of the Coldest Month, Mean Temperature of the Wettest Quarter, Annual Precipitation and Precipitation of the Driest Quarter.

We retrieved a second set of spatial variables to represent the effects of local-scale conditions on the species' distribution across the island. These variables were Land Use and Land Cover Classes (LULC), namely: agricultural and agroforestry areas, banana plantations, bushes, densely urban areas, forests and other natural environments, public spaces (e.g., parks and gardens), sparse urban areas and water bodies; and several indicators representing human demographics and building typology: number of buildings, number of inhabitants, number of lowest buildings (fewer than 4 flats), number of most recent buildings (post-1990), number of oldest buildings (prior to 1981), number of residential housing and number of tallest buildings (more than 5 floors). We collected the LULC data from the Regional Administration of Environment and Climate Changes (DRAAC) of the Madeira Government, while the data representing the human demographics and type of buildings were collected from the Portuguese National Statistics Institute (INE). Both types of data had a minimum mapping width of 1 ha.

Considering that the occurrence of *Tarentola mauritanica* is likely to be influenced by nearby environmental conditions, we quantified variables for a buffer with a 250 m radius around each data point, instead of solely for the location of the distributional record itself. For LULC, we calculated the percentage value of each class, while for the remaining variables we estimated an approximate value according to the area of the buffer that intersected the spatial layer containing the variables' values. Finally, we considered the proneness of *T. mauritanica* to inhabit humanized areas during variable selection and - as performed for the bioclimatic variables - redundant variables were excluded based on Pearson correlation and VIF (Arnold and Ovenden, 2002). Additionally, given the large number of variables that remained after the multicollinearity analysis, we also conducted a wrapper feature selection to reduce the number of variables. In this procedure we generated different subsets of input variables and then selected those that resulted in the best performing model according to the adopted metrics - Area Under the Curve (AUC) and True Skill Statistics (TSS) (Kuhn and Johnson, 2013). Thus, the following variables were retained to perform the local model: the LULC classes of Banana Plantations, Public Spaces, Bushes, Densely Urban Areas and Sparse Urban Areas; and the variables related to the type of buildings - Number of Tallest Buildings and Number of Oldest Buildings.

2.4. Modelling procedures

We performed the models using an ensemble modelling approach through the “SDM” package (Naimi and Araújo, 2016). Four modelling algorithms were used: generalized additive models (GAM), generalized linear models (GLM), boosting regression trees (BRT), and random forest (RF). However, regarding the local model we could not use the GAM algorithm, as the number of distribution records was insufficient for model fitting. The models were calibrated through the set of variables retained from the known observations, and a set of pseudo-absences records randomly generated over the same area. The use of pseudo-absence data is commonly adopted to overcome the lack of true absence data (Chapman et al., 2019). Following Barbet-Massin et al. (2012), we created a number of pseudo-absences similar to the known species’ observations, resulting in 2260 records for the climatic model and 40 for the local model.

To evaluate the predictive performance of each modelling algorithm, we used a fivefold cross validation procedure with 10 repetitions. AUC and TSS were used to assess model accuracy (Zhang et al., 2019). Only algorithms providing ‘good’ predictive performance, i.e., with values of these metrics above 0.8 and 0.5 (Nüchel et al., 2018; Ren-Yan et al., 2014), respectively, were retained to integrate the ensemble (see above).

Since buffer areas were used to collect the local predictor variables, we built a grid of regular hexagons (250 m radius) to provide a continuous prediction surface covering the whole island. Each hexagon represents the values of percentage of land classes and the indicators of human occupation – following the same procedures used to attain the predictor variables.

Afterwards, we estimated the potential distribution of the species by combining both types of models. For this purpose, the continuous values of probability were converted into predictions of suitable and unsuitable conditions through threshold values based on the maximum specificity and sensitivity method (Freeman and Moisen, 2008). We then summed the binary classifications and mapped the combinations of the two using a bivariate gradient. We evaluated the relative importance of each model variable through independent AUC tests by calculating model performance while including or excluding each variable, through a cross-validation procedure (Naimi and Araújo, 2016). Furthermore, the response curves of each variable were evaluated through an adaptation of the “evaluation strip” (Elith et al., 2005) which is also available in the “SDM” package. This procedure allows the marginal effect of a specific variable on the response variable to be evaluated, meaning that the response curves show the sensitivity of the model to a specific variable when the others remain at a constant value (in the “evaluation range” proposed by Elith et al., 2005 the remaining variables are set to the mean).

3. Results

Overall, the models had a good performance in predicting the distribution of *T. mauritanica* in Madeira Island. The predictive performance values did not present a significant inter-model variability, except for the differences observed between the GLM and the remaining models, concerning the TSS values. For the climatic model, the AUC values ranged from 0.85 (GLM) to 0.97 (RF), and the TSS values from 0.7 (GLM) to 0.94 (RF) (Table 1). As for the local model, AUC and TSS values range from 0.68 (GLM) to 0.78 (RF) and 0.47 (GLM) to 0.59 (FR), respectively (Table 1). In both metrics the results suggest that the RF algorithm provides the best performance, while the GLM the worst. According to the threshold values adopted to classify their predictive performance as ‘good’, all modelling algorithms were selected to perform the global ensemble modelling (climatic), while for the local use ensemble we excluded the GLM.

The SDM results suggest that the south and south-east of Madeira Island present the most suitable habitats for *T. mauritanica*. This could be observed from the climatic model (Fig. 2), which revealed that potentially ca. 56% of Madeira’s south and south-east territories offer suitable conditions for *T. mauritanica* (Fig. 2b). Surprisingly, the model predicts that the northern region around Santana also presents high environmental suitability for the species, despite currently no occurrence records are known for the area. Furthermore, model predictions also suggest that *T. mauritanica* can occupy more locations at the center of the island (north of Ribeira Brava), although with lower probability of suitability (Fig. 2a).

The contribution of each bioclimatic variable to the climatic models is reported in Table 2. The Minimum Temperature of the Coldest Month is clearly the variable with the most explanatory power (76.5%), followed by the Mean Temperature of the Wettest Quarter (15.3%), with the remaining ones having a very residual explanatory performance. The response curves of the variables reveal that the most suitable climatic conditions for *T. mauritanica* are higher Minimum Temperatures in the Coldest Month, Lower Mean

Table 1

Area Under the Curve (AUC) and True Skill Statistics (TSS) values for all tested models. “Climatic” refers to the models based only on bioclimatic variables and covering all the distribution range of *Tarentola mauritanica* (i.e., native and introduced, see Fig. 1 and Fig. B.1). “Local” refers to models based on land use and land cover variables, including only the distribution of *T. mauritanica* in Madeira Island.

