Management of Biological Invasions (2024) Volume 15, Issue 1: 145–158

Research Article

Alien turtles in Spain: Modeling a growing problem

Daniel Escoriza[1], Santiago Poch[1,2], Albert Martínez-Silvestre[3], Joan Budó[4], Guillem Pascual[5], Albert Bertolero[6], Marc Franch[7,8], Joaquim Soler[3], Ramón Mascort[4,9], Sergi Garcia[5], Quim Pou[10], Sofia Rivaes[11], Miquel Campos[12,13], Iago Pérez[14], Esther Fanlo[15], Diego Martínez[16], Eloi Cruset[10], Andreu Porcar[10], Pau Sunyer-Sala[2,17], Júlia Ferrer-Morell[2], Badis Bakhouche[18] and Dani Boix[1]

[1]*GRECO, Institute of Aquatic Ecology, University of Girona, Maria Aurèlia Capmany, 69, 17003 Girona, Spain;* [2]*Fundació Emys, Carretera de Santa Coloma, Km 21, 17421 Riudarenes, Spain;* [3]*CRARC, Catalonian Reptiles and Amphibians Rescue Center, 08783 Masquefa, Barcelona, Spain;* [4]*Centre de Reproducció de Tortugues de l'Albera, Santuari de la Mare de Déu del Camp, 17780 Garriguella, Spain;* [5]*Galanthus, 17460 Celrà, Spain;* [6]*Associació Ornitològica Picampall de les Terres de l'Ebre, La Galera, 43870 Amposta, Spain;* [7]*Biologia Animal Research Group - Departament de Ciències Ambientals, University of Girona, 17003 Girona, Spain;* [8]*CICGE - Centro de Investigação em Ciências Geo-Espaciais, Observatório Astronómico Prof. Manuel de Barros, University of Porto,4430-146 Vila Nova de Gaia, Portugal;* [9]*C. la Jonquera 17, 2, 17600 Figueres, Alt Empordà, Spain;* [10]*Sorelló, Parc Científic i Tecnològic de la Universitat de Girona. Carrer Emili Grahit n°91, Edifici Narcís Monturiol, Despatx P1, B1,17007 Girona, Spain;* [11]*Oficina Tècnica de SEO/BirdLife al Delta de l'Ebre - Reserva Natural de Riet Vell, Carretera Amposta-Eucaliptus, Km 18.5,43870 Amposta, Spain;* [12]*Wildlife Conservation Medicine Research Group (WildCoM), Departament de Medicina i Cirurgia Animals, Universitat Autònoma de Barcelona, 08193 Bellaterra, Spain;* [13]*Consorci de l'Estany, Plaça dels Estudis 2, 17820 Banyoles, Spain;* [14]*Associació La Sorellona, Claveria 4, 17004 Girona, Spain;* [15]*Ajuntament de Lleida, Secció Ecologia i Sostenibilitat, 25007 Lleida, Spain;* [16]*Iberá. Consultoría Medio Ambients, Lluis Companys 107, 43597 Arnes, Tarragona Spain;* [17]*Vivers Tres Turons, Camps de Mas Olivet s/n, 08211 Castellar del Vallès, Spain;* [18]*Laboratory of Biological Oceanography and the Marine Environment (LOBEM), Faculty of Biological Sciences, University of Science and Technology of Houari Boumediene (USTHB), BP 32, 16111 Algiers, Algeria*

Corresponding author: Daniel Escoriza (drdanielescoriza@gmail.com)

Citation: Escoriza D, Poch S, Martínez-Silvestre A, Budó J, Pascual G, Bertolero A, Marc Franch, Joaquim Soler, Mascort R, Garcia S, Pou Q, Rivaes S, Campos M, Pérez I, Fanlo E, Martínez D, Cruset E, Porcar A, Sunyer-Sala P, Ferrer-Morell J, Bakhouche B, Boix D (2024) Alien turtles in Spain: Modeling a growing problem. *Management of Biological Invasions* 15(1): 145–158, https://doi.org/10.3391/mbi.2024.15.1.09

Received: 17 July 2023
Accepted: 6 October 2023
Published: 29 November 2023

Handling editor: Vivek Srivastava
Thematic editor: Catherine Jarnevich

Abstract

Four native chelonians species occur in Spain, three of which are severely threatened. In recent surveys, 25 species of alien turtles and tortoises were reported, some of which had established breeding populations and interfered with native species. In this study, we used ecological niche models to evaluate which regions are more vulnerable to colonization by alien turtles and tortoises and which alien chelonians show substantial environmental overlap with native species. The parameters of the ecological niche models were iteratively optimized using Akaike procedures, and we assessed the projection transferability between donor and recipient geographic regions using Mobility-Oriented Parity estimation. Our results indicated that the Mediterranean and some Atlantic rivers (Miño-Sil and Guadalquivir) are particularly vulnerable to colonization by semi-aquatic alien turtles, while southwestern Spain is exposed to colonization by alien tortoises. The aquatic species most susceptible to overlap with the four species of native turtles are those native to the cold and warm temperate regions of North America and China: *Apalone spinifera, Chelydra serpentina, Chrysemys picta, Mauremys mutica, Mauremys reevesii, Mauremys sinensis, Pelodiscus sinensis, Sternotherus odoratus*, and *Trachemys scripta*. These results highlight the importance of establishing stricter trade regulations for certain species with a focus on protecting vulnerable areas.

Key words: conservation, Ecological Niche Models, invasive species, Mediterranean region, Mobility-Oriented Parity Estimation, reptiles, trade regulation

Introduction

The Iberian Peninsula is considered a biodiversity hotspot in the Mediterranean ecoregion, due to its climatic heterogeneity and its role as an environmental refugium during recent Pleistocene glacial episodes (López-López et al. 2011).

However, this diversity is threatened by the profound alteration of landscapes due to the anthropic impacts of urbanization and agricultural activity (Lloret et al. 2002). This alteration of natural landscapes simplifies native biotic communities, generating empty niches that favour commensal species with high reproductive rates (Reino et al. 2009). A new disturbance factor has recently been introduced, fueled by this simplification of communities, the increasing presence of alien species (Angulo et al. 2021; Sáez-Gómez and Prenda 2022).

Alien species typically begin their colonization process in disturbed areas, usually close to urban centers. From these habitats, they progressively expand toward more natural environments, frequently displacing or exterminating native species, either through competition or predation (Thomson et al. 2010; Li et al. 2011). Once an alien species has become established, control measures are difficult to implement and often ineffective. Therefore, it is critical to quickly identify those species that have a higher probability of successful colonization and also overlap with native species (Chang et al. 2022).

Four species of native turtles occur on the Iberian Peninsula: two tortoises of the genus *Testudo* (*T. graeca* and *T. hermanni*) and two semi-aquatic turtles, *Emys orbicularis* and *Mauremys leprosa* (Salvador 2014). Three of these species are severely threatened, occupying small, often pristine, and protected areas, with low population numbers (Díaz-Paniagua et al. 2001; Couturier et al. 2014; Bertolero et al. 2020). The fragility of these populations suggests that the expansion of alien species can be very detrimental to endangered native species, since alien species remove populations of native species through competition, predation, pathogen transmission, or even hybridization (Fujii et al. 2014; Polo-Cavia et al. 2014; Martínez-Silvestre et al. 2015a; Ueno et al. 2021).

