

From introduction to the establishment of alien species: bioclimatic differences between presence and reproduction localities in the slider turtle

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ABSTRACT

Aim Understanding the factors determining the transition from introduction of aliens to the establishment of invasive populations is a critical issue of the study of biological invasions, and has key implications for management. Differences in fitness among areas of introduction can define the zones where aliens become invasive. The American slider turtle *Trachemys scripta* has been introduced worldwide, and has negative effects on freshwater communities, but only a subset of introduced populations breed successfully. We used species distribution models to assess the factors influencing the slider distribution in Italy, by analysing bioclimatic features that can cause the transition from presence of feral adults to breeding populations. We also evaluated whether climate change might increase the future suitability for reproduction.

Location Central and Northern Italy.

Methods The distribution of slider turtle was obtained from the literature, unpublished reports and field surveys. We used Maxent to build bioclimatic models.

Results Reproductive populations are associated to a clear bioclimatic envelope with warmer climate, more solar radiation and higher precipitations than populations where reproduction is not observed. Several Mediterranean areas currently have climatic features suitable for sliders. Scenarios of climate change predict the expansion of these areas. In the near future (2020), the proportion of populations in areas suitable for reproduction will dramatically increase.

Main conclusion Our study shows that bioclimatic differences can determine the areas where aliens become invaders. Management should be focused to these source areas. However, climate change can increase fitness in the future, and therefore the interactions between climate change and fitness can boost the invasiveness of this alien species.

Keywords

Bioclimatic envelope, biological invasions, climate change, fitness, MAXENT, problematic alien species, reproduction, species distribution models.

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INTRODUCTION

Alien invasive species (AIS) are a major cause of biodiversity loss (Strayer *et al.*, 2006; Ricciardi, 2007). They can negatively affect native species through predation and competition, can diffuse pathogens, can modify ecosystem functioning and abiotic features of the environments (Strayer *et al.*, 2006; Ricciardi, 2007). The prevention and control of AIS is thus a priority for conservation (Hulme, 2006).

Biological invasions can be described as a multistep process, comprising three major phases: initial dispersal (i.e. an organism moves long distances to areas outside its native range, for example through human assisted dispersal); establishment of self-sustaining populations within the non-native range; and invasion of the new range (Richardson *et al.*, 2000; Puth & Post, 2005). However, when species are invasive, they have strongly positive demographic trends and are often numerous, therefore their management can be extremely difficult and expensive (Hulme, 2006). For these

reasons, the first stages of invasions are the most critical for conservation (Puth & Post, 2005; Hulme, 2006). Preventing new introductions is currently considered the most effective management tool (Leung *et al.*, 2002; Keller *et al.*, 2008). However, some species will become introduced even in the presence of strict protocols of prevention and screening. In these cases, a rapid response may still stop the invasion (Hulme, 2006).

Unfortunately, studying and managing the first steps of invasions (i.e. before that species become invasive) is often difficult. First of all, only a small subset of introduced species become invasive (approximately 1%: Williamson & Fitter, 1996; but see also Suarez *et al.*, 2005), and the active control and monitoring of all non-native species may be not feasible. Moreover, many AIS often undergo a clear 'lag phase' before they show any sign of becoming invasive (Crooks & Soulé, 1999). During lag phases, species are usually rare; the low detection rate limits our power to detect presence, assess demographic changes and to find the factors determining the transition from establishment to invasion (Hulme, 2006). Molecular genetics can provide insights into the demography of early stages of invasions (Lindholm *et al.*, 2005; Ficetola *et al.*, 2008), but these studies are usually performed *post hoc*, i.e. when species are already invasive.