Models	Climatic		Local	
	AUC	TSS	AUC	TSS
BRT	0.95	0.93	0.73	0.58
GAM	0.95	0.92	None	None
GLM	0.85	0.70	0.68	0.47
RF	0.97	0.94	0.78	0.60
Ensemble	0.95	0.89	0.76	0.59

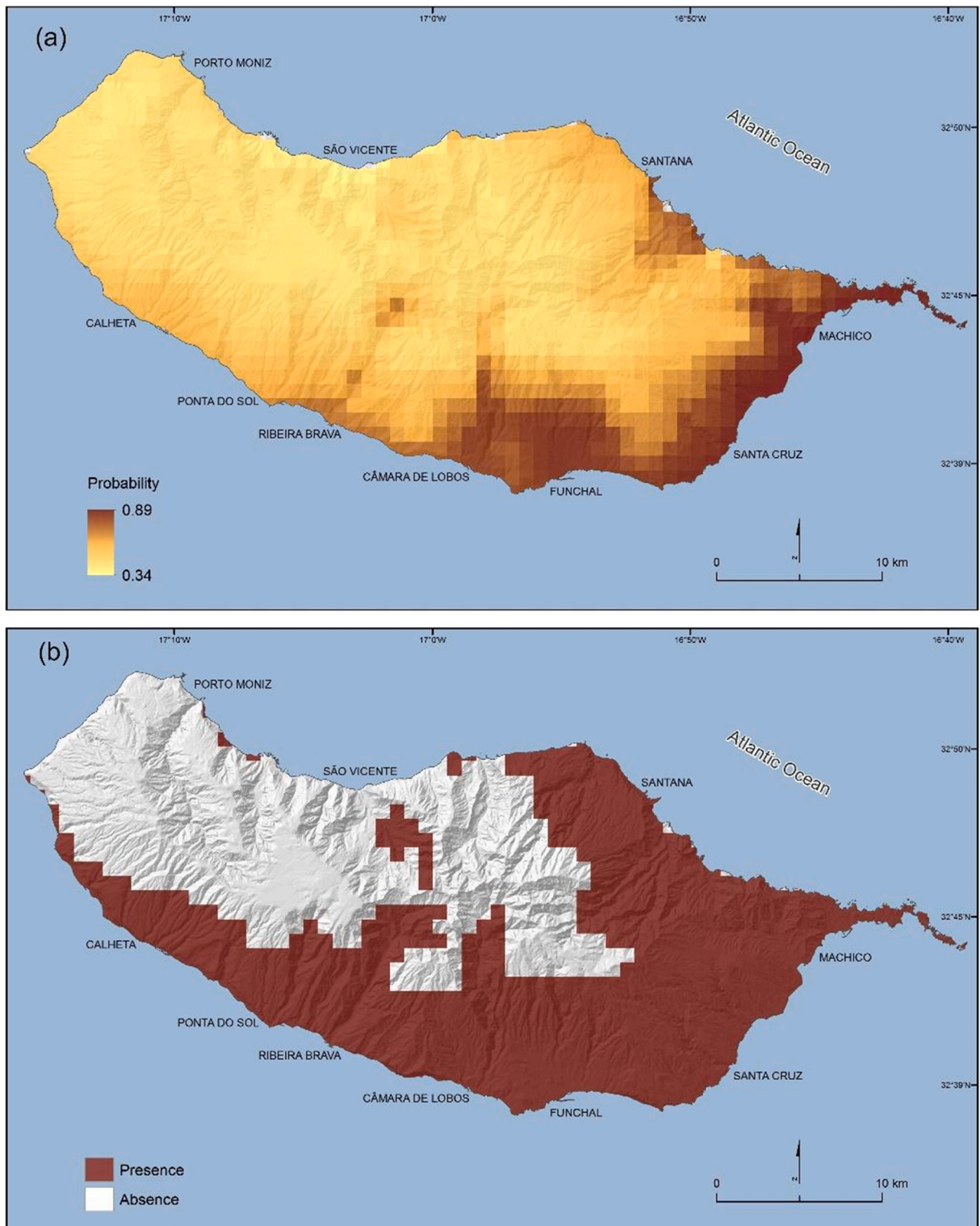


Fig. 2. Bioclimatic model of habitat suitability of *Tarentola mauritanica* in Madeira Island. a) Map of suitability based on probability of presence; b) Map of suitability based on the threshold. of 0.52.

Table 2
Importance of each variable to explain the distribution of *Tarentola mauritanica* in Madeira Island.

Model	Variable	Importance (%)
Climatic model	Minimum Temperature of Coldest Month	76.5
	Mean Temperature of Wettest Quarter	15.3
	Annual Precipitation	5.8
	Precipitation of Driest Quarter	2.4
Local model	Densely Urban Areas	62.1
	Bushes	7.3
	Sparse Urban Areas	5.8
	Number of Higher Buildings	2.4

Temperature of Wettest Quarter, Lower Annual Precipitation and Higher Precipitation of the Driest Quarter (Fig. D.1). Regarding the performance of the ensemble climatic model, an AUC value of 0.95 and a TSS value of 0.89 reveal a good capacity to predict the distribution in Madeira Island.

The local model, based on the land use and land cover variables (Fig. 3), predicted a wider distribution of *T. mauritanica*, covering all the coastal areas of the island. Similarly, to the climatic model, it also suggests that the species is likely to expand to the center of the island, with a relatively high suitability percentage (see Table 2 for the contribution of each land use and land cover variable). The variable Densely Urban Areas had the most explanatory power (62.1%), whereas the remaining three local variables had a relatively poor performance in explaining the distribution of the gecko in Madeira Island. The response curves indicate that the occurrence of *T. mauritanica* is determined by high values of dense or sparse urban areas, with somewhat low bush concentration and with higher buildings (Fig. D.2). The performance of the local model is also good, with an AUC value of 0.76 and a TSS value of 0.59.

The overlap of the climatic model with the land use model supports the high habitat suitability of both the south and south-east regions (center of the island, north from Ribeira Brava), as well as the north-east coastal areas, for the occurrence of *T. mauritanica* (Fig. 4).

4. Discussion

Our results suggest that Madeira Island, and in particular its south-east region, is suitable for *Tarentola mauritanica*. At present, the species' distribution is still somewhat restricted, but both the climatic and local models indicate that the geographic range of *T. mauritanica* is likely to expand, either naturally or assisted by humans. We found that the Moorish gecko prefers niches encompassing high temperatures during the coldest month, low mean temperatures during the wettest quarter, low annual values of precipitation, and high precipitation during the driest quarter. Hence, although introduced in a subtropical island, this temperate gecko has a clear bias for regions with more Mediterranean-like climates - i.e., characterized by dry summers and cold and wet winters (Blondel et al., 2010b). This pattern of niche conservatism was also observed in the Mediterranean house gecko *Hemidactylus turcicus* throughout its non-native range (Rödder and Lötters, 2009).

Matching our results, Rato et al. (2015b) identified humidity and temperature seasonality as the key determinants of niche shift and genetic diversification in *Tarentola mauritanica*. The introduced populations of *T. mauritanica* from Madeira cluster phylogenetically with the European lineage (Harris et al., 2004a, 2004b), which apart from being distributed along the Western Mediterranean coast (Rato et al., 2012), is also the only lineage with a widespread distribution across the species' introduced range (Maçát et al., 2014; Rato et al., 2021a, 2015c). Furthermore, this lineage has a higher plasticity regarding water loss in comparison to another closely related clade, reinforcing the hypothesis of its high colonizing capacity (Rato and Carretero, 2015). This ecophysiological trait is likely to be a key aspect for the success of the introduced geckos in Madeira Island.