Despite these risks and evidence that an increasing number of alien turtle species are becoming naturalized in Spain (Martínez-Silvestre et al. 2001; Soler et al. 2010; Poch et al. 2020; González de la Vega et al. 2021), there have been only a few studies on the impact of these species on native species, such as habitat overlap or agonistic behaviours of *Trachemys scripta* (Martínez-Silvestre et al. 2012; Escoriza et al. 2021). In this study, we evaluated the level of overlap in ecological niches between alien freshwater turtles and tortoises and native species from Spain. We hypothesize that (i) given the climatic heterogeneity of Spain, there are more favourable areas for the colonization of alien chelonian species (regions particularly sensitive to invasion) and (ii) there are differences in niche overlap between the native and alien species, due to niche partitioning between the native species of turtles and tortoises (Escoriza and Ben Hassine 2022) (species particularly sensitive to invasion).

Materials and methods

Study region and surveys

The study was carried out in Spain (Iberian Peninsula, Balearic Islands and Canary Islands). The climate of the Iberian Peninsula and Balearic Islands is mostly warm Mediterranean, humid-subhumid type (*Csa* Köppen classification), or steppe type (*Bsk* Köppen classification). In the northwest, the climate is sub-Mediterranean/temperate oceanic (*Csb-Cwa* Köppen classification) (Beck et al. 2018). In the Canary Islands, a hot desert climate (*BWh* Köppen classification) predominates in the eastern islands (Lanzarote and Fuerteventura) and subtropical subhumid in the western islands (La Palma, El Hierro and La Gomera) with transitional stages in Tenerife and Gran Canaria (Beck et al. 2018).

We surveyed rivers, lakes, reservoirs, ponds, urban parks, open forests, and traditional agricultural lands in northeastern Spain. Surveys were carried out using visual transects with binoculars and baited funnel traps, between April and October 2000–2021. Data from rescue centers have also been included. Individuals were identified at the species level following Conant and Collins (1998), Bonin et al. (2006), and Ernst and Lovich (2009). The data obtained during the samplings was used to compile a list of species presence and not to calibrate the ecological niche models, since in most cases these records did not correspond to naturalized populations (Poch et al. 2020).

Environmental Data

We obtained data on 19 bioclimatic variables and elevation from the WorldClim 2 database, with a spatial resolution of 30 arc seconds (Fick and Hijmans 2017). The final number of variables used to build predictive models was evaluated using the variance inflation factor (VIF) (Dormann et al. 2013). To estimate the VIF, we defined buffer polygons of 200 km around the location of each species and generated 1000 random points within these polygons. The climate data obtained for the random points and the species occurrences were used to perform a logistic regression. We started with a simple model that included only BIO10 (mean temperature of the warmest quarter), BIO11 (mean temperature of the coldest quarter), BIO12 (annual precipitation), and elevation. These variables were initially chosen because of their relevance to the life history of the target species (Pearson et al. 2014), and included winter and summer temperatures (associated with hibernation and the development of embryos) and environmental water availability (Storey et al. 1988; Stephens and Wiens 2003). Terrain elevation was also added because this variable has an additional effect independent of climate since many species of aquatic turtles only occupy low-elevation areas where rivers are wider and slower (Ernst and Lovich 2009; Legler and Vogt 2013). Variables with VIF values > 10 were excluded from subsequent analyses (Schroeder et al. 1990). The variables finally included in the models were BIO10 + BIO11 + BIO12 + elevation + BIO3+ BIO8 + BIO9 + BIO15.

Occurrence data

To generate ecological niche models, the occurrence data of 20 species of aquatic turtles and five species of tortoises were obtained from the GBIF database and scientific publications (Supplementary material Table S1).

To reduce spatial autocorrelation bias (Boria et al. 2014), records that are closer than 10 km from each other were removed from the analysis using spThin routines (Aiello-Lammens et al. 2015) in R (R Development Team 2023). Bias grids were also constructed to compensate for possible spatial clustering in species records (Syfert et al. 2013). The use of these grids assumes that the occurrence data could be observer-biased (Elith et al. 2011). However, turtles are often not randomly distributed, and their presence is circumscribed to areas with very specific environmental conditions (e.g. threatened species in nature reserves; Mazzotti 2004; Zenboudji et al. 2016). Therefore, the use of bias grids in these species may result in a significant reduction in the model performance (Warren et al. 2014). For this reason, in this study, we built niche models with and without bias grids. These grids were generated with the species-occurrence data as binary layers using the raster package (Hijmans 2023) in R and Quantum GIS (Quantum GIS Development Team 2023).

The niche models were calibrated from data obtained for the native distributions of alien species and in regions where these species were introduced and showed evidence of reproduction (e.g., *Pelusios castaneus* in Guadaloupe or *Testudo marginata* in Sardinia; Soflanidou et al. 1990; Fritz et al. 2011). Therefore, we did not include locations within the tolerance limits of the adult individuals where reproduction is unlikely under natural conditions (Pupins 2007; Cathrine and Monir 2022) and consequently the species cannot be considered invasive.

Data analysis

The analyses evaluated (i) the climatic suitability of Spain for alien turtle species and (ii) the overlap of niches between invasive and native species. The regions most vulnerable to colonization by invasive species were evaluated separately for aquatic and terrestrial species. A suitability map was generated after calibrating Maxent niche models with only occurrence data (Elith et al. 2011). Several candidates were tested through an iterative process and the best statistical model was selected using the Akaike information criterion corrected for finite samples (AICc) with ENMval functions (Muscarella et al. 2014) in R. The Maxent models were built using various features (L: linear; Q: quadratic; H: hinge; P: product; T: threshold) and regularization multipliers (RM). The features and the RM for the best model were used to generate a mapped projection in Maxent 3.4.4 (Phillips et al. 2006), calibrated using 70% of the species occurrences. The background regions were defined using a rectangle that encompasses the occurrences of each species, thus maximizing the inclusion of environmental variation around the occurrence areas while minimizing the effect of noninformative regions (Acevedo et al. 2012). The predictive capacity of the models was evaluated using the area under the receiver operating characteristic curve (AUC) and the continuous Boyce index (CIB) (Hirzel et al. 2006). In general, CIB provides a better estimate of the predictive ability of presence data models (Hirzel et al. 2006).

Models with positive CBI values close to 1 show almost perfect predictive ability, while those with negative values are not predictive (Hirzel et al. 2006).

The best ecological niche models (ENM) were used to estimate the relationships between climate and species presence in our study region (Lei and Liu 2021). The environmental similarity between the donor and recipient regions was tested using Mobility-Oriented Parity (MOP) analysis (Owens et al. 2013). MOP allows for evaluating model transferability between geographically separated regions depending on the degree of environmental similarity (Owens et al. 2013). Maps showing MOP estimates were built using kuenm (Cobos et al. 2019) in R and Quantum GIS.

Maxent models were also used to estimate niche overlap (Warren et al. 2021). To do so, 1000 random points were generated throughout Spain and similarities in the predicted suitability values between native and alien species were assessed with their kernel density distributions (KDD; Geange et al. 2011). This analysis was carried out with the package overlapping (Pastore et al. 2022) in the R environment and is summarized in the Supplementary material (Table S2).

