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What does the future hold for a thermophilic and widely introduced gecko, *Tarentola mauritanica* (Squamata: Phyllodactylidae)?

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Abstract The continuous growth and movement of the human population is increasing the frequency of translocating species from their native ranges to novel environments. However, biological invasions offer a rare opportunity to investigate how species can colonise and adapt to new conditions. In that sense, Ecological Niche Models (ENMs) can be a powerful tool to predict where invasive species will spread over the next decades, although they depend heavily on climatic niche conservatism between native and exotic ranges. To reduce these uncertainties, ENMs can be refined by accounting for dispersal constraints. The common wall gecko, *Tarentola mauritanica* is a native and widespread Mediterranean lizard that has been introduced across different tropical and subtropical regions. In this study, we aim to predict the potential and future distribution of *T. mauritanica* geckos using correlative models, its potential colonization regions under a dispersal model, and the niche overlap between native and introduced populations. The correlative models predict that the most suitable geographic areas for this gecko correspond to Mediterranean-type ecosystems, such as California, central Chile, the Cape Region of South Africa, around the Caspian Sea, south-eastern Asia, and south-western and southern Australia. The species distribution models projected to 2061–2080, forecast that the range of *T. mauritanica* is likely to shift towards northern latitudes but, surprisingly, not to expand. According to the dispersal models, *T. mauritanica* will be able to colonise a similar geographic range compared to the one obtained with the correlative models for the future. Finally, the niche overlap results demonstrate that *T. mauritanica*'s realised niche has not been conserved over space, as the naturalised climatic niche of the introduced populations differs significantly from its native one. The latter results suggest that there has been no climatic niche conservatism during the several introductions of *T. mauritanica* and that this species seems to be able to cope with novel and more humid environments, typical from the tropics.

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Introduction

The movement of species beyond their native habitats, driven by human activities, is leading to new populations (Wilson et al. 2009). Some introduced species adapt and cause environmental problems, such as biodiversity loss and disrupted ecosystem services (Butchart et al. 2010; Gurevitch and Padilla 2004). Invasive reptiles significantly contribute to global biodiversity decline. A recent meta-analysis by Capinha et al. (2017) found nearly 200 reptile species established in various regions worldwide, with invasions increasing. This is especially concerning in biodiversity hotspots, where invasive species richness is high (Li et al. 2016).

Climate change compounds these issues by affecting the introduction of new invasive species and the distribution of existing ones (Hellmann et al. 2008). However, the effects vary among species, with some benefiting from climate change while others struggle. Species distribution models (SDMs), or ecological niche models (ENMs), are crucial in invasion biology (Srivastava et al. 2019). They predict invasion risk (e.g., Kramer et al. 2017; Tingley et al. 2018) and guide control strategies (e.g., Giljohann et al. 2011; Tulloch et al. 2014). ENMs also apply to other conservation areas, including assessing climate change impacts on genetic and functional diversity (e.g., Pauls et al. 2013; Weterings et al. 2019), and selecting protected areas (e.g., Guisan et al. 2013). ENM studies often reveal similarities in climatic niches between native and introduced species populations (e.g., Petitpierre et al. 2012; Zhu et al. 2020), and that models based on native distributions can predict spread in introduced areas (e.g., Thuiller et al. 2005). In general terms, the concordance between the realised climatic niches of a species' native and introduced distributions may provide evidence of niche conservatism (e.g., Petitpierre et al. 2012; Wiens and Graham 2005). The assumption of niche conservatism entails that niche divergence will be negligible over the timeframe of prediction, and this assumption is used to predict the impacts of anthropogenic climate change on species distributions and persistence (e.g., Petitpierre et al. 2012). Yet, shifts between climatic niches of native and introduced populations are common (e.g., Atwater et al. 2018; Fernández and Hamilton 2015; Parravicini et al. 2015). Introduced populations' shifts may provide insights into species'

responses to climate change (e.g., Fernández and Hamilton 2015; Guisan et al. 2014; Moran and Alexander 2014).

Gecko lizards excel in long-distance dispersals, natural or human-mediated (e.g., Agarwal et al. 2021; Perella and Behm 2020; Rocha et al. 2022). Their success is due to factors like their association with humans, small size, nocturnal habitats, calcareous eggs, and high population densities (Locey and Stone 2006; Rödder and Lötters 2009; Weterings and Vetter 2018). Some invasive geckos are nearly cosmopolitan (Baldo et al. 2008). The genus *Hemidactylus*, with over 165 species (Agarwal et al. 2021), includes about 10 with intercontinental distributions (Capinha et al. 2017; Weterings and Vetter 2018). The common wall gecko *Tarentola mauritanica* (Linnaeus, 1758), a species complex with six putative distinct taxa (Rato et al. 2016), is native to the west coastal Mediterranean Basin (Vogrin et al. 2017). However, due to its association with human settlements and long-distance dispersal (Carranza et al. 2000), it has been introduced to various regions in the eastern Mediterranean, Macaronesia, North and South America (e.g., Deso et al. 2020; Díaz-Fernández et al. 2019; Ortiz-Medina et al. 2019; Rato et al. 2015b). The environmental impacts of *T. mauritanica* in these new habitats are largely unknown (Baldo et al. 2008; Deso et al. 2020). In Croatia, they compete with *Hemidactylus turcicus* through spatial displacement (Lisičić et al. 2012). On Madeira Island, they may influence arthropod communities (Martins et al. 2022). *Tarentola mauritanica* is well adapted to living near humans, frequently feeding on insects attracted to artificial light (Valverde 1967). These behaviours contribute to their success, as they inadvertently disperse long distances via human transportation (e.g., Arredondo and Núñez 2014; Díaz-Fernández et al. 2019; Ortiz-Medina et al. 2019). While individuals reach various parts of the world, climatic conditions can limit their establishment. However, with climate change, some populations may thrive. Evidence shows a northward shift in the Iberian Peninsula and France (Geniez and Cheylan 2012; Moreno-Rueda et al. 2011), and expansion in Mediterranean-like regions of Madeira Island (Silva-Rocha et al. 2022). Climatic variables related to humidity and temperature seasonality drive niche shifts and genetic diversification in native *T. mauritanica* (Rato et al. 2015a). They also affect the successful establishment of the