The expansion of *Tarentola mauritanica* towards northern areas of Madeira suggests that the species can cope with more humid environments. However, as the response curves demonstrate, when humidity is too high, as in the mountains or in the northern coast of the island, the habitat becomes unsuitable for *T. mauritanica*. This is most likely due to the limited favorable conditions viable for gekkotan reproduction, particularly concerning humid environments. Like most gecko lizards, *T. mauritanica* produces rigid-shelled eggs, which are a pre-adaptation to arid environments but in conditions of high humidity, oxygen diffusion can limit embryo development (Pike et al., 2012). Moreover, evidence from the gecko *Chondrodactylus turneri* suggests that under high moisture conditions, fungal infections can decrease the viability of hard-shelled gekkotan eggs (Andrews, 2015). Therefore, unless the individuals inhabiting the north and center parts of Madeira can select suitable micro-habitats for egg laying, the future of these populations might be compromised under current climatic conditions. Yet, climate is changing at a global scale and at such a fast pace that species are more likely to change their distributions as a response than to adapt in situ (Bradshaw and Holzapfel, 2006). In fact, at least in the Iberian Peninsula and France, there is evidence of a northward shift of Moorish gecko's populations as a response to global warming (Geniez and Cheylan, 2012; Moreno-Rueda et al., 2012). However, without long-term data, one can only hypothesize that the same might be taking place in Madeira.

When it comes to local drivers, the positive effect of urban area density on the habitat suitability of *Tarentola mauritanica* was expected due to the species' common association to humanized areas (e.g., in use or abandoned buildings) where they find abundant arthropod prey attracted by artificial lights (Arnold and Ovenden, 2002). Notwithstanding that shrubs are known to affect the occupancy of *Tarentola* geckos (Penado et al., 2015), it was interesting to observe that bush density had a positive effect on the habitat suitability of *Tarentola mauritanica*. Yet, bush density had only a positive influence up to a certain value and, if too dense, the habitat

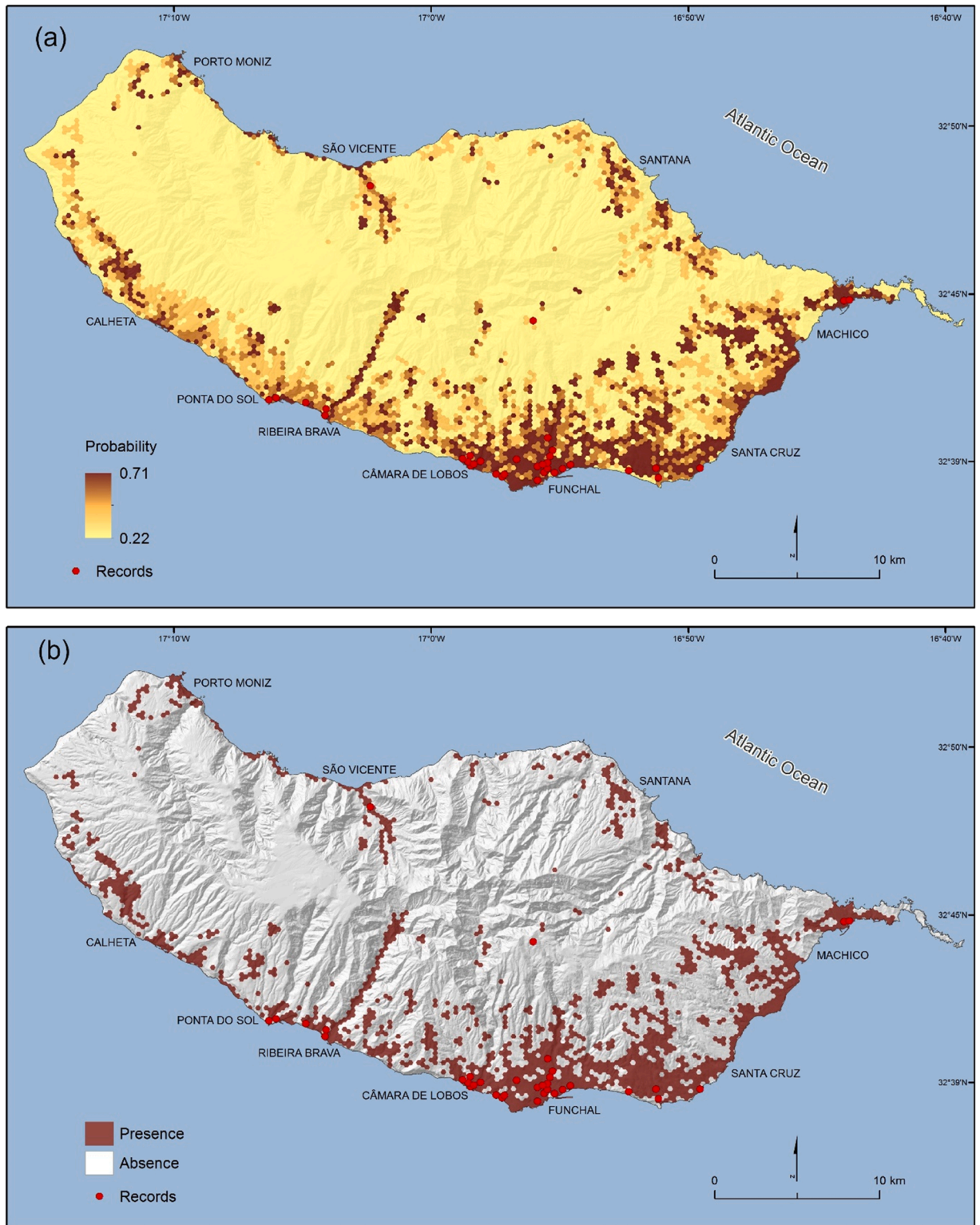


Fig. 3. Local model of habitat suitability of *Tarentola mauritanica* in Madeira Island. a) Map of suitability based on probability of presence; b) Map of suitability based on the threshold of 0.47.