Results

In total, 5927 individuals of 25 alien species (20 semi-aquatic turtles and 5 tortoises) were captured. AUC and CBI values indicated that most of the models performed well and were reliable, except for the models generated for *Cyclemys dentata* and *Kinixys belliana*, which were not included in the mapped projections and analyses (Tables S3–S5). The models corrected or not corrected for observation biases in the occurrences provided different mapped projections. In general, there was a decrease in the logistic values of the corrected projections, which tended to be almost zero in some sparsely distributed species (e.g., native *T. hermanni*), making the overlap niche values little informative (Tables 1 and 2). For this reason, in Figure 1 only the overlap between the uncorrected projections is shown.

Projections over Spain showed that certain regions were more vulnerable to colonization by alien turtle species (Figures 2 and 3). For aquatic species, these regions included mainly the basins of Ebro (northeast), Guadalquivir (southwest), Miño-Sil drainage (northwest) and the northern and central Mediterranean coast (including Menorca and Mallorca, Balearic Islands), based on both types of projections (corrected or not for occurrence data biases) (Figure 2). In the case of tortoises, the most vulnerable regions were located in the southwest of Spain and the northeast, including the Balearic Islands (Figure 3). However, the bias-corrected projection showed lower suitability values for the northeastern region of the Peninsula and the Balearic Islands (Figure 3). Overall, the donor and recipient regions are environmentally similar, with low risk of extrapolation, and therefore these projections can be considered statistically reliable (Figure 4).

Table 1. Estimation of niche overlap by kernel density distribution, between alien and the two native turtles. Values close to 1 indicated almost complete overlap in the environmental suitable regions in Spain for the species pairs. NB, uncorrected for potential data collection biases; B, using a bias grid.

	Emys orbicularis		*Mauremys leprosa*	
	NB	B	NB	B
Apalone ferox	0.045	0.005	0.049	0.013
Apalone spinifera	0.822	0.549	0.835	0.381
Chelydra serpentina	0.658	0.312	0.696	0.233
Chrysemys picta	0.778	0.366	0.753	0.479
Graptemys ouachitensis	0.089	0.011	0.104	0.017
Graptemys pseudogeographica	0.069	0.001	0.079	0.001
Macrochelys temminckii	0.091	0.011	0.099	0.023
Mauremys mutica	0.673	0.546	0.710	0.396
Mauremys reevesii	0.675	0.545	0.687	0.373
Mauremys sinensis	0.629	0.451	0.693	0.296
Pelodiscus sinensis	0.830	0.714	0.838	0.477
Pelusios castaneus	0.000	0.000	0.138	0.066
Phrynops hilarii	0.190	0.098	0.216	0.109
Pseudemys concinna	0.152	0.058	0.173	0.090
Pseudemys nelsoni	0.029	0.001	0.008	0.039
Pseudemys peninsularis	0.001	0.006	0.008	0.011
Pseudemys rubiventris	0.018	0.004	0.021	0.001
Sternotherus odoratus	0.379	0.159	0.409	0.154
Trachemys ornata	0.009	0.002	0.016	0.006
Trachemys scripta	0.830	0.726	0.849	0.495

Table 2. Estimation of niche overlap by kernel density distribution, between alien and the two native tortoises. Values close to 1 indicated almost complete overlap in the environmental suitable regions in Spain for the species pairs. NB, uncorrected for potential data collection biases; B, using a bias grid.

	Testudo graeca		*Testudo hermanni*	
	NB	B	NB	B
Terrapene carolina	0.008	0.027	0.234	0.012
Testudo graeca eastern subspecies	0.740	0.336	0.276	0.005
Testudo hermanni eastern subspecies	0.727	0.421	0.201	0.002
Testudo horsfieldii	0.591	0.223	0.328	0.004
Testudo marginata	0.558	0.242	0.420	0.001

As expected, estimates of niche overlap indicated important differences between alien species (Table 1). The aquatic species that showed greater overlap in the niche (KDD ≥ 0.25) with native turtles were *Apalone spinifera, Chelydra serpentina, Chrysemys picta, Mauremys mutica, Mauremys reevesii, Mauremys sinensis, Pelodiscus sinensis, Sternotherus odoratus* and *Trachemys scripta* (Table 1), and the terrestrial species were *Testudo graeca ibera, Testudo hermanni boettgeri, Testudo horsfieldii* and *Testudo marginata* (Table 2).

Discussion

This study provides a framework for evaluating the invasive potential of alien species traded in a region, and thus initiate rapid measures to regulate their local importation, whether they are pets or garden plants (Head 2017; Lockwood et al. 2019). These preventive measures could help reduce the establishment of new invasive species, a growing problem on a global scale and whose management is usually difficult and expensive (Strayer 2010).

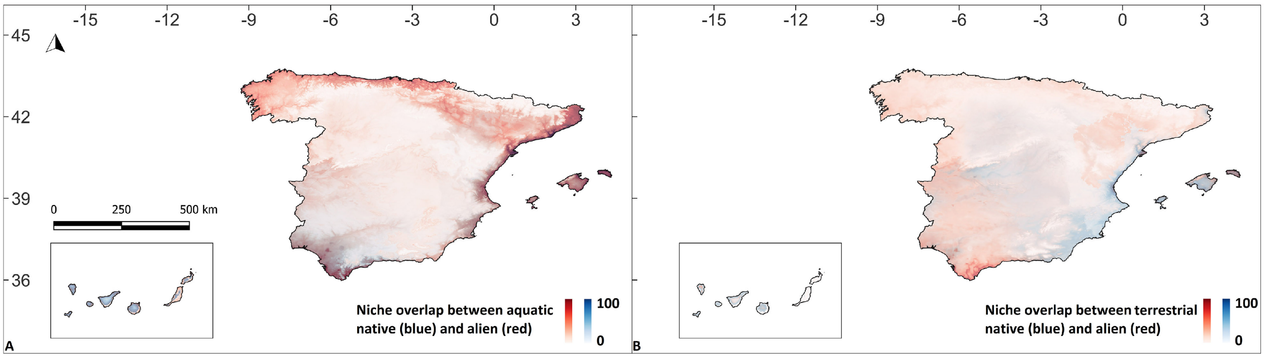

Figure 1. Map of Spain representing the modeled niche overlap (projections without bias corrections) between native (blue) and alien (red) species of the alien species of turtles (A) and tortoises (B). The inset shows the Canary Islands.

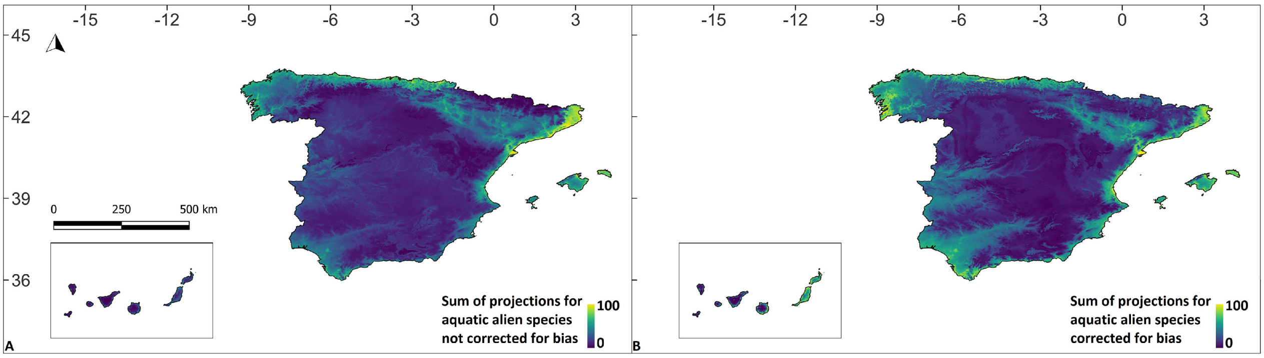

Figure 2. Map of Spain representing the sum of the projections of the alien species of aquatic turtles. A) projections without bias correction; B) bias-corrected projections. The inset shows the Canary Islands.