common wall gecko on Madeira Island (Silva-Rocha et al. 2022). Additionally, their plasticity in response to water loss is likely crucial for the success of introduced populations worldwide (Rato and Carretero 2015). Although the current distribution of both native and introduced *T. mauritanica* populations is well documented (Vogrin et al. 2017), attempts to infer their potential geographic distribution have been limited to a local scale (Geniez and Cheylan 2012; Moreno-Rueda et al. 2011; Silva-Rocha et al. 2022). Given their transcontinental dispersal, this knowledge gap on a broader scale is significant.

In this study, we aimed to (1) predict the potential and future distribution of *T. mauritanica* geckos using correlative models; (2) forecast their potential invasive range under future climates using dispersal models; and (3) evaluate niche overlap between native and introduced populations. Given the global geographic distribution of the model species, we expect a larger predicted range of habitat suitability than the one currently known. Considering its thermophilic nature, we anticipate that future climate change will expand suitable habitats. Finally, we also hypothesize divergent environmental niches between native and introduced populations due to the extensive geographic range of the latter and novel environmental conditions these populations are subject to.

Materials and methods

Species occurrence

Species occurrence records of *Tarentola mauritanica* from native and introduced ranges were compiled from the Global Biodiversity Information Facility (GBIF) database (November 2022, www.gbif.org), personal databases (Catarina Rato and Ricardo Rocha), and recently published records (Arredondo and Núñez 2014; Baldo et al. 2008; Díaz-Fernández et al. 2019; Huerta-Vera 2016; Mačát et al. 2014; Mizerakis and Strachinis 2017; Mizsei et al. 2017; Ortiz-Medina et al. 2019; Strachinis and Artavanis 2017; Strachinis and Pafilis 2018). From GBIF, we only included records containing animal pictures to be sure about the taxonomic assignment. The combination of all these different record sources allowed covering the entire known distribution (native and introduced) of *T. mauritanica*. Species occurrences were cleaned

and filtered for duplicates (i.e., records from the same location) and erroneous geo-referenced records, and later removed from the final dataset. Additionally, to reduce the effects of sampling bias, we performed a spatial thinning on the native and introduced records which were less than 20- and 10 km apart respectively, with the spThin R package (Aiello-Lammens et al. 2015). In the end, a total of 723 records comprising the entire distribution (native and introduced), were used to perform all further analyses.

Environmental data

Using the function *worldclim_global* from the geodata R package (Hijmans et al. 2022), a set of 19 bioclimatic variables was downloaded from WorldClim v2.1 (http://www.worldclim.org) at a resolution of 2.5 arc minutes, used to estimate the realised ecological niche (sensu Sillero 2011) of the species across the globe. The bioclimatic variables were masked to a hypothesis of accessible area for *T. mauritanica* (Anderson and Raza 2010; Barve et al. 2011; Soberón and Peterson 2005). The mask was a 0.5-degree buffered spatial polygon using the occurrence points (Phillips et al. 2009). To test for multicollinearity among environmental variables, we used the function *vif* from the usdm R package (Naimi et al. 2014). To reduce the number of highly correlated variables, we applied a Pearson correlation with the function *layerStats* from the package raster (Hijmans 2022), and a hierarchical cluster analysis to select the most relevant variables among collinear variables with a correlation < |0.75|. In the end, the following variables were selected: Mean Diurnal Range (bio2), Temperature Seasonality (bio4), Max Temperature of Warmest Month (bio5), Min Temperature of Coldest Month (bio6), Mean Temperature of Wettest Quarter (bio8), Annual Precipitation (bio12), Precipitation Seasonality (bio15), Precipitation of Driest Quarter (bio17), Precipitation of Warmest Quarter (bio18), and Precipitation of Coldest Quarter (bio19).

Ecological niche models (ENMs)

Potential changes in the spatial distribution of the target species were implemented using six different algorithms/models in the biomod2 R package (Thuiller et al. 2009), a computer-based platform for ensemble forecasting of species distributions,

enabling the treatment of a range of methodological uncertainties in models, and the examination of species–environment relationships (Araújo and New 2007; Thuiller et al. 2009). The algorithms we used were: GLM (generalised linear model), GBM (generalised boosted regression model), GAM (generalised additive model), CTA (classification tree analysis), RF (random forest), and the MAXENT.Phillips (maximum-entropy model).