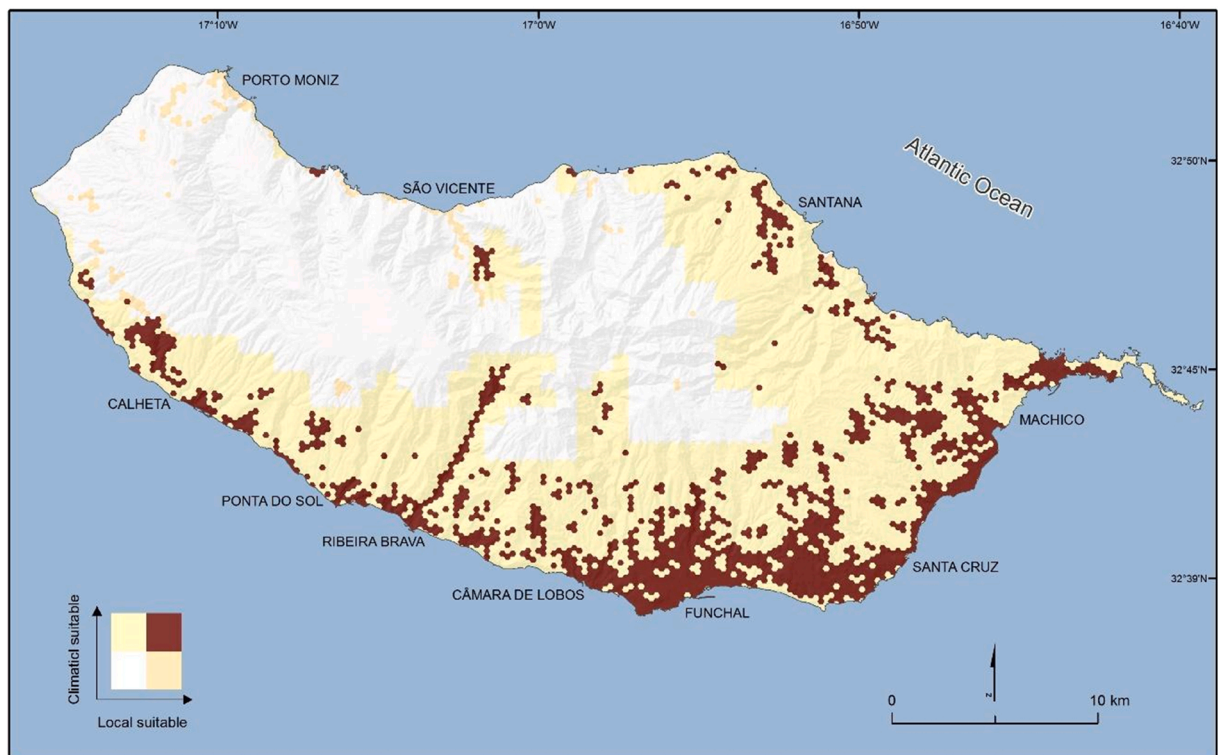


Fig. 4. Habitat suitability of *Tarentola mauritanica* in Madeira Island based on the overlap of bioclimatic and local models. The darker areas represent a match between climatic and local models.

was deemed as unsuitable for the species. These results highlight the importance of including local variables in habitat suitability models; when active, the Moorish gecko frequently uses vertical walls and hides behind sparsely dense bushes (Rato, C., personal obs.).

In general, both models (climatic and local) do overlap, with the climatic one predicting a larger suitable area than the local, and the local presenting projections on the west of the island, which do not match with the outputs of the climatic one. Interestingly, both SMDs predict the region around Santana as suitable, but so far, we are not aware of any records for that area. Indeed, a proper survey in this region is imperative to validate these models.

Studies suggest that climatic variables normally capture the species distribution at a global or continental scale, but not at more local levels (Bradie and Leung, 2017; Wang et al., 2018). To assess which drivers shape the distribution of species at regional and local scales, abiotic variables such as topography, vegetation types and land use should be used. Indeed, local scales identify more accurately the different habitats the species can occupy (Bradie and Leung, 2017; Hortal et al., 2010; Oliveira et al., 2021). In this study, the integration of both models seems to result in the combination of suitable climatic areas with preferred habitats of *T. mauritanica*. It also reinforces that the use of different predictors and the combination among them can contribute to models with a better performance and a more realistic distribution of the species at a regional level.

The current distribution of *Tarentola mauritanica* and its potential to expand in the future reflect the ability of geckos in general to thrive in new environments. Geckos are one of the reptile families with greatest numbers of introduction events and, simultaneously, with greatest numbers of naturalized populations (Kraus, 2009). In the case of the Mediterranean islands, for example, geckos are within the groups with more putative alien species, being *Hemidactylus turcicus* and *T. mauritanica* the species with more introduced populations (Silva-Rocha et al., 2019). This is not a surprise since most gecko species are small and synanthropic, which makes them prone to be transported in cargo to a variety of places. Apart from the obvious exchange of goods between Madeira and mainland Portugal, this Atlantic island is also a renowned tourist destination, especially among Europeans, with frequent daily flights from and to several European destinations, apart from regular cruise ships also connecting the island to other archipelagos and continental regions. Hence, there is an abundance of opportunities for plants, animals and even pathogens to be introduced in Madeira. This was most likely the mode of introduction of *T. mauritanica* in Madeira and Porto Santo. From these islands, *T. mauritanica* can easily be transported to other nearby islands or islets, and in particular to the Selvagens Islands, where the closely related - and endemic - *Tarentola bischoffi* can be found. Furthermore, Madeira can also act as a recipient for future introductions, due to the abundance of commercial and touristic routes connecting the island and unoccupied regions with suitable habitats for *T. mauritanica*. In fact, Madeira Island was already the point of entrance for *Aedes* mosquitoes from Venezuela (Seixas et al., 2019) and for *Hemidactylus mabouia*, another introduced gecko, potentially introduced from Brazil (Rato et al., 2021b). It can also serve as a source to other regions, as in the case of *Teira dugesii*, the Madeiran lizard, which was introduced in Lisbon, Azores and the Canary Islands (Silva-Rocha

et al., 2016).

5. Conclusions

Globalization is increasing the frequency of translocation of species from their native ranges to alien environments, and a wide array of plants, animals and pathogens are finding their way to remote islands, with the assistance of humans. The Moorish gecko is currently well established in Madeira and over the last three decades its area of occurrence in the island has increased more than 20 km. Our climatic and local land use SDMs confirm the south and south-eastern sections of the island as holding the most suitable areas for the species, with the climatic model predicting that over 50% of this region could be colonized. Surprisingly, both approaches predicted some areas of the northern coast of the island to be suitable, despite the current absence of records for those areas. Clearly, although introduced in a subtropical island, the Moorish gecko has an overall preference for more Mediterranean-like microclimates, similar to the one from its native range. Although the impact of *T. mauritanica* on Madeira's native biodiversity is still unknown, the fact is that its geographic distribution is predicted to increase in the future, reinforcing the need for strong and serious monitoring actions, which should be extended to other alien species in Madeira and in other Macaronesian islands.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors wish to thank Beatriz Martins for helping during fieldwork and to all those that shared their observations of Moorish geckos. This research was funded by the project PTDC/BIA-EVL/27958/2017 (to CR), financed by the Portuguese Foundation for Science and Technology (FCT). C.R. and R.R. were supported by FCT contracts (DL57/2016/CP1440/CT0005 - C.R.; 2020.01129. CEECIND/CP1601/CT0004 - R.R.), ISR was supported by FCT through a post-doc grant within project PTDC/BIA-EVL/27958/2017 and MS was supported by FCT through a PhD research scholarship (SFRH/BD/139753/2018). R.R. further acknowledges the support from ARDITI – Madeira's Regional Agency for the Development of Research, Technology and Innovation (grant M1420-09-5369-FSE-000002).

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2022.e02164](https://doi.org/10.1016/j.gecco.2022.e02164).