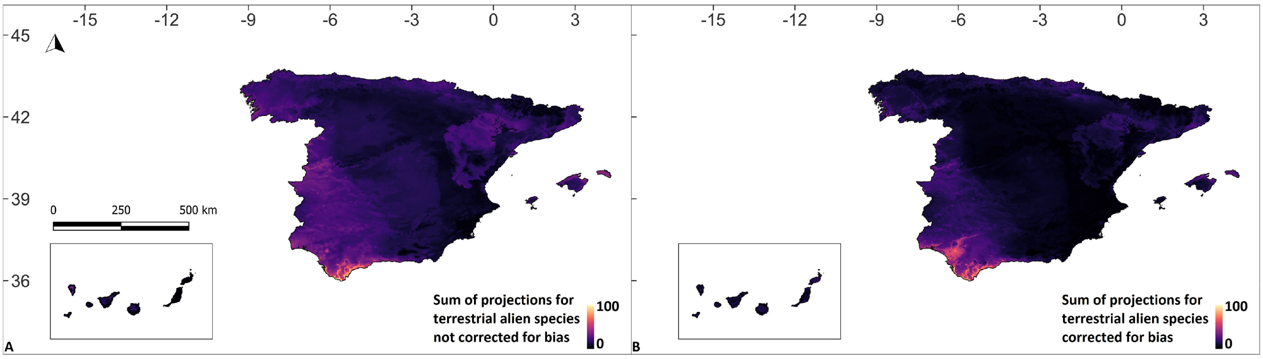

Figure 3. Map of Spain representing the sum of the projections of the alien species of tortoises. A) projections without bias correction; B) bias-corrected projections. The inset shows the Canary Islands.

In this study, we applied bias grids to reduce the effect of sampling biases (Rondinini et al. 2006). However, this method can cause a significant loss of information, especially evident in species that are not uniformly distributed in a geographic region. The latter is the case for numerous species of turtles, whose occurrence is altered by anthropogenic causes and appear to be distributed in a clustered manner (Vyas 2017; Chessman et al. 2020; Lamichhane and Khadka 2020). In these cases, the results of the models generated with bias grids may be partially unreliable and should be compared with those produced from standard models.

Our results revealed that not all regions of Spain are equally vulnerable to invasion by alien chelonians species. Projections showed that several large

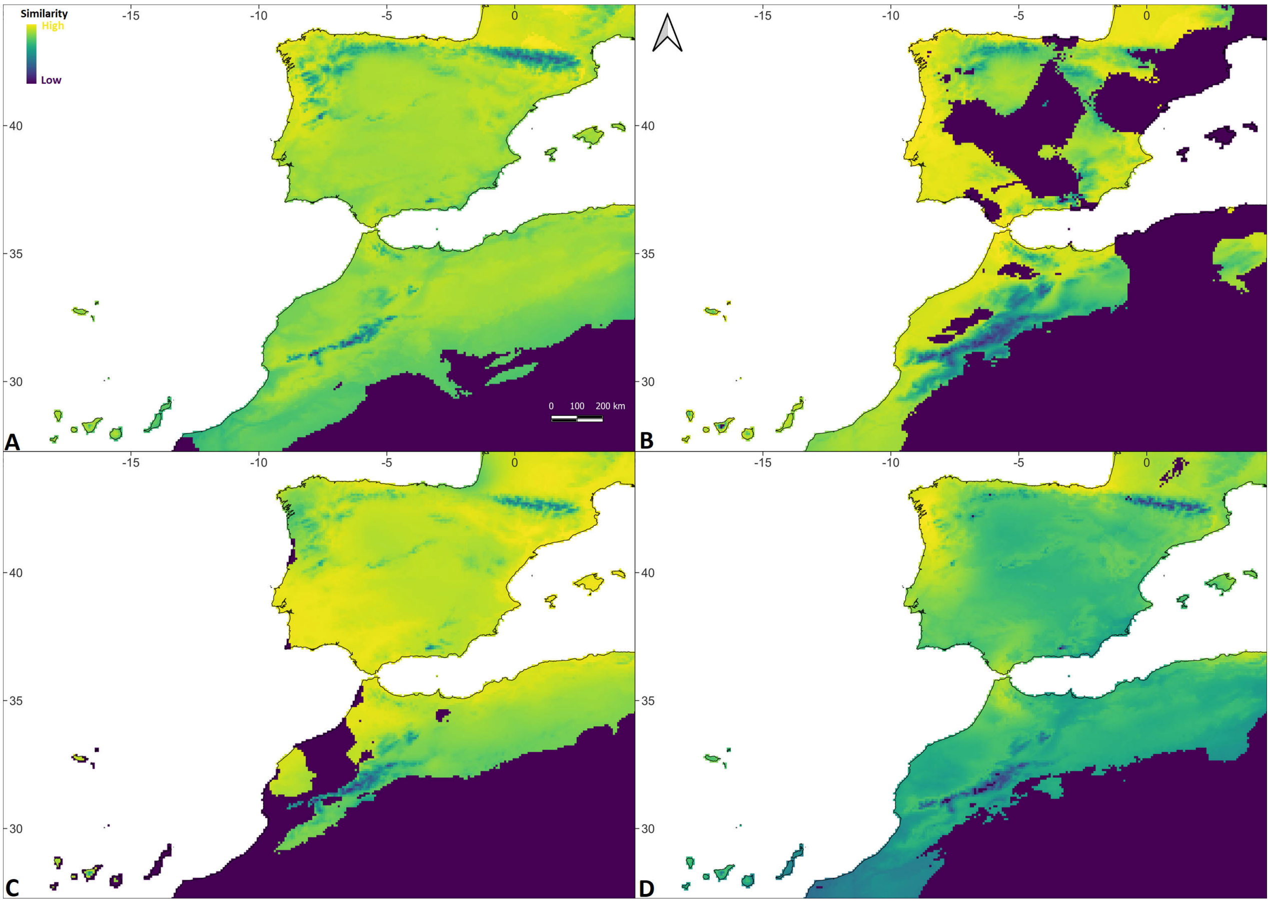

Figure 4. Mobility-Oriented Parity estimation of the environmental similarity between donor and recipient regions. Lighter colors indicate greater similarity and higher model transferability. Clockwise, modeled similarity with North America (A), South America (B), eastern Mediterranean (C), and eastern Asia (D).

hydrographic basins are highly susceptible to invasion, such as the Ebro, Miño-Sil and Guadalquivir basins, and the smaller basins of the Mediterranean coast (e.g., the Jucar, Ter, and Llobregat rivers). These basins are already populated by several alien species of turtles, some of which may be established as breeders, such as *Trachemys scripta* (Lacomba and Sancho 2004; Polo-Cavia et al. 2010; Martínez-Silvestre et al. 2015b, 2017; Costas and Ayres 2018). These basins still include populations of native turtles, many of which are restricted to stretches with high-quality riparian habitats and composed of low numbers of individuals, and are therefore potentially vulnerable to negative interactions with other species of turtles (Lacomba and Sancho 2004; Díaz-Paniagua et al. 2014; Escoriza et al. 2020). In contrast, other regions, such as the central and southeast parts of the Iberian Peninsula and most of the Canary Islands, show potentially lower invasiveness, due to prevailing cold steppe or subtropical desert conditions (Rodríguez et al. 2005; Ollero and van Staalduinen 2012), unfavourable for the establishment of aquatic turtles (McGaugh 2012).