Standard procedures were followed to compute the realised niche models (Sillero et al. 2021; Sillero and Barbosa 2021). Species occurrence data were coupled with 10,000 randomly generated pseudo-absences, following Barbet-Massin et al. (2012). Ten replicate models were built using 70% of the native and introduced occurrences and pseudo-absence data, and the remaining 30% were withheld for evaluating predictions. As not all algorithms have the same output range, we scaled all model outputs within a range between 0 and 1000 to calculate the ensemble modelling afterwards, using the parameter scale.models from the BIOMOD_Modeling() function. Hence, we evaluated a total of 60 models: 1 pseudo-absence set × 10 iterations × 6 models. Models' performance was evaluated using two discrimination measures: the true skill statistic (TSS) (Allouche et al. 2006) and the area under the receiver operating characteristic (ROC) curve (AUC) (Fielding and Bell 1997). For the ensemble modelling, only those models with TSS and ROC scores above 0.8, and 0.9, respectively were considered (Allouche et al. 2006; Shabani et al. 2018). To choose the best models, a preliminary screening was carried out to investigate which variables and algorithms would be more suitable for predicting the target species' ENMs, based on model evaluation (i.e., TSS, and ROC), and projections to the current conditions (See Supplementary Material). One of the main features of the biomod2 software is the ability to combine predictions made in single models in an ensemble.

For the best models, we projected the current potential distribution of *T. mauritanica*, using the *BIOMOD_Projection* function from biomod2, and generated an ensemble model as the mean of all models.

To project the potential species distribution under climate change (2061–2080), we used nine CMIP6 climate models (BCC-CSM2-MR, CanESM5, CNRM-CM6-1, CNRM-ESM2-1, CMCC-ESM2, IPSL-CM6A-LR, MIROC6, MIROC-ES2L, MRI-ESM2-0), each within the four shared socio-economic pathways (SSP126, SSP245, SSP370 and SSP585), downloaded from WorldClim v2.1, using the function *cmip6_world* from the geodata R package (Hijmans et al. 2022). The final future projections were performed using the *BIOMOD_Projection* function from biomod2, and an ensemble model was generated by averaging all climatic models for each SSP.

Species dispersion model

A cellular automaton model was implemented using the MigClim R package (Engler and Guisan 2009; Engler et al. 2012) to incorporate dispersal constraints of *T. mauritanica* and predict the potential dispersal movements towards future climatic scenarios. Succinctly, a cellular automaton is a matrix of cells containing values that change over time based on regulations influenced by adjacent cells, as explained by Sarkar (2000). Datasets to simulate dispersal (i.e., the biomod2 models) had a resolution of 2.5 arcmin per pixel (~ 3.5 km). MigClim enables the implementation of species-specific dispersal constraints and demographic parameters into projections of species distribution models under environmental change and/or landscape fragmentation scenarios (Engler et al. 2012). It can equally well be used to simulate dispersal in stable environments and undisturbed landscapes (e.g., for modelling the potential spread of invasive species) (Engler et al. 2012). MigClim calculates the probability of each grid cell being colonised as a function of its distance to the source cells, its future habitat suitability, the dispersal ability of the species, and the propagule production potential of source cells over time.

We used MigClim to model the dispersal of *T. mauritanica* under a no-barrier dispersal scenario, that is, the species can disperse to any suitable cell (following Carranza et al. 2000). To do that, we provided MigClim with the following inputs: a map defining the species' initial distribution, the species' dispersal parameters, and maps of the current and future species' habitat suitability obtained previously from biomod2. We chose a reclassification threshold of 0 (i.e., continuous mode), meaning that habitat suitability model output will not be converted into binary values (i.e. presence and absence). Instead, we used the raw values of the realised models, that is, the

habitat suitability index values, as a conditional probability that a cell becomes colonized; thus, the habitat suitability index is interpreted as a value of "habitat invasibility". We also defined a dispersal kernel of 0.1 (i.e., the probability of colonizing a directly adjacent cell). Long distance dispersal frequency was set to 0.1 and the min-max distance range as 25 cells and 2857 cells, respectively, since the minimum recorded dispersal event is 89 km from the Iberian Peninsula to Alborán islet (Rato et al. 2021a), and the maximum from France to Chile (10.000 km in Arredondo and Núñez 2014). Propagule production potential was set to 1. We had 2 environmental change steps (present, and future 2061–2080) with 30 dispersal steps in each environmental change step. Accordingly, the total number of dispersal steps simulated was equal to [envChgSteps] × [dispSteps], here 60, which corresponds to 60 years from 2023 to 2080. Simulations were repeated 100 times.

Ecological niche overlap

To characterise and compare the niches of both native and introduced populations of *T. mauritanica*, we created ellipsoidal envelope ecological niche models for each group of interest.

Ellipsoidal envelopes were built using the first three PCAs of the variables previously used in the species distribution modelling (see *Environmental data*). Then, we retrieved the environmental information of the occurrence points for each group and fit three-dimensional minimum volume ellipsoids (Van Aelst and Rousseeuw 2009). PCAs were obtained using the *kuenm_rpca* function from the kuenm R package (Cobos et al. 2019).