References

- Alsos, I.G., Ehrlich, D., Thuiller, W., Eidesen, P.B., Tribsch, A., Schönswetter, P., Lagaye, C., Taberlet, P., Brochmann, C., 2012. Genetic consequences of climate change for northern plants. *Proc. R. Soc. B Biol. Sci.* 279, 2042–2051. <https://doi.org/10.1098/RSPB.2011.2363>.
- Andrews, R.M., 2015. Rigid shells enhance survival of gekkotan eggs. *J. Exp. Zool. Part A Ecol. Genet. Physiol.* 323, 607–615. <https://doi.org/10.1002/JEZ.1951>.
- Arnold, E.N., Oviden, D.W., 2002. A field guide to the reptiles and amphibians of Britain and Europe. Herper Collins, London.
- Báez, M., Biscoito, M., 1993. First record of *Tarentola mauritanica* (Linnaeus, 1758) from the island of Madeira (NE Atlantic), in: First Symposium of Fauna and Flora of the Atlantic Islands. Funchal, Madeira.
- Baldo, D., Borteiro, C., Brusquetti, F., García, J.E., Prigioni, C., 2008. Reptilia, Gekkonidae, Hemidactylus mabouia, Tarentola mauritanica: distribution extension and anthropogenic dispersal. *Check List* 4, 434. <https://doi.org/10.15560/4.4.434>.
- Barbet-Massin, M., Jetz, W., 2015. The effect of range changes on the functional turnover, structure and diversity of bird assemblages under future climate scenarios. *Glob. Chang. Biol.* 21, 2917–2928. <https://doi.org/10.1111/GCB.12905>.
- Barbet-Massin, M., Jiguet, F., Albert, C.H., Thuiller, W., 2012. Selecting pseudo-absences for species distribution models: how, where and how many? *Methods. Ecol. Evol.* 3, 327–338. <https://doi.org/10.1111/J.2041-210X.2011.00172.X>.
- Blackburn, T.M., Delean, S., Pyšek, P., Cassey, P., Field, R., 2016. On the island biogeography of aliens: a global analysis of the richness of plant and bird species on oceanic islands. *Glob. Ecol. Biogeogr.* 25, 859–868. <https://doi.org/10.1111/geb.12339>.
- Blackburn, T.M., Pyšek, P., Bacher, S., Carlton, J.T., Duncan, R.P., Jarošík, V., Wilson, J.R.U., Richardson, D.M., 2011. A proposed unified framework for biological invasions. *Trends Ecol. Evol.* 26, 333–339. <https://doi.org/10.1016/j.tree.2011.03.023>.
- Blondel, J., Aronson, J., Bodiou, J.-Y., Boeuf, G., 2010a. The Mediterranean Region - Biological Diversity in Space and Time, second ed. Oxford University Press, Oxford. https://doi.org/10.1163/1872-5287_bdr_COM_00277.
- Blondel, J., Aronson, J., Bodiou, J., Boeuf, G., 2010b. *The Mediterranean Region: Biological Diversity in Space and Time*, second ed. Oxford University Press, New York.
- Bradie, J., Leung, B., 2017. A quantitative synthesis of the importance of variables used in MaxEnt species distribution models. *J. Biogeogr.* 44, 1344–1361. <https://doi.org/10.1111/jbi.12894>.
- Bradley, B.A., Wilcove, D.S., Oppenheimer, M., 2009. Climate change increases risk of plant invasion in the Eastern United States. *Biol. Invasions* 12, 1855–1872. <https://doi.org/10.1007/S10530-009-9597-Y>.
- Bradshaw, W.E., Holzapfel, C.M., 2006. Evolutionary response to rapid climate change. *Science* 312, 1477–1478. <https://doi.org/10.1126/science.1127000>.
- Brun, P., Thuiller, W., Chauvier, Y., Pellissier, L., Wüest, R.O., Wang, Z., Zimmermann, N.E., 2020. Model complexity affects species distribution projections under climate change. *J. Biogeogr.* 47, 130–142. <https://doi.org/10.1111/jbi.13734>.
- Capinha, C., Seebens, H., Cassey, P., García-Díaz, P., Lenzner, B., Mang, T., Moser, D., Pyšek, P., Rödder, D., Scalera, R., Winter, M., Dullinger, S., Essl, F., 2017. Diversity, biogeography and the global flows of alien amphibians and reptiles. *Divers. Distrib.* 23, 1313–1322. <https://doi.org/10.1111/ddi.12617>.