Our analyses also allowed us to identify a priori which species are more likely to establish populations in regions suitable for native turtles. These include several species of North American and Northeast Asian origin.

Alien species can compete with native species for basking places and trophic resources (e.g., *Trachemys scripta*; Cadi and Joly 2004; Martínez-Silvestre et al. 2012), but they can also act as predators (e.g., *Chelydra serpentina*; Ernst and Lovich 2009). In addition, two alien species found during surveys (*Trachemys scripta* and *Mauremys sinensis*), are reservoirs for various pathogens, including viruses, bacteria, and endoparasites that can be transmitted to and harm native species (Martínez-Silvestre et al. 2013; Hidalgo-Vila et al. 2011, 2020).

In the niche overlap analysis, *E. orbicularis* and *M. leprosa* show similar overlap values with the alien species. However, our analyses only assessed broad environmental requirements. It is possible that local overlap between species could increase or decrease depending on specific habitat conditions, although within the pool of species present in similar climates. For example, Iberian species are adapted to using temporary aquatic habitats, both in their adult and juvenile phases (Keller et al. 1995), while this type of habitat is not used by some North American species (Ernst and Lovich 2009).

In the case of terrestrial species, the projections indicate that southwestern Spain, and possibly also the Mediterranean coast and the Balearic Islands, are the most suitable regions to be colonized by alien tortoises. These zones include healthy populations of native tortoises and would be very sensitive to invasion, particularly if they are conspecific individuals of the eastern *Testudo graeca* and *T. hermanni* subspecies, with which hybridization is frequent in captivity and may also occur in natural populations (Bertolero 2006; Soler et al. 2012; Zenboudji et al. 2016). Overlap analyses indicated that *T. graeca* populations are potentially more vulnerable if any of these alien tortoises can establish naturalized populations, particularly those of southwestern Spain. The implantation of alien species could hinder the capacity for future natural expansion of native species, which in western Andalusia are entirely confined to protected areas (Doñana National Park; Díaz-Paniagua et al. 2001).

In conclusion, our findings indicated that the native species are potentially susceptible to ecological overlap with alien species of turtles. Therefore, the trade of these alien species should be banned in Spain and other Mediterranean countries, even if they are not yet listed as harmful or invasive (Toland et al. 2020; Di Blasio et al. 2021). These include aquatic turtles of the temperate regions of North America and China (like *Pelodiscus sinensis*, *Apalone spinifera*, *Trachemys scripta*, or *Chrysemys picta*) and the species of the genus *Testudo* (*T. marginata* or the eastern clades of *T. graeca*). Overall, this and future studies can help identify lists of species whose trade must be regulated (i.e., negative lists) but also for the preparation of positive lists (Toland et al. 2020). However, both positive and negative lists must be built after rigorous ecological assessments and scientific consensus to be useful tools for conservation management (Oficialdegui et al. 2023).

Therefore, we recommend that imports within the studied territory be limited to species that are not potentially invasive. Species of subtropical-tropical origin can be used as alternatives to harmful invasive species, as they have more difficulty adapting to the conditions imposed by the highly seasonal climates of the Mediterranean and temperate European region (Kobelt and Nentwig 2008; Bianco 2014).

Acknowledgements

We thank to the Centre de Fauna dels Aiguamolls de l'Empordà (Generalitat de Catalunya) and to ADENC (Associació per la Defensa i l'Estudi de la Natura) for providing data for this study. We also thank the editor and anonymous referees for their valuable comments.

Funding

Part of this research has received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement No 869296 – The PONDERFUL Project.

Authors' contribution

Research conceptualization: D.E., S.P., A.M., J.B. and D.B.; sample design and methodology: D.E., S.P., A.M., J.B. and D.B.; investigation and data collection: all authors; funding provision: S.P. and D.B.; writing – original draft: D.E.; writing – review and editing: D.E., S.P., A.M., J.B. and D.B.

References

Acevedo P, Jiménez-Valverde A, Lobo JM, Real R (2012) Delimiting the geographical background in species distribution modelling. *Journal of Biogeography* 39: 1383–1390, https://doi.org/10.1111/j.1365-2699.2012.02713.x

Aiello-Lammens ME, Boria RA, Radosavljevic A, Vilela B, Anderson RP (2015) spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. *Ecography* 38: 541–545, https://doi.org/10.1111/ecog.01132

Angulo E, Ballesteros-Mejia L, Novoa A, Duboscq-Carra VG, Diagne C, Courchamp F (2021) Economic costs of invasive alien species in Spain. *NeoBiota* 67: 267–297, https://doi.org/10.3897/neobiota.67.59181

Beck HE, Zimmermann NE, McVicar TR, Vergopolan N, Berg A, Wood EF (2018) Present and future Köppen-Geiger climate classification maps at 1-km resolution. *Scientific Data* 5: 180214, https://doi.org/10.1038/sdata.2018.214

Bertolero A (2006) La tortue d'Hermann *Testudo hermanni* sur les îles de Majorque et Minorque, *Chéloniens* 1: 12–19

Bertolero A, Budó J, Torres N (2020) Característiques poblacionals de la tortuga mediterrània *Testudo hermanni hermanni* Gmelin a la serra de l'Albera (Reptilia: Testudinidae). *Butlletí de la Institució Catalana d'Història Natural* 84: 131–136

Bianco PG (2014) An update on the status of native and exotic freshwater fishes of Italy. *Journal of Applied Ichthyology* 30: 62–77, https://doi.org/10.1111/jai.12291

Bonin F, Devaux B, Dupré A (2006) Turtles of the World. Johns Hopkins University Press, Baltimore, 416 pp

Boria RA, Olson LE, Goodman SM, Anderson RP (2014) Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. *Ecological Modelling* 275: 73–77, https://doi.org/10.1016/j.ecolmodel.2013.12.012

Cadi A, Joly P (2004) Impact of the introduction of the red-eared slider (*Trachemys scripta elegans*) on survival rates of the European pond turtle (*Emys orbicularis*). *Biodiversity & Conservation* 13: 2511–2518, https://doi.org/10.1023/B:BIOC.0000048451.07820.9c

Cathrine C, Monir T (2022) Turtles (Testudines) of Glasgow Botanic Gardens including the first record of *Mauremys reevesii* (Gray, 1831) for the U.K. outwith captivity. *The Glasgow Naturalist* 27: 65–68, https://doi.org/10.37208/tgn27420