To measure overlap using these ellipsoids, we followed two different approaches. First, the full overlap, which considers the background data that overlap between the two ellipsoids. To this end, a cloud of points uniformly distributed in the multi-dimensional environmental space that covers the two ellipsoids is used to detect how those envelopes overlap (Qiao et al. 2016). Secondly, we measured the background overlap, which considers only the subset of the full overlap corresponding to environments that are accessible to the groups of interest (which may or may not fill all the volume of the two ellipsoids) (Nuñez-Penichet et al. 2021). The overlap is measured using the Jaccard Index (Mammola 2019), where the value of overlap is the ratio between the number of points within the intersection of two ellipsoids (E1 ∩ E2) and the total number of points contained by two ellipsoids (E1 ∪ E2): J = E1 ∩ E2/E1 ∪ E2. To perform the analyses of overlap using the environmental combinations accessible to each group, we used the values of the PCs for each group. To test the statistical significance of our observed values of overlap, we compared the observed results to a null distribution of 1,000 overlapped values derived from comparing ellipsoid envelopes created from points randomly sampled from each group's accessible environment. The null hypothesis is that the two ellipsoids fitted to actual observations overlap at least as much as random-data ellipsoids. If the observed niche overlap value falls inside the upper 95% of the null distribution, the null hypothesis cannot be rejected. As the full overlap analysis uses points that are uniformly distributed, significance tests (which rely on available conditions) were performed only for analyses of background overlap. Analyses of niche overlap were carried out in R using the package ellipsenm (Cobos et al. 2020).

Results

All six algorithms (GLM, CTA, RF, GBM, GAM, and MAXENT.Phillips) produced species distribution models with TSS and ROC evaluation scores over 0.8 and 0.9, respectively (Fig. S1). However, both RF and CTA algorithms were removed from the modelling and projection analyses; the CTA exhibited a low mean ROC score (< 0.75; Fig. S2), and they both delivered unsuitable ENMs for *T. mauritanica*, such as Scandinavia (in CTA), Alaska, and Siberia (in RF) (Fig. S5). Moreover, most of the environmental variables contributed very little to the RF model (Fig. S3), which might explain its poor capacity to estimate accurately suitable habitats for *T. mauritanica*. As for the initially considered environmental variables, they were all kept for further analysis.

In general, the most suitable areas for *T. mauritanica* correspond to regions with low to moderate precipitation, moderate to high temperatures, low-temperature seasonality, and low to moderate mean diurnal range (Fig. S4).

Tarentola mauritanica's ensembled potential distribution is predicted to be wider than the range it is

known today (Figs. 1 and 2). For instance, the regions around the Black and Caspian Seas present high habitat suitability, as well as south-eastern Asia, the south-western coast of South Africa and the southern coast of Australia. In Europe, suitable regions also include the northern latitudes of this continent.

As for the habitat suitability to 2061–2080 (Fig. 3), all SSP scenarios support very similar models for the future distribution of *T. mauritanica*. In Europe, a shift to northern latitudes is forecasted, reaching the southern UK and the southern Scandinavian Peninsula. In North America, the north-eastern region of the USA will become suitable in the future. Moreover, south-eastern Spain and North Africa are predicted to become less suitable for this gecko species. The same is observed for south-eastern Asia, Argentina, and Uruguay.

Again, the species dispersal models among the different future scenarios are very similar (Fig. 4), and they also predict that over the next 60 years, *T.* *mauritanica* will be able to colonise a similar geographic range compared to the one obtained with the correlative models for the future (Fig. 3).

The full niche overlap between native and introduced ellipsoids was 0.43, and the overlap using the available conditions was 0.58 (Fig. 5). The null hypothesis of niche overlap (using the background) was rejected (p-value$=0.00$), with the observed values of niche overlap being smaller than expected, falling below the 5% confidence limit.

Discussion

Across its native Mediterranean geographic range, the common wall gecko, *T. mauritanica* is subject to mild wet winters, and warm and dry summers (Lionello et al. 2006). These specific climatic conditions coincide with the obtained response curves for the several temperature and precipitation variables used in this