Habitat modelling is a powerful approach to evaluate the factors determining species invasions. Through modelling, data on the distribution of AIS can be used to find the environmental features determining species distribution, and therefore to build maps for risk assessment (Thuiller *et al.*, 2005; see also Elith *et al.*, 2006). Modelling is usually based on distribution within the native range (Roura-Pascual *et al.*, 2004; Thuiller *et al.*, 2005; Ficetola *et al.*, 2007b), on records in the invasive range (Bossenbroek *et al.*, 2007; Ward, 2007; Nielsen *et al.*, 2008) or both (Broennimann *et al.*, 2007). Nevertheless, the presence of a species does not necessarily imply that it has positive fitness in an environment. This can be extremely important for species that are introduced multiple times, sometimes in suboptimal areas. Particularly in long-lived species, adults can survive long periods in suboptimal habitats, and may even attain high densities if massively released, but can fail to achieve key steps of their life cycle, such as reproduction. This can determine human-mediated source-sink dynamics. The distinction between localities of presence, and localities where non-native species have positive fitness, can be the key to understanding the causes of the transition among the different steps of invasions. However, comparisons of fitness among areas are rarely included in models of distribution of non-native species.

Turtles are long-lived organisms, and adults can survive for decades in suboptimal habitats where environmental features are unsuitable for breeding (Gariboldi & Zuffi, 1994; Spinks *et al.*, 2003). Therefore, even if they can negatively affect native populations, the presence of non-native turtles does not necessarily imply that a species is invasive and colonizing new habitats. The long life cycle of turtles determines slow population dynamics (Congdon *et al.*, 1993), making turtles particularly suitable for the study of transition between the different steps of invasions, and to find the factors influencing these transitions. The slider turtle *Trachemys scripta* Schoepffs, 1972 is a native of Eastern

Northern and Central America, but has been introduced as a pet in some 30 countries around the world, with several million individuals sold during the past decades (Lever, 2003). Young sliders are sold at a size of just a few centimetres, but can grow quickly, and are released by owners in natural and seminatural wetlands. The importation of *T. scripta elegans* has been banned in the European Union (Commission Regulation 349/2003), although other subspecies are still sold, and individuals traded before the ban continue to be released in natural and seminatural wetlands. Sliders are considered a potential threat to European freshwater ecosystems. They compete for food and basking places with the threatened European pond turtle *Emys orbicularis*, and can increase its mortality (Cadi & Joly, 2003, 2004). Moreover, at high densities sliders can modify wetland vegetation and the communities of macroinvertebrates and amphibians (Teillac-Deschamps & Prevot-Julliard, 2006). However, not all the European slider 'populations' are reproductively active. Reproduction has been observed only in a limited number of localities of southern Europe (Spain (Pleguezuelos, 2002); France (Cadi *et al.*, 2004); Italy (Sindaco *et al.*, 2006)), while most feral sliders are assumed to live in areas too cold for a successful reproduction. Nevertheless, we lack large scale and quantitative analysis of environmental features discriminating between reproductive and non-reproductive populations. An objective assessment of these features would identify populations that have the highest risk of becoming invasive, and thus the priority areas for management actions such as eradication.

The aim of this study was twofold. First, we assessed the factors influencing the distribution of the slider turtle in Italy, by analysing bioclimatic features that can cause the transition from presence of feral adults to breeding populations. Ongoing climate change is quickly modifying environmental conditions, and can affect invasion dynamics (Thuiller *et al.*, 2007). We therefore evaluated whether climate change might increase the suitability for reproduction, and boost the risk of establishment and invasion of this species in the near future.

METHODS

Distribution data

To obtain reliable distribution data over extensive areas throughout Italy, we combined data from the literature, from regional herpetological atlas (Lapini *et al.*, 1999; Bologna *et al.*, 2000; Bologna *et al.*, 2003; Fiacchini, 2003; Bernini *et al.*, 2004; Ragni *et al.*, 2006; Vanni & Nistri, 2006), the Italian fauna data base (Ruffo & Stoch, 2005), the ongoing Italian herpetological monitoring (Societas Herpetologica Italica, 2008), direct field surveys and personal communications from field herpetologists. We defined 'reproducing populations' to be populations where hatchling emergence has been observed (e.g. Lapini *et al.*, 1999; Ficetola *et al.*, 2003) excluding localities where females lay eggs but hatchling emergence has never been observed.