Chang B, Kim I, Choi K, Cho W, Ko DW (2022) Population dynamics of American Bullfrog (*Lithobates catesbeianus*) and implications for control. *Animals* 12: 2827, https://doi.org/10.3390/ani12202827

Chessman BC, McGilvray G, Ruming S, Jones HA, Petrov K, Fielder DP, Spencer RJ, Georges A (2020) On a razor's edge: Status and prospects of the critically endangered Bellinger River snapping turtle, *Myuchelys georgesi*. *Aquatic Conservation: Marine and Freshwater Ecosystems* 30: 586–600, https://doi.org/10.1002/aqc.3258

Cobos ME, Peterson AT, Barve N, Osorio-Olvera L (2019) kuenm: an R package for detailed development of ecological niche models using Maxent. *PeerJ* 7: e6281, https://doi.org/10.7717/peerj.6281
Conant R, Collins JT (1998) A field guide to reptiles & amphibians: eastern and central North America. Houghton Mifflin, Boston, USA, 494 pp
Costas MD, Ayres C (2018) Nuevos datos sobre la reproducción de *Trachemys scripta* en Galicia. *Boletín de la Asociación Herpetológica Española* 29: 75–76
Couturier T, Besnard A, Bertolero A, Bosc V, Astruc G, Cheylan M (2014) Factors determining the abundance and occurrence of Hermann's tortoise *Testudo hermanni* in France and Spain: Fire regime and landscape changes as the main drivers. *Biological Conservation* 170: 177–187, https://doi.org/10.1016/j.biocon.2013.12.028
Di Blasio L, Santoro R, Ferri V, Battisti C, Soccini C, Egidi A, Scalici M (2021) First successful reproduction of the Chinese striped-necked turtle *Mauremys sinensis* (Gray, 1834) in a European wetland. *BioInvasions Records* 10: 721–729, https://doi.org/10.3391/bir.2021.10.3.22
Díaz-Paniagua C, Keller C, Andreu AC (2001) Long-term demographic fluctuations of the spur-thighed tortoise *Testudo graeca* in SW Spain. *Ecography* 24: 707–721, https://doi.org/10.1111/j.1600-0587.2001.tb00532.x
Díaz-Paniagua C, Andreu AC, Marco A, Nuez M, Hidalgo-Vila J, Perez-Santigosa N (2014) Data on nesting, incubation, and hatchling emergence in the two native aquatic turtle species (*Emys orbicularis* and *Mauremys leprosa*) from Doñana National Park. *Basic and Applied Herpetology* 28: 147–151, http://dx.doi.org/10.11160/bah.13010/
Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, García Marquéz JR, Gruber B, Lafoucarde B, Leitão PJ, Münkemüller T, McClean C, Osborne PE, Reineking B, Schröder B, Skidmore AK, Zurell D, Lautenbach S (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36: 27–46, https://doi.org/10.1111/j.1600-0587.2012.07348.x
Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE, Yates CJ (2011) A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions* 17: 43–57, https://doi.org/10.1111/j.1472-4642.2010.00725.x
Ernst CH, Lovich JE (2009) Turtles of the United States and Canada. Johns Hopkins University Press, Baltimore, USA, 827 pp
Escoriza D, Ben Hassine J (2022) Niche diversification of Mediterranean and southwestern Asian tortoises. *PeerJ* 10: e13702, https://doi.org/10.7717/peerj.13702
Escoriza D, Franch M, Ramos S, Sunyer-Sala P, Boix D (2020) Demographics and survivorship in the European pond turtle (*Emys orbicularis*): a 31-year study. *Herpetological Conservation and Biology* 15: 41–48
Escoriza D, Sunyer P, Poch S, Boix D (2021) Habitat overlap and body condition in aquatic turtles: are there additive effects between invasive and native species? *Knowledge & Management of Aquatic Ecosystems* 422: 2, https://doi.org/10.1051/kmae/2021002
Fick SE, Hijmans RJ (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* 37: 4302–4315, https://doi.org/10.1002/joc.5086
Fritz U, Branch WR, Hofmeyr MD, Maran J, Prokop H, Schleicher A, Široký P, Stuckas H, Vargas-Ramírez M, Vences M, Hundsdörfer AK (2011) Molecular phylogeny of African hinged and helmeted terrapins (Testudines: Pelomedusidae: *Pelusios* and *Pelomedusa*). *Zoologica Scripta* 40: 115–125, https://doi.org/10.1111/j.1463-6409.2010.00464.x
Fujii R, Ota H, Toda M (2014) Genetic and morphological assessments of hybridization between two non-native Geoemydid turtles, *Mauremys reevesii* and *Mauremys mutica*, in northcentral Japan. *Chelonian Conservation and Biology* 13: 191–201, https://doi.org/10.2744/CCB-1067.1
Geange SW, Pledger S, Burns KC, Shima JS (2011) A unified analysis of niche overlap incorporating data of different types. *Methods in Ecology and Evolution* 2: 175–184, https://doi.org/10.1111/j.2041-210X.2010.00070.x
González de la Vega JP, García-de-Lomas J, Rodríguez-Andrés JL (2021) New records of the Chinese turtles *Mauremys reevesii* (Gray, 1831) and *Mauremys sinensis* (Gray, 1834) (Testudines, Geoemydidae) in southern Spain. *Graellsia* 77: e142, https://doi.org/10.3989/graellsia.2021.v77.306
Head L (2017) The social dimensions of invasive plants. *Nature Plants* 3: 1–7, https://doi.org/10.1038/nplants.2017.75
Hidalgo-Vila J, Martínez-Silvestre A, Ribas A, Casanova JC, Pérez-Santigosa N, Díaz-Paniagua C (2011) Pancreatitis associated with the helminth *Serpinema microcephalus* (Nematoda: Camallanidae) in exotic Red-eared slider turtles (*Trachemys scripta elegans*). *Journal of Wildlife Diseases* 47: 201–205, https://doi.org/10.7589/0090-3558-47.1.201
Hidalgo-Vila J, Martínez-Silvestre A, Pérez-Santigosa N, León-Vizcaíno L, Díaz-Paniagua C (2020) High prevalence of diseases in two invasive populations of red-eared slider (*Trachemys scripta elegans*) in southwestern Spain. *Amphibia-Reptilia* 41: 509–518, https://doi.org/10.1163/15685381-bja10021

Hirzel AH, Le Lay G, Helfer V, Randin C, Guisan A (2006) Evaluating the ability of habitat suitability models to predict species presences. *Ecological Modelling* 199: 142–152, https://doi.org/10.1016/j.ecolmodel.2006.05.017

Keller C, Paniagua CD, Andreu A, Bravo MA (1995) Distribution pattern of freshwater turtles in the Doñana National Park (SW Spain). In: Devaux B (ed), Proceedings of the International Congress of Chelonian Conservation. SOPTOM (Gonfaron), pp 192–195

Kobelt M, Nentwig W (2008) Alien spider introductions to Europe supported by global trade. *Diversity and Distributions* 14: 273–280, https://doi.org/10.1111/j.1472-4642.2007.00426.x

Lacomba I, Sancho V (2004) Advances in the action plan for *Emys orbicularis* in the Valencia region, Spain. *Biologia Bratislava* 59: 173–176