Fig. 1 Geographic distribution of the records used in this study, after a spatial thinning of the points that were less than 10 km apart for the introduced records (red dots) and less than 20 km for the native (black dots).
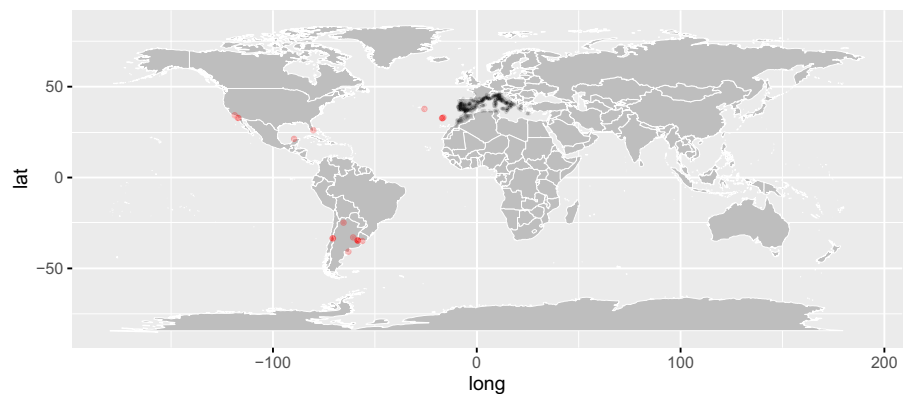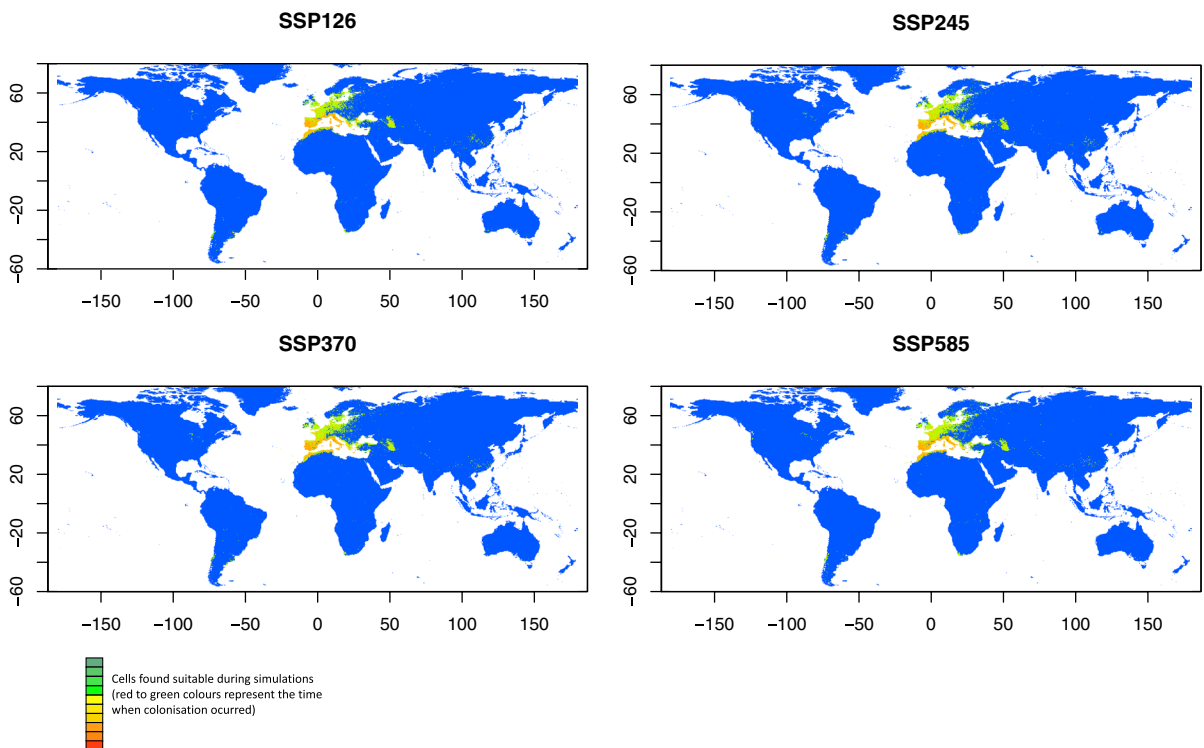