- Carranza, S., Arnold, E.N., Mateo, J.A., López-Jurado, L.F., 2000. Long-distance colonization and radiation in gekkonid lizards, *Tarentola* (Reptilia: Gekkonidae), revealed by mitochondrial DNA sequences. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* 267, 637–649. <https://doi.org/10.1098/RSPB.2000.1050>.
- Chapman, D., Pescott, O.L., Roy, H.E., Tanner, R., 2019. Improving species distribution models for invasive non-native species with biologically informed pseudo-absence selection. *J. Biogeogr.* 46, 1029–1040. <https://doi.org/10.1111/JBI.13555>.
- Cole, N.C., Jones, C.G., Harris, S., 2005. The need for enemy-free space: the impact of an invasive gecko on island endemics. *Biol. Conserv.* 125, 467–474. <https://doi.org/10.1016/j.biocon.2005.04.017>.
- Dawson, W., Moser, D., Kleunen, M., Van, Kreft, H., Pergl, J., Pyšek, P., Weigelt, P., Winter, M., Lenzner, B., Blackburn, T., Dyer, E., Cassey, P., Scrivens, S., Economo, E., Guénard, B., Capinha, C., Seebens, H., García-Díaz, P., Nentwig, W., García-Berthou, E., Casal, C., Mandrak, N., Fuller, P., Meyer, C., Essl, F., 2017. Global hotspots and correlates of alien species richness across taxonomic groups. *Nat. Ecol. Evol.* 1, 1–7. <https://doi.org/10.1038/s41559-017-0186>.
- Didham, R.K., Tylianakis, J.M., Hutchison, M.A., Ewers, R.M., Gemmill, N.J., 2005. Are invasive species the drivers of ecological change? *Trends Ecol. Evol.* 20, 470–474.
- Domisch, S., Araújo, M.B., Bonada, N., Pauls, S.U., Jähnig, S.C., Haase, P., 2013. Modelling distribution in European stream macroinvertebrates under future climates. *Glob. Chang. Biol.* 19, 752–762. <https://doi.org/10.1111/GCB.12107>.
- Dueñas, M.A., Hemming, D.J., Roberts, A., Diaz-Soltero, H., 2021. The threat of invasive species to IUCN-listed critically endangered species: a systematic review. *Glob. Ecol. Conserv.* 26, e01476. <https://doi.org/10.1016/J.GECCO.2021.E01476>.
- Elith, J., Ferrier, S., Huettmann, F., Leathwick, J., 2005. The evaluation strip: a new and robust method for plotting predicted responses from species distribution models. *Ecological Modelling* 186 (3), 280–289.
- Figueira, C., Prada, S., Sequeira, M., Perestrelo, A., Silva, M., 2006. Estudo da precipitação oculta em dois tipos de vegetação da Ilha da Madeira. *8o Congr. Da Água* 1–10.
- Freeman, E.A., Moisen, G.G., 2008. A comparison of the performance of threshold criteria for binary classification in terms of predicted prevalence and kappa. *Ecol. Modell.* 217, 48–58. <https://doi.org/10.1016/J.ECOLMODEL.2008.05.015>.
- García, R.A., Burgess, N.D., Cabeza, M., Rahbek, C., Araújo, M.B., 2012. Exploring consensus in 21st century projections of climatically suitable areas for African vertebrates. *Glob. Glob. Chang. Biol.* 18, 1253. <https://doi.org/10.1111/J.1365-2486.2011.02605.X>.
- Geniez, P., Cheylan, M., 2012. Les amphibiens et les reptiles du Languedoc-Roussillon et régions limitrophes atlas biogéographique.
- Giljohann, K.M., Hauser, C.E., Williams, N.S.G., Moore, J.L., 2011. Optimizing invasive species control across space: willow invasion management in the Australian Alps. *J. Appl. Ecol.* 48, 1286–1294. <https://doi.org/10.1111/J.1365-2664.2011.02016.X>.
- Guisan, A., Tingley, R., Baumgartner, J.B., Naujokaitis-Lewis, I., Sutcliffe, P.R., Tulloch, A.I.T., Regan, T.J., Brotons, L., McDonald-Madden, E., Mantyka-Pringle, C., Martin, T.G., Rhodes, J.R., Maggini, R., Setterfield, S.A., Elith, J., Schwartz, M.W., Wintle, B.A., Broennimann, O., Austin, M., Ferrier, S., Kearney, M.R., Possingham, H.P., Buckley, Y.M., 2013. Predicting species distributions for conservation decisions. *Ecol. Lett.* 16, 1424–1435. <https://doi.org/10.1111/ELE.12189>.
- Hannah, L., Midgley, G., Anelman, S., Araújo, M., Hughes, G., Martinez-Meyer, E., Pearson, R., Williams, P., 2007. Protected area needs in a changing climate. *Front. Ecol. Environ.* 5, 131–138. [https://doi.org/10.1890/1540-9295\(2007\)5\[131:PANIAC\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2007)5[131:PANIAC]2.0.CO;2).
- Harris, D.J., Batista, V., Carretero, M.A., Ferrand, N., 2004a. Genetic variation in *Tarentola mauritanica* (Reptilia: Gekkonidae) across the Strait of Gibraltar derived from mitochondrial and nuclear DNA sequences. *Amphib. -Reptil.* 25, 451–459. <https://doi.org/10.1163/156853807779799144>.
- Harris, D.J., Batista, V., Lymberakis, P., Carretero, M.A., 2004b. Complex estimates of evolutionary relationships in *Tarentola mauritanica* (Reptilia: Gekkonidae) derived from mitochondrial DNA sequences. *Mol. Phylogenet. Evol.* 30, 855–859. [https://doi.org/10.1016/S1055-7903\(03\)00260-4](https://doi.org/10.1016/S1055-7903(03)00260-4).
- Harris, D.J., Batista, V., Lymberakis, P., Carretero, M.A., 2004b. Complex estimates of evolutionary relationships in *Tarentola mauritanica* (Reptilia: Gekkonidae) derived from mitochondrial DNA sequences. *Mol. Phylogenet. Evol.* 30, 855–859. [https://doi.org/10.1016/S1055-7903\(03\)00260-4](https://doi.org/10.1016/S1055-7903(03)00260-4).
- Hortal, J., Roura-Pascual, N., Sanders, N.J., Rahbek, C., 2010. Understanding (insect) species distributions across spatial scales. *Ecography* 31, 51–53. <https://doi.org/10.1111/j.1600-0587.2009.06428.x>.
- James, G., Witten, D., Hastie, T., Tibshirani, R., 2021. An Introduction to Statistical Learning. *Springer Texts Stat.* <https://doi.org/10.1007/978-1-0716-1418-1>.
- Jesus, J., Lemos, A., Gonçalves, R., Brehm, A., 2008. First record of *Tarentola mauritanica* (LINNAEUS, 1758) on Porto Santo Island. *Herpetozoa* 20, 175–177.
- Jiménez-Valverde, A., Peterson, A.T., Soberón, J., Overton, J.M., Aragón, P., Lobo, J.M., 2011. Use of niche models in invasive species risk assessments. *Biol. Invasions* 13, 2785–2797. <https://doi.org/10.1007/s10530-011-9963-4>.
- Karger, D.N., Conrad, O., Böhrer, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Zimmermann, N.E., Linder, H.P., Kessler, M., 2017. Climatologies at high resolution for the earth's land surface areas. *Sci. Data* 4, 1–20. <https://doi.org/10.1038/sdata.2017.122>.
- Kramer, A.M., Annis, G., Wittmann, M.E., Chadderton, W.L., Rutherford, E.S., Lodge, D.M., Mason, L., Beletsky, D., Riseng, C., Drake, J.M., 2017. Suitability of Laurentian Great Lakes for invasive species based on global species distribution models and local habitat. *Ecosphere* 8, e01883. <https://doi.org/10.1002/ECS2.1883>.
- Kraus, F., 2009. Impacts of alien reptiles and amphibians. *Alien. Reptil. Amphib. A Sci. Compend. Anal.* 57–93. <https://doi.org/10.1007/978-1-4020-8946-6>.
- Kuhn, M., Johnson, K., 2013. Applied predictive modeling. *Appl. Predict. Model.* <https://doi.org/10.1007/978-1-4614-6849-3>.
- Lecocq, T., Rasmont, P., Harpke, A., Schweiger, O., 2016. Improving international trade regulation by considering intraspecific variation for invasion risk assessment of commercially traded species: the bombus terrestris case. *Conserv. Lett.* 9, 281–289. <https://doi.org/10.1111/CONL.12215>.
- Li, Y., Liu, X., Li, X., Petitpierre, B., Guisan, A., 2014. Residence time, expansion toward the equator in the invaded range and native range size matter to climatic niche shifts in non-native species. *Glob. Ecol. Biogeogr.* 23, 1094–1104.
- Lisicic, D., Drakulic, S., Herrel, A., Dikic, D., Benkovic, B., Tadic, Z., 2012. Effect of competition on habitat utilization in two temperate climate gecko species. *Ecol. Res.* 27, 551–560. <https://doi.org/10.1007/s11284-011-0921-5>.
- Lockwood, J.L., Hoopes, M.F., Marchetti, M.P., 2009. *Invasion Ecology*, second ed. Wiley-Blackwell Publishing., Oxford.
- Macát, Z., Starcová, M., Červenka, J., Jablonski, D., Šandera, M., 2014. A molecular assessment and first record of *Tarentola mauritanica* (Squamata: Phyllodactylidae) on Corfu. *Greece Salama* 50, 172–176.
- Macdougall, A.S., Turkington, R., 2005. Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology* 86, 42–55.
- Maiorano, L., Faluccci, A., Zimmermann, N.E., Psomas, A., Pottier, J., Baisero, D., Rondinini, C., Guisan, A., Boitani, L., 2011. The future of terrestrial mammals in the Mediterranean basin under climate change. *Philos. Trans. R. Soc. B Biol. Sci.* 366, 2681. <https://doi.org/10.1098/RSTB.2011.0121>.
- Mammola, S., Goodacre, S.L., Isaia, M., 2018. Climate change may drive cave spiders to extinction. *Ecography* 41, 233–243. <https://doi.org/10.1111/ECOG.02902>.
- Marini, M.A., Barbet-Massin, M., Lopes, L.E., Jiguet, F., 2009. Major current and future gaps of Brazilian reserves to protect Neotropical savanna birds. *Biol. Conserv.* 142, 3039–3050. <https://doi.org/10.1016/J.BIOCON.2009.08.002>.
- Martins, B., 2021. Can an introduced gecko act as biological pest controller? Exploring the diet of *Tarentola mauritanica* in Madeira Island. *Faculdade de Ciências da Universidade do Porto*.
- Mittermeier, R.A., Gil, P.R., Hoffman, M., Pilgrim, J., Brooks, T., Mittermeier, C.G., Lamoreux, J., Fonseca, G.A.B., 2005. Hotspots: earth's biologically richest and most endangered terrestrial ecoregions. University of Chicago Press., Chicago. <https://doi.org/10.5860/choice.38-0922>.
- Moreno-Rueda, G., Pleguezuelos, J.M., Pizarro, M., Montori, A., 2012. Northward shifts of the distributions of Spanish reptiles in association with climate change. *Conserv. Biol.* 26, 278–283. <https://doi.org/10.1111/j.1523-1739.2011.01793.x>.
- Naimi, B., Araújo, M.B., 2016. Sdm: A reproducible and extensible R platform for species distribution modelling. *Ecography* 39, 368–375. <https://doi.org/10.1111/ECOG.01881>.
- Novosolov, M., Rodda, G.H., Feldman, A., Kadison, A.E., Dor, R., Meiri, S., 2016. Power in numbers. Drivers of high population density in insular lizards. *Glob. Ecol. Biogeogr.* 25, 87–95. <https://doi.org/10.1111/geb.12390>.
- Nüchel, J., Bocher, P.K., Xiao, W., Zhu, A.X., Svenning, J.C., 2018. Snub-nosed monkeys (*Rhinopithecus*): potential distribution and its implication for conservation. *Biodivers. Conserv.* 27, 1517–1538. <https://doi.org/10.1007/S10531-018-1507-0/FIGURES/7>.