Lamichhane S, Khadka BB (2020) First distribution record of *Pangshura flaviventer*, *Chitra indica*, and *Aspideretes gangeticus* in the major rivers of Chitwan National Park, Nepal. *Herpetology Notes* 13: 157–159

Legler J, Vogt RC (2013) The turtles of Mexico: land and freshwater forms. University of California Press, Berkeley, USA, 416 pp, https://doi.org/10.1525/9780520956896

Lei Y, Liu Q (2021) Tolerance niche expansion and potential distribution prediction during Asian openbill bird range expansion. *Ecology and Evolution* 11: 5562–5574, https://doi.org/10.1002/ece3.7456

Li Y, Ke Z, Wang Y, Blackburn TM (2011) Frog community responses to recent American bullfrog invasions. *Current Zoology* 57: 83–92, https://doi.org/10.1093/czoolo/57.1.83

Lloret F, Calvo E, Pons X, Díaz-Delgado R (2002) Wildfires and landscape patterns in the Eastern Iberian Peninsula. *Landscape Ecology* 17: 745–759, https://doi.org/10.1023/A:1022966930861

Lockwood JL, Welbourne DJ, Romagosa CM, Cassey P, Mandrak NE, Strecker A, Leung B, Stringham OC, Udell B, Episcopio-Sturgeon DJ, Tlusty MF, Sinclair J, Springborn MR, Pienaar EF, Rhyne AL, Keller R (2019) When pets become pests: the role of the exotic pet trade in producing invasive vertebrate animals. *Frontiers in Ecology and the Environment* 17: 323–330, https://doi.org/10.1002/fee.2059

López-López P, Luigi M, Alessandra F, Emilio B, Luigi B (2011) Hotspots of species richness, threat and endemism for terrestrial vertebrates in SW Europe. *Acta Oecologica* 37: 399–412, https://doi.org/10.1016/j.actao.2011.05.004

Martínez-Silvestre A, Soler-Massana J, Solé R, Medina D (2001) Reproducción de quelonios alóctonos en Cataluña en condiciones naturales. *Boletín de la Asociación Herpetológica Española* 12: 41–43

Martínez-Silvestre A, Flecha C, Soler J (2012) Observaciones de interacciones entre *Trachemys scripta elegans* y *Mauremys leprosa* en el pantano del Foix (Barcelona). *Boletín de la Asociación Herpetológica Española* 23: 106–109

Martínez-Silvestre A, Guinea D, Soler J, Ferrer D (2013) Presencia del parásito autóctono *Serpinema microcephalus* (Nematoda: Camallanidae) en las tortugas *Trachemys scripta* y *Pseudemys concinna* asilvestradas en Barcelona. *Boletín de la Asociación Herpetológica* 24: 48–50

Martínez-Silvestre A, Guinea D, Ferrer D, Pantchev N (2015a) Parasitic enteritis associated with the camallanid nematode *Serpinema microcephalus* in wild invasive turtles (*Trachemys*, *Pseudemys*, *Graptemys*, and *Ocadia*) in Spain. *Journal of Herpetological Medicine and Surgery* 25: 48–52, https://doi.org/10.5818/1529-9651-25.1.48

Martínez-Silvestre A, Cano JM, Soler J (2015b) Tortuga mordedora (*Chelydra serpentina*) en Cataluña (NE de la Península Ibérica): nuevas citas y consideraciones sobre su riesgo invasor. *Boletín de la Asociación Herpetológica Española* 26: 91–93

Martínez-Silvestre A, Soler J, Verdaguer I, Cano JM (2017) Confirmación de la reproducción en condiciones naturales de (*Trachemys emolli*) en Cataluña (NE península ibérica). *Boletín de la Asociación Herpetológica Española* 28: 78–80

Mazzotti S (2004) Hermann's tortoise (*Testudo hermanni*): current distribution in Italy and ecological data on a population from the north Adriatic coast (Reptilia, Testudinidae). *Italian Journal of Zoology* 71: 97–102, https://doi.org/10.1080/11250003.2004.9525543

McGaugh SE (2012) Comparative population genetics of aquatic turtles in the desert. *Conservation Genetics* 13: 156–176, https://doi.org/10.1007/s10592-012-0403-5

Muscarella R, Galante PJ, Soley-Guardia M, Boria RA, Kass JM, Uriarte M, Anderson RP (2014) ENM eval: An R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. *Methods in Ecology and Evolution* 5: 1198–1205, https://doi.org/10.1111/2041-210X.12261

Oficialdegui FJ, Zamora-Marín JM, Guareschi S, Anastácio PM, García-Murillo P, Ribeiro F, Miranda R, Cobo F, Gallardo B, García-Berthou E, Boix D, Arias A, Cuesta J,A, Medina L, Almeida D, Banha F, Barca S, Biurrun I, Cabezas M,P, Calero S, Campos J,A, Capdevila-Argüelles L, Capinha C, Casals F, Clavero M, Encarnaçao J, Fernández-Delgado C, Franco J, Guillén A, Hermoso V, Machordom A, Martelo J, Mellado-Díaz A, Morcillo F, Ozcoz J, Perdices A, Pou-Rovira Q, Rodríguez-Merino A, Ros M, Ruiz-Navarro A, Sánchez MI, Sánchez-Fernández D, Sánchez-González JR, Sánchez-Gullón E, Teodósio MA, Torralva M, Vieira-Lanero R, Oliva-Paterna FJ (2023) A horizon scan exercise for aquatic invasive alien species in Iberian inland waters. *Science of the Total Environment* 869: 161798, https://doi.org/10.1016/j.scitotenv.2023.161798

Ollero HS, van Staalduinen MA (2012) Iberian steppes. In: Werger M, van Staalduinen M (eds), Eurasian steppes. Ecological problems and livelihoods in a changing world. Plant and vegetation, vol 6. Springer, Dordrecht, The Netherlands, pp 273–286, https://doi.org/10.1007/978-94-007-3886-7_9

Owens HL, Campbell LP, Dornak LL, Saupe EE, Barve NV, Soberón J, Ingenloff K, Lira-Noriega A, Hensz CM, Myers CE, Peterson AT (2013) Constraints on interpretation of ecological niche models by limited environmental ranges on calibration areas. *Ecological Modelling* 263: 10–18, https://doi.org/10.1016/j.ecolmodel.2013.04.011

Pearson RG, Stanton JC, Shoemaker KT, Aiello-Lammens ME, Ersts PJ, Horning N, Fordham DA, Raxworthy CJ, Ryu HY, McNess J, Akçakaya HR (2014) Life history and spatial traits predict extinction risk due to climate change. *Nature Climate Change* 4: 217–221, https://doi.org/10.1038/nclimate2113

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190: 231–259, https://doi.org/10.1016/j.ecolmodel.2005.03.026

Poch S, Sunyer P, Pascual G, Boix D, Campos M, Cruset E, Quer-Feo C, Fuentes MA, Molina A, Porcar A, Pérez-Novo I, Pou-Rovira Q, Ramos S, Escoriza D (2020) Alien chelonians in north-eastern Spain: new distributional data. *The Herpetological Bulletin* 151: 1–5, https://doi.org/10.33256/hb151.15