Fig. 2 Ensemble forecast of global habitat suitability for *T. mauritanica* under current environmental conditions, highlighting a highly suitable area in south-western Iran
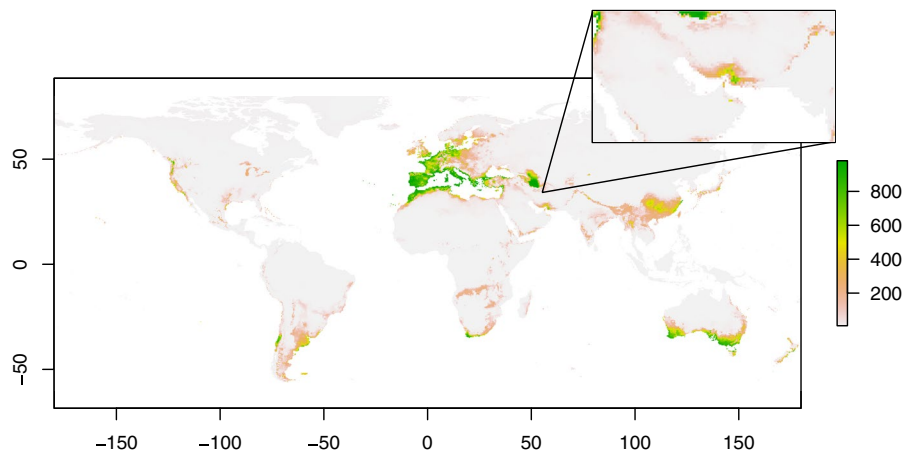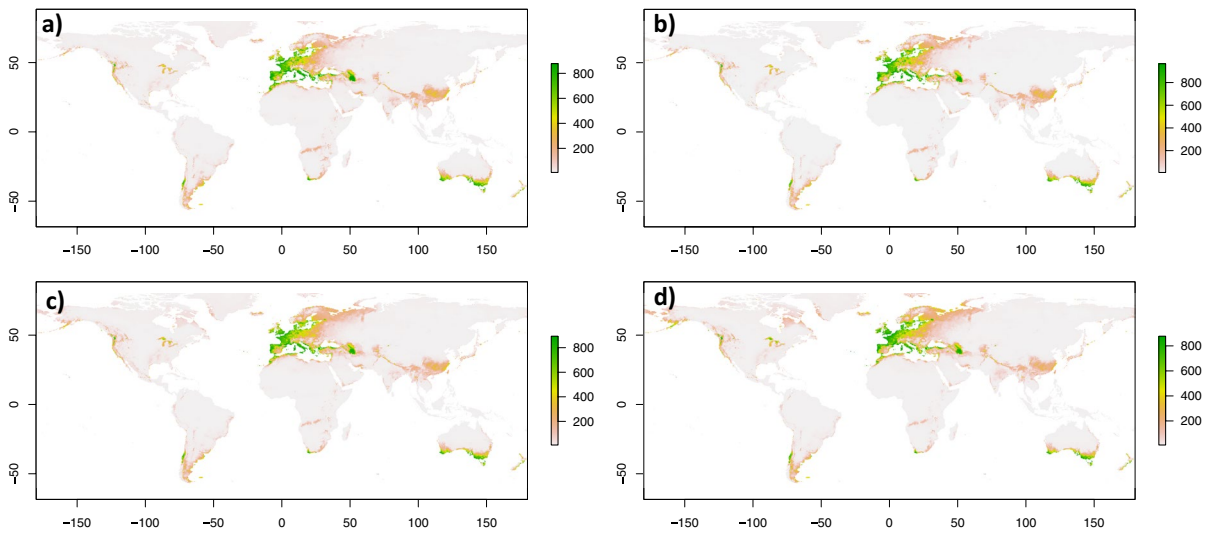
Fig. 3 Results from the ensemble models for *T. mauritanica* projected to 2061-2080 under four socio-economic pathways: SSP126 (**a**), SSP245 (**b**), SSP370 (**c**), and SSP585 (**d**)

Fig. 4 Global estimated expansion of *T. mauritanica* over the next 60 years for each SSP derived from the MigClim R package. Red to green gradient represents the time when colonisation occurred, with regions in red representing the initial distribution and in green the most recent colonised areas
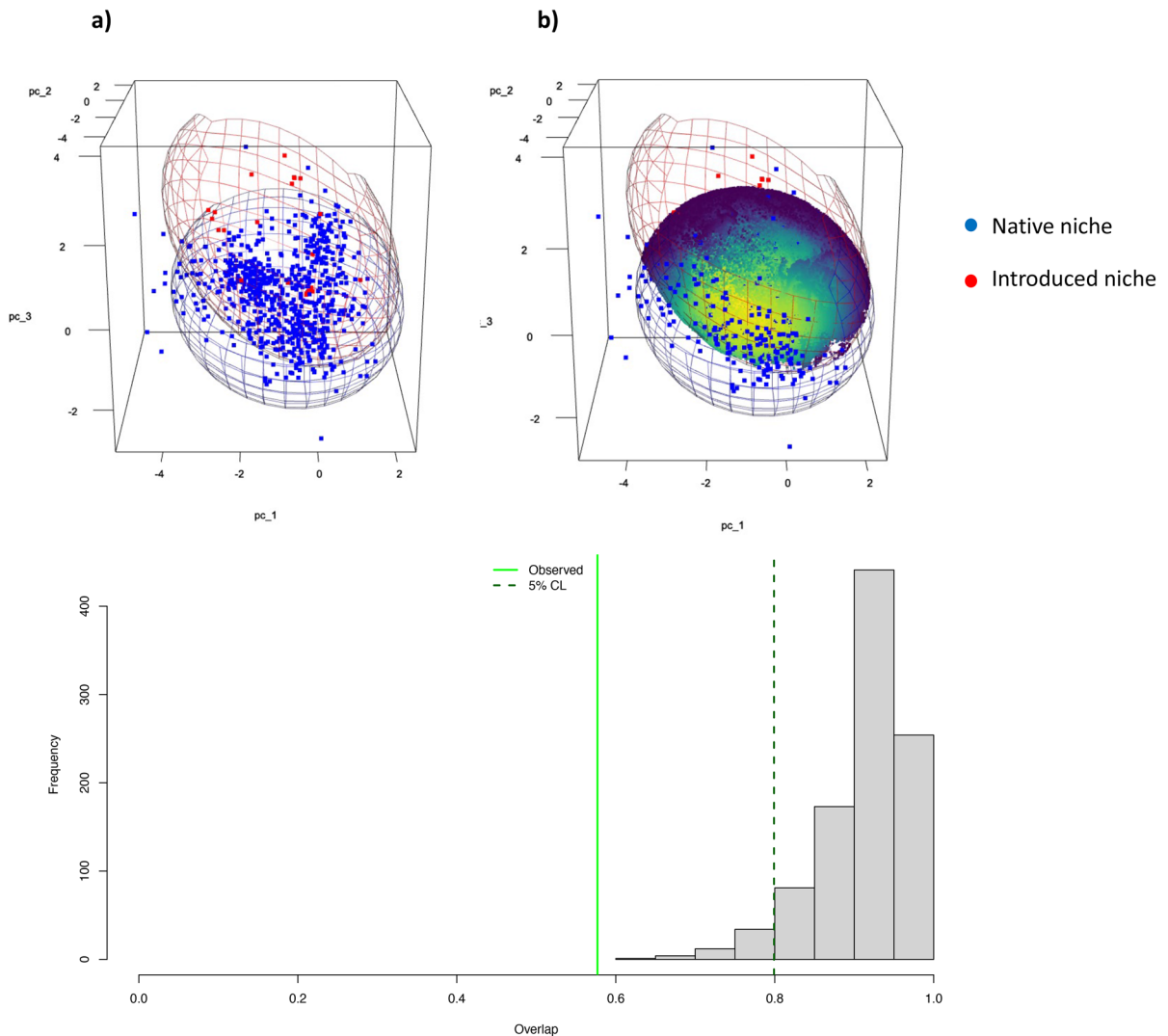
Fig. 5 Representation of the two types of overlap analyses used: full overlap (**a**) and background overlap (**b**). The background in **b** corresponds to the actual values of the climatic variables in the study region. Each ellipsoid represents the ecological niche of *T. mauritanica* species (the native niche represented in blue and the introduced one represented in red). Comparison of observed values of niche overlap against the null distribution of 1000 overlap values of random ellipsoids (**c**). Solid green line shows the observed values, and the dashed green line the 5 % confidence interval (CL)