- Oliveira, M.R., Tomas, W.M., Guedes, N.M.R., Peterson, A.T., Szabo, J.K., Júnior, A.S., Camilo, A.R., Padovani, C.R., Garcia, L.C., 2021. The relationship between scale and predictor variables in species distribution models applied to conservation. *Biodivers. Conserv.* 30, 1971–1990. <https://doi.org/10.1007/s10531-021-02176-w>.
- Ortiz-Medina, J.A., Cabrera-Cen, D.I., Chan-Noh, M.M., Cedeño-Vázquez, J.R., 2019. First record of the Moorish Gecko, *Tarentola mauritanica* (Linnaeus, 1758) (Squamata: Phyllodactylidae), in Mexico. *Herpetol. Notes* 12, 971–974.
- Pauls, S.U., Nowak, C., Bálint, M., Pfenniger, M., 2013. The impact of global climate change on genetic diversity within populations and species. *Mol. Ecol.* 22, 925–946. <https://doi.org/10.1111/MEC.12152>.
- Penado, A., Rocha, R., Sampaio, M., Gil, V., Carreira, B.M., Rebelo, R., 2015. Where to “Rock”? Choice of retreat sites by a gecko in a semi-arid habitat. *Acta Herpetol.* 10, 47–54. https://doi.org/10.13128/ACTA_HERPETOL-15304.
- Perella, C.D., Behm, J.E., 2020. Understanding the spread and impact of exotic geckos in the greater Caribbean region. *Biodivers. Conserv.* 29, 1109–1134. <https://doi.org/10.1007/s10531-020-01939-1>.
- Pike, D.A., Andrews, R.M., Du, W.G., 2012. Eggshell morphology and gekkotan life-history evolution. *Evol. Ecol.* 26, 847–861. <https://doi.org/10.1007/s10682-011-9527-1>.
- W. Pitt, D. Vice M. Pitzler Challenges of invasive reptiles and amphibians D.L. Nolte K.A. Fagerstone 11th Wildlife Damage Management Conference 2005 Wildlife Damage Management Fort Collins Colorado 112 119.
- Pyšek, P., Hulme, P.E., Simberloff, D., Bacher, S., Blackburn, T.M., Carlton, J.T., Dawson, W., Essl, F., Foxcroft, L.C., Genovesi, P., Jeschke, J.M., Kühn, I., Liebhold, A.M., Mandrak, N.E., Meyerson, L.A., Pauchard, A., Pergl, J., Roy, H.E., Seebens, H., van Kleunen, M., Vilà, M., Wingfield, M.J., Richardson, D.M., 2020. Scientists’ warning on invasive alien species. *Biol. Rev.* 95, 1511–1534. <https://doi.org/10.1111/brv.12627>.
- Quintal, R., 2007. Estudo fitogeográfico dos jardins, parques e quintas do concelho do Funchal. Universidade de Lisboa.
- Rato, C., Carranza, S., Harris, D.J., 2012. Evolutionary history of the genus *Tarentola* (Gekkota: Phyllodactylidae) from the Mediterranean Basin, estimated using multilocus sequence data. *BMC Evol. Biol.* 12, 14. <https://doi.org/10.1186/1471-2148-12-14>.
- Rato, C., Carretero, M.A., 2015. Ecophysiology tracks phylogeny and meets ecological models in an Iberian gecko. *Physiol. Biochem. Zool.* 88, 564–575. <https://doi.org/10.1086/682170>.
- Rato, C., Harris, D.J., Carranza, S., Machado, L., Perera, A., 2016. The taxonomy of the *Tarentola mauritanica* species complex (Gekkota: Phyllodactylidae): Bayesian species delimitation supports six candidate species. *Mol. Phylogenet. Evol.* 94, 271–278. <https://doi.org/10.1016/j.ympev.2015.09.008>.
- Rato, C., Harris, D.J., Perera, A., Carvalho, S.B., Carretero, M.A., Rödder, D., 2015a. A Combination of divergence and conservatism in the niche evolution of the Moorish gecko, *Tarentola mauritanica* (Gekkota: Phyllodactylidae). *PLoS One* 10. <https://doi.org/10.1371/journal.pone.0127980>.
- Rato, C., Harris, D.J., Perera, A., Carvalho, S.B., Carretero, M.A., Rödder, D., 2015b. A Combination of divergence and conservatism in the niche evolution of the Moorish gecko, *Tarentola mauritanica* (Gekkota: Phyllodactylidae). *PLoS One* 10, 1–16. <https://doi.org/10.1371/journal.pone.0127980>.
- Rato, C., Marques, V., Paracuellos, M., Tortolero, J., Nevado, J., Carretero, M., 2021a. Alborán Island, a small meeting point for three invasive lizards, whose geographic origin is uncovered by molecular analysis. *Biol. Invasions Rec.* 10, 977–990. <https://doi.org/10.3391/bir.2021.10.4.22>.
- Rato, C., Martins, B., Rocha, R., Silva-Rocha, I., 2021b. Uncovered genetic diversity in *Hemidactylus mabouia* (Reptilia: Gekkonidae) from Madeira Island reveals uncertain sources of introduction. *Amphib. Reptil.* 42, 369–375. <https://doi.org/10.1163/15685381-bja10052>.
- Rato, C., Resendes, R., Cunha, R., Harris, J., 2015c. First Rec. *Tarentola substituta* JOGER, 1984. *Genet. Identif. Tarentola mauritanica* (LINNAEUS, 1758. *Herpetozoa* 27, 182–187.
- Ren-Yan, D., Xiao-Quan, K., Min-Yi, H., Wei-Yi, F., Zhi-Gao, W., 2014. The predictive performance and stability of six species distribution models. *PLoS One* 9, e112764. <https://doi.org/10.1371/JOURNAL.PONE.0112764>.
- Ricciardi, A., Blackburn, T.M., Carlton, J.T., Dick, J.T.A., Hulme, P.E., Iacarella, J.C., Jeschke, J.M., Liebhold, A.M., Lockwood, J.L., MacIsaac, H.J., Pyšek, P., Richardson, D.M., Ruiz, G.M., Simberloff, D., Sutherland, W.J., Wardle, D.A., Aldridge, D.C., 2017. Invasion Science: a horizon scan of emerging challenges and opportunities. *Trends Ecol. Evol.* 32, 464–474. <https://doi.org/10.1016/j.tree.2017.03.007>.
- Richardson, D.M., 2011. Fifty Years Invasion Ecol., Fifty Years Invasion Ecol.: Leg. Charles Elton. <https://doi.org/10.1002/9781444329988>.