Our study was focused on Central and Northern Italy, because most of observations came from this area (Fig. 1). Observations in Southern Italy were scant, and this was probably related to

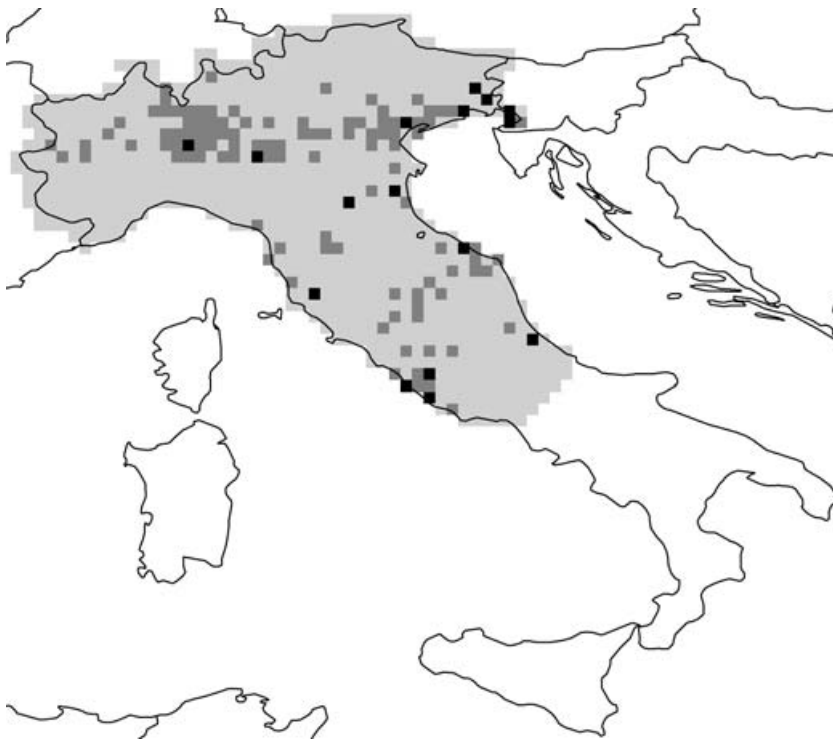


Figure 1 Study area in Italy (pale grey), and distribution of localities with feral (dark grey) and reproducing populations (black) of *Trachemys scripta*.

both reduced frequency of introduction and lower monitoring effort in these areas (see Sindaco *et al.*, 2006).

We did not use data of distribution of the slider turtle within the native range, since *T. scripta* has complex systematic with strong differentiation among subspecific entities (Stephens & Wiens, 2003). Individuals with different origin might have different climatic tolerance, but the subspecies and the origin of individuals introduced in Europe are often unknown and changed in time. In these conditions, models based on the introduced range only can be more informative (Steiner *et al.*, 2008). Therefore, our analysis describes the realized niche of introduced populations.

Environmental data

For the climatic parameters, the CRU CL 2.0 global data set at $10' \times 10'$ served as the base data set (New *et al.*, 2002). At the latitude of the study area, each $10' \times 10'$ cell corresponds to a rectangle of approximately 13×18 km. Two temperature variables (winter temperature: average temperature in the coldest month; summer temperature: average temperature in the warmest month) and annual solar radiation ($\text{Wh/m}^2/\text{day}$) described the species thermal tolerance and the availability of thermal energy. Summed annual precipitation described the water availability. To avoid the multicollinearity issue, we did not include other climatic variables (such as annual temperature and seasonal precipitation) that were strongly correlated to linear combinations of the four climatic variables used. Furthermore, we used the human footprint at $10' \times 10'$, a measure of human influence on global surface, combining data of population density, land transformation, human access and presence of infrastructures. This information was based on nine geographical data sets including satellite

images, vector maps and census data (Sanderson *et al.*, 2002). Human footprint was used because the slider turtle and many other alien species are often associated with human modified landscapes (Ficetola *et al.*, 2004; Leprieux *et al.*, 2008).