study. Not surprisingly, the correlative models predicted California, central Chile, the Cape Region of South Africa, around the Caspian Sea, south-eastern Asia, and south-western and southern Australia, as some of the most suitable geographic areas for this gecko to occur, which also correspond to the areas of the world with Mediterranean-type ecosystems (Esler et al. 2018; Sayre et al. 2020). Nevertheless, the cool temperate climate we find in Northern Europe is also predicted as moderately suitable for *T. mauritanica*.

Although this gecko species has been successfully introduced across several sub-tropical and tropical regions of the world (e.g., Madeira, Azores, Yucatán, Florida, Uruguay and Argentina in Arredondo and Núñez 2014; Báez and Biscoito 1993; Baldo et al. 2008; Barreiros et al. 2010; Díaz-Fernández et al. 2019; Huerta-Vera 2016; Jesus et al. 2008; Rato et al. 2015b), our ENMs have identified only one (not yet colonised) highly suitable

tropical region located in south-western Iran, facing the United Arab Emirates Peninsula.

Despite some known limitations (Araújo and Peterson 2012), ENMs can be a powerful tool to predict where invasive species will spread next. However, until the last stage of invasion, an introduced species is not yet at equilibrium with its environment, as demonstrated in previous studies focusing on other invasive species (e.g., Barbet-Massin et al. 2018; Gallien et al. 2012; Václavík and Meentemeyer 2012). The equilibrium hypothesis is an important assumption, and its violation has to be acknowledged when interpreting ENM predictions (Garcia et al. 2012). Indeed, violating the equilibrium hypothesis has some consequences when modelling species distribution, such as the underestimation of the potential climatic niche of a species, which can in turn underestimate the geographical area the species can invade (Václavík and Meentemeyer 2012). Considering that the introduction of *T. mauritanica* into tropical ecosystems has taken place only in the last 20–30 years, it is reasonable to assume that these populations have not yet reached an equilibrium with the novel environmental conditions and that the habitat suitability models might be underestimating the probabilities of species occurrences. Actually, over the last three decades, the occurrence area of *T. mauritanica* on Madeira Island has increased by more than 20 km (Silva-Rocha et al. 2022). Moreover, the same study demonstrates that despite preferring Mediterranean-like climate areas, more humid regimes seem also suitable for the introduced populations of the common wall gecko in sub-tropical Madeira Island.

Furthermore, our niche overlap results demonstrate that *T. mauritanica*'s realised niche has not been conserved over space, as the naturalised climatic niche of the introduced populations differs significantly from its native one (e.g., Early and Sax 2014; Medley 2010; Parravicini et al. 2015). These results highlight two important aspects: first, there has been no climatic niche conservatism during the several introductions of *T. mauritanica*; and second, this species seems to be able to cope with novel and more humid environments.

Undoubtedly, biological invasions offer a rare opportunity to investigate how species colonise new environments (Kueffer et al. 2013; Richardson and Pyšek 2008; Sax et al. 2007), and whether they preserve their climatic niche in a new range (Pearman et al. 2008). Addressing this question has proven important in recent years as a test for ecological niche models, which depend heavily on climatic niche conservatism between native and exotic ranges (Colwell and Rangel 2009; Pearman et al. 2008; Peterson 2011). Evidence exists both for (e.g., Peterson 2011; Petitpierre et al. 2012; Strubbe et al. 2013), and against (e.g., Broennimann et al. 2007; Fitzpatrick et al. 2007; Lauzeral et al. 2011; Li et al. 2014; Medley 2010; Rödder and Lötters 2009) climatic niche conservatism during invasions, which is most likely related to the different types of niche change, biological and/methodological study contexts, data types, species characteristics, or methods being used (see references in Guisan et al. 2014).