Polo-Cavia N, Gonzalo A, López P, Martín J (2010) Predator recognition of native but not invasive turtle predators by naïve anuran tadpoles. *Animal Behaviour* 80: 461–466, https://doi.org/10.1016/j.anbehav.2010.06.004

Polo-Cavia N, López P, Martín J (2014) Interference competition between native Iberian turtles and the exotic *Trachemys scripta*. *Basic and Applied Herpetology* 28: 5–20, http://dx.doi.org/10.11160/bah.13014/

Pupins M (2007) First report on recording of the invasive species *Trachemys scripta elegans*, a potential competitor of *Emys orbicularis* in Latvia. *Acta Universitatis Latviensis* 723: 37–46

Reino L, Moya-Laraño J, Cláudio Heitor A (2009) Using survival regression to study patterns of expansion of invasive species: will the common waxbill expand with global warming? *Ecography* 32: 237–246, https://doi.org/10.1111/j.1600-0587.2008.05354.x

Rodríguez AR, Mora JL, Arbelo C, Bordon J (2005) Plant succession and soil degradation in desertified areas (Fuerteventura, Canary Islands, Spain). *Catena* 59: 117–131, https://doi.org/10.1016/j.catena.2004.07.002

Rondinini C, Wilson KA, Boitani L, Grantham H, Possingham HP (2006) Tradeoffs of different types of species occurrence data for use in systematic conservation planning. *Ecology Letters* 9: 1136–1145, https://doi.org/10.1111/j.1461-0248.2006.00970.x

Sáez-Gómez P, Prenda J (2022) Freshwater fish biodiversity in a large Mediterranean basin (Guadalquivir River, S Spain): Patterns, threats, status and conservation. *Diversity* 14: 831, https://doi.org/10.3390/d14100831

Salvador A (2014) Reptiles: 2ª edición. Museo Nacional de Ciencias Naturales-CSIC, Madrid, Spain, 1372 pp

Schroeder MA, Lander J, Levine-Silverman S (1990) Diagnosing and dealing with multicollinearity. *Western Journal of Nursing Research* 12: 175–187, https://doi.org/10.1177/019394599001200204

Soflanidou TS, Psallidas VK, Belcheva RG (1990) A karyological study of the tortoise *Testudo marginata*. *Amphibia-Reptilia* 11: 185–189, https://doi.org/10.1163/156853890X00582

Soler J, Martínez-Silvestre A, Budó J, Capalleras X, Juárez JL (2010) Análisis de la presencia de tortugas terrestres alóctonas y autóctonas asilvestradas en Cataluña (NE España). *Boletín de la Asociación Herpetológica Española* 21: 63–68.

Soler J, Pfau B, Martínez-Silvestre A (2012) Detecting intraspecific hybrids in *Testudo hermanni* (Gmelin 1789). *Radiata* 21: 4–29

Stephens PR, Wiens JJ (2003) Explaining species richness from continents to communities: the time-for-speciation effect in emydid turtles. *The American Naturalist* 161: 112–128, https://doi.org/10.1086/345091

Storey KB, Storey JM, Brooks SP, Churchill TA, Brooks RJ (1988) Hatchling turtles survive freezing during winter hibernation. *Proceedings of the National Academy of Sciences* 85: 8350–8354, https://doi.org/10.1073/pnas.85.21.8350

Strayer DL (2010) Alien species in fresh waters: ecological effects, interactions with other stressors, and prospects for the future. *Freshwater Biology* 55: 152–174, https://doi.org/10.1111/j.1365-2427.2009.02380.x

Syfert MM, Smith MJ, Coomes DA (2013) The effects of sampling bias and model complexity on the predictive performance of MaxEnt species distribution models. *PLoS ONE* 8: e55158, https://doi.org/10.1371/journal.pone.0055158

Thomson RC, Spinks PQ, Shaffer HB (2010) Distribution and abundance of invasive red-eared sliders (*Trachemys scripta elegans*) in California's Sacramento River Basin and possible impacts on native western pond turtles (*Emys marmorata*). *Chelonian Conservation and Biology* 9: 297–302, https://doi.org/10.2744/CCB-0820.1

Toland E, Bando M, Hamers M, Cadenas V, Laidlaw R, Martínez-Silvestre A, van der Wielen P (2020) Turning negatives into positives for pet trading and keeping: A review of positive lists. *Animals* 10: 2371, https://doi.org/10.3390/ani10122371

Ueno S, Kamezaki N, Mine K, Suzuki D, Hosoya S, Kikuchi K, Okamoto K, Torii M, Kadowaki K, Okamoto K, Sano M (2021) Reproductive Ability of Hybrids between Japanese Pond Turtle (*Mauremys japonica*) and Reeves' Pond Turtle (*Mauremys reevesii*). *Zoological Science* 39: 186–192, https://doi.org/10.2108/zs210047

Vyas R (2017) A Northern River Terrapin (*Batagur baska*) from Kutch, with comments on the species' distribution in western India and Pakistan. *Reptiles & Amphibians* 24: 128–131, https://doi.org/10.17161/randa.v24i2.14167

Warren DL, Wright AN, Seifert SN, Shaffer HB (2014) Incorporating model complexity and spatial sampling bias into ecological niche models of climate change risks faced by 90 California vertebrate species of concern. *Diversity and Distributions* 20: 334–343, https://doi.org/10.1111/ddi.12160

Warren DL, Matzke NJ, Cardillo M, Baumgartner JB, Beaumont LJ, Turelli M, Glor RE, Huron NA, Simões M, Iglesias TL (2021) ENMTools 1.0: An R package for comparative ecological biogeography. *Ecography* 44: 504–511, https://doi.org/10.1111/ecog.05485

Zenboudji S, Cheylan M, Arnal V, Bertolero A, Leblois R, Astruc G, Bertorelle G, Pretus JL, Valvo ML, Sotgiu G (2016) Conservation of the endangered Mediterranean tortoise *Testudo hermanni hermanni*: The contribution of population genetics and historical demography. *Biological Conservation* 195: 279–291, https://doi.org/10.1016/j.biocon.2016.01.007

Websites, online databases and software

Hijmans RJ (2023) raster: Geographic Data Analysis and Modeling. R package version 3.6–14. https://CRAN.R-project.org/package=raster (accessed 19 January 2023)

Pastore M, Di Loro PA, Mingione M, Calcagni A (2022) overlapping: Estimation of overlapping in empirical distributions. R package version 2.1. https://CRAN.R-project.org/package=overlapping (accessed 19 January 2023)

Quantum GIS Development Team (2023) https://www.qgis.org/es/site/ (accessed 29 January 2023)

R Development Team (2023) R: A language and environment for statistical computing. https://cran.r-project.org/ (accessed 29 January 2023)

Supplementary material

The following supplementary material is available for this article:

Table S1. Data sources used in this study.
Table S2: ODMAP (Overview, Data, Model, Assessment and Prediction) protocol.
Table S3: Best ENM candidates generated by ENMval for alien semi-aquatic species.
Table S4: Best ENM candidates generated by ENMval for alien terrestrial species.
Table S5: Best ENM candidates generated by ENMval for native species.

This material is available as part of online article from:
http://www.reabic.net/journals/mbi/2024/Supplements/MBI_2024_Escoriza_etal_SupplementaryMaterial.pdf