- Rocha, R., Reino, L., Sepúlveda, P., Ribeiro, J., 2020. Introduced population of ring-necked parakeets *Psittacula krameri* in Madeira Island, Portugal – Call for early action. *Manag. Biol. Invasions* 11, 576–587. <https://doi.org/10.3391/mbi.2020.11.3.15>.
- Rödder, D., Lötters, S., 2009. Niche shift versus niche conservatism? Climatic characteristics of the native and invasive ranges of the Mediterranean house gecko (*Hemidactylus turcicus*). *Glob. Ecol. Biogeogr.* 18, 674–678.
- Santos, J.M.F., 2018. Análise e modelação espaço-temporal do mosquito vetor do dengue na ilha da Madeira. Universidade de Lisboa.
- Seixas, G., Salgueiro, P., Bronzato-Badial, A., Gonçalves, Y., Reyes-Lugo, M., Gordicho, V., Ribolla, P., Viveiros, B., Silva, A.C., Pinto, J., Sousa, C.A., 2019. Origin and expansion of the mosquito *Aedes aegypti* in Madeira Island (Portugal). *Sci. Rep.* 9, 1–13. <https://doi.org/10.1038/s41598-018-38373-x>.
- Silva-Rocha, I., Sá-Sousa, P., Fariña, B., Carretero, M.A., 2016. Molecular analysis confirms madeira as source for insular and continental introduced populations of *Teira dugesii* (Sauria: Lacertidae). *Salamandra* 52, 269–272.
- Silva-Rocha, I., Vieira, V., Aguiar, A.F., Boeiro, M., Borges, P.A.V., Cravo, D., Jesus, J., Matos, M., Monteiro, M., Rego, C., Reino, L., Serrano, A.R.M., Soares, A.O., Sousa, A., 2018. Animais exóticos e invasores em ecossistemas terrestres. In: Vicente, J.R., Queiroz, A.I., Dias e Silva, L.F., Marchante, E., Honrado, J. P. (Eds.), *As Invasões Biológicas Em Portugal: História, Diversidade e Gestão. Arte e Ciência - Universidade do Porto, Porto*, pp. 142–168.
- Silva-Rocha, I.R., Salvi, D., Carretero, M.A., Ficetola, G.F., 2019. Alien reptiles on Mediterranean islands: a model for invasion biogeography. *Divers. Distrib.* 25, 995–1005. <https://doi.org/10.1111/ddi.12911>.
- Silva, L., Ojeda Land, E., Rodríguez-Luengo, J.L., 2008. Flora e Fauna Terrestre Invasora na Macaronésia Flora y Fauna Terrestre Invasora en la Macaronesia Top 100 nos Açores, Madeira e Canárias.
- Srinivasulu, A., Srinivasulu, B., Srinivasulu, C., 2021. Ecological niche modelling for the conservation of endemic threatened squamates (lizards and snakes) in the Western Ghats. *Glob. Ecol. Conserv.* 28, e01700. <https://doi.org/10.1016/J.GECCO.2021.E01700>.
- Srivastava, V., Lafond, V., Griess, V.C., 2019. Species distribution models (SDM): applications, benefits and challenges in invasive species management. *CAB Rev. Perspect. Agric. Vet. Sci. Nutr. Nat. Resour.* 14. <https://doi.org/10.1079/PAVSNRR201914020>.
- Thuiller, W., Maiorano, L., Mazel, F., Guilhaumon, F., Ficetola, G.F., Lavergne, S., Renaud, J., Roquet, C., Mouillot, D., 2015. Conserving the functional and phylogenetic trees of life of European tetrapods. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 370, 20140005. <https://doi.org/10.1098/rstb.2014.0005>.
- Tingley, R., García-Díaz, P., Arantes, C.R.R., Cassey, P., 2018. Integrating transport pressure data and species distribution models to estimate invasion risk for alien stowaways. *Ecography* 41, 635–646. <https://doi.org/10.1111/ECOG.02841>.
- Tulloch, A.I.T., Tulloch, V.J.D., Evans, M.C., Mills, M., 2014. The value of using feasibility models in systematic conservation planning to predict landholder management uptake. *Conserv. Biol.* 28, 1462–1473. <https://doi.org/10.1111/COBI.12403>.
- Vogrin, M., Corti, C., Mellado, V.P., Sá-Sousa, P., Cheylan, M., Pleguezuelos, J., El Din, S.B., 2017. *Tarentola mauritanica*, IUCN Red. List Threat. Species. <https://doi.org/10.2305/IUCN.UK.2017-2.RLTS.T61578A63716927.en>.
- Wang, H.H., Wonkka, C.L., Treglia, M.L., Grant, W.E., Smeains, F.E., Rogers, W.E., 2018. Incorporating local-scale variables into distribution models enhances predictability for rare plant species with biological dependencies. *Biodivers. Conserv.* 28, 171–182. <https://doi.org/10.1007/s10531-018-1645-4>.
- Weterings, R., Barbetti, M., Buckley, H.L., 2019. Hypothesis: Do invasive house geckos exacerbate dengue fever epidemics? *Biol. Invasions* 21, 3533–3543. <https://doi.org/10.1007/s10530-019-02066-x>.
- Weterings, R., Vetter, K.C., 2018. Invasive house geckos (*Hemidactylus* spp.): their current, potential and future distribution. *Curr. Zool.* 64, 559–573. <https://doi.org/10.1093/cz/zox052>.
- Wetterer, J.K., Espadaler, X., Wetterer, A.L., Aguin-Pombo, D., Franquinho-Aguiar, A.M., 2007. *Ants (Hymenoptera: Formicidae) of the madeiran archipelago. Sociobiology* 49, 265–297.

- Whittaker, R.J., Fernandez-Palacios, J.M., 2007. *Island biogeography: ecology, Evolution, and Conservation*. Oxford University Press.
- Yang, D., González-Bernal, E., Greenlees, M., Shine, R., 2012. Interactions between native and invasive gecko lizards in tropical Australia. *Austral Ecol.* 37, 592–599. <https://doi.org/10.1111/j.1442-9993.2011.02319.x>.
- Zhang, Z., Xu, S., Capinha, C., Weterings, R., Gao, T., 2019. Using species distribution model to predict the impact of climate change on the potential distribution of Japanese whiting *Sillago japonica*. *Ecol. Indic.* 104, 333–340. <https://doi.org/10.1016/J.ECOLIND.2019.05.023>.