The introduction and expansion of the common wall gecko populations across different tropical ranges (Arredondo and Núñez 2014; Baldo et al. 2008; Silva-Rocha et al. 2022), suggests that the species can cope with more humid environments. However, as the response curves demonstrate, when humidity is too high, the habitat becomes unsuitable for *T. mauritanica*. This is most likely due to the limited favourable conditions viable for gecko reproduction, particularly concerning humid environments. Like most gecko lizards, *T. mauritanica* produces rigid-shelled eggs (a pre-adaptation to arid environments) that in conditions of high humidity 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). While the excess of humidity/water vapour is a limitation to gecko groups with highly calcified rigid-shelled eggs (e.g., Sphaerodactylidae, Phyllodactylidae, and Gekkonidae), parchment-shelled eggs are highly permeable and benefit from water vapour (Andrews 2015). Hence, in a humid environment, depending on the gecko group, females will either choose drier microhabitats and/or reproduce during the drier seasons (if they have hard-shelled eggs) (e.g., Somaweera 2009), or deposit their eggs in humid places (if they lay parchment-shelled eggs). Unless the individuals inhabiting the tropics can select suitable micro-habitats for egg laying, the future of these populations might be compromised under current climatic conditions. Yet, the 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).

Indeed, the species distribution models projected to 2061–2080, forecast that the range of *T. mauritanica* is likely to shift towards northern latitudes. South-eastern Spain and parts of North Africa will become unsuitable, while the south of the UK and the Scandinavian Peninsula seem to offer more relevant environmental conditions for this gecko species. Furthermore, the climate in the tropics will become unsuitable, while parts of the north-eastern USA seem to favour the establishment of *T. mauritanica*. At least in the Iberian Peninsula and France, a northward shift in the range of the common wall gecko populations has already been documented as a response to global warming (Geniez and Cheylan 2012; Moreno-Rueda et al. 2011). According to Sumner et al. (2003), by the late twenty-first century, the far south of Spain will undergo a continued spread of aridity of the climate, extending westwards. This is already the hottest and one of the aridest parts of Spain, and the predicted environmental changes will be disastrous to several taxa of the region (e.g., *Algyroides marchii* in Rato et al. 2021b), including a thermophilic reptile such as *T. mauritanica*.

Contrary to what we obtained with the species distribution models, the dispersal models forecast that colonization by the common wall gecko will still take place across southern Spain and North Africa. Indeed, the largest colonisation is predicted to take place in the European continent, with *T. mauritanica* expanding its territory towards the northern and eastern regions. In South America, the dispersal models also predicted a potential expansion to the south, and towards the north following the Atlantic coast of Brazil. The population from California is also expected to disperse to more northern territories.

The common wall gecko occurs naturally in a typical Mediterranean climate and has mostly crepuscular activity. It thermoregulates during the first 2–3 h of the day near the refugium, to where it returns once its optimal temperature is achieved (Martínez-Rica 1974). In comparison to other sympatric similar-sized lacertid lizards, this gecko has a higher resistance to dehydration (García-Muñoz and Carretero 2013; Osojnik et al. 2013), with great plasticity among populations for this trait (Rato and Carretero 2015). Indeed, this feature conveys the common wall gecko with a great capacity to withstand long periods without water, and able to survive during transmarine trips. Moreover, future global warming would not be a limiting factor for this species, as already documented in previous studies (Geniez and Cheylan 2012; Moreno-Rueda et al. 2011). In fact, Moreno-Rueda et al. (2011) saw that the southern range of *T. mauritanica* has not been affected by global warming during the last 70 years. Therefore, both the predicted future range and colonization models are in line with the ecophysiological requirements and dispersal capacity of this species.

The way organisms respond to environmental change may be complex, since such responses are usually nonlinear, often have thresholds, and (as demonstrated in this study) could change with novel conditions (Beissinger and Riddell 2021; Huey et al. 2012). Therefore, there is a growing acknowledgment that we need to accurately characterize how organisms experience their environments and the biological mechanisms by which they respond to improve our predictions (Helmuth et al. 2005; Keith et al. 2008; Urban et al. 2016). In ectotherms, biophysical models can be used to estimate the body temperature of a single life stage in a particular microclimate (Levy et al. 2015). However, to identify *T. mauritanica*'s constraints and improve the results obtained here by the correlative models, body temperature predictions from biophysical models should ideally be combined with data on the temperature dependence of development, sex, activity, growth, survival, or reproduction.

Overall, globalisation is increasing the frequency of translocating species from their native ranges to novel transmarine environments. Over the last 30 years, the native Mediterranean common wall gecko, *Tarentola mauritanica*, has been introduced across several tropical and subtropical regions of the globe, where it has found novel environmental conditions. Our results confirm that the realised niche occupied by these introduced populations is significantly different from their native ones, highlighting the capacity of this species to cope with novel ecosystems, which is key to successful colonisation. Over the next 60 years, the geographic range of this gecko is likely to shift, benefiting from global climate change. The lack of knowledge on the effects it might have on local species and ecosystems reinforces the need for strong and serious monitoring actions.

Data availability The datasets generated and/or analysed, and R scripts used during the current study are available in the Figshare repository [link will be made available upon acceptance of the manuscript].

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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