Four climate-change scenarios were derived from HadCM3 (Hadley Centre for Climate Prediction and Research's General Circulation Model) for the period of 2010 to 2039 (referred to as the 2020 scenario) to obtain estimates of likely climatic conditions in the near future. The different global circulation model was run using four IPCC SRES (Intergovernmental Panel on Climate Change, Special Report on Emission Scenarios) storyline runs, reflecting different assumptions about demographic changes, socioeconomic and technological development (Nakicenovic & Swart, 2000). These include A1, A2, B1 and B2, ranging from fossil-fuel intensive to alternative futures involving rapid adoption of new technologies. This range of scenarios gives some idea of the range of greenhouse gas emission pathways that might be taken during the next decades.

Data analysis

Environmental suitability was modelled using Maxent 3.1 (Phillips *et al.*, 2006; Phillips & Dudík, 2008). Maxent is a machine learning method that estimates the distribution of a species by finding the probability distribution of maximum entropy (i.e. that is closest to uniform) subject to constraints representing our incomplete information about the distribution. The constraints are that the expected value of each environmental variable should match its average over sampling locations derived from environmental layers (Phillips *et al.*, 2006). The model evaluates the suitability of each grid cell as a function of

environmental variables at that cell. Some advantages of Maxent are that it requires presence-only data, deterministic algorithms have been developed that always converge to the optimal probability distribution, and can calculate the relative importance of different environmental variables (Phillips *et al.*, 2006). We used a logistic output of Maxent, with suitability values ranging from 0 (unsuitable habitat) to 1 (optimal habitat) (Phillips & Dudík, 2008). Following Pearson *et al.* (2007), we used the 10th percentile training presence as a suitability threshold, i.e. we assumed that a cell is suitable if its suitability score is greater than the 10th percentile of training presence points. We developed models using linear, quadratic and hinge functions (Phillips & Dudík, 2008). In recent comparisons among several techniques of prediction of species distribution, Maxent was among the most effective methods using presence-only data, and showed a particularly good performance when analysing data sets with a small number of presence records (Elith *et al.*, 2006; Hernandez *et al.*, 2006). The reliability of the results of Maxent has been confirmed by its good capacity to predict novel presence localities for poorly known species (Pearson *et al.*, 2007) and the outcome of introductions of invasive species outside the native range (Ficetola *et al.*, 2007b).

Using Maxent, we built two models to compare the bioclimatic envelopes corresponding to different levels of fitness. First, we built a model using presence data. This model describes the environmental features needed for the presence and survival of adults, independently from reproduction. The second model used data on the distribution of breeding localities, and described the environmental features required for successful reproduction (i.e. for the establishment of naturalized populations). All models included the five environmental variables as predictors.

We used null-models to test for significance of Maxent models (Raes & ter Steege, 2007). For each model based on turtle distribution, we generated 99 null-distributions of random points in the study area; the number of random points per distribution was equal to the actual number of presence points. Next, we used Maxent to create models relating the null-distributions to the environmental layers. We then compared the area under the curve of the receiver operator plot (AUC) (Manel *et al.*, 2001) of the randomly generated models with the AUC of the models generated using the actual distribution data. These randomly generated models can be thus used as a null-hypothesis against which to test the significance of species distribution models. If the AUC of the slider turtle models was significantly higher than the AUC of randomly generated models, it was considered as evidence that the species distribution model performs significantly better than expected by chance (Raes & ter Steege, 2007).

We used the jackknife procedure developed by Pearson *et al.* (2007) to evaluate the predictive performance of our model, i.e. the ability to correctly predict new localities of reproduction. Each observed locality of reproduction was removed once from the data set and a model was built using the remaining $n - 1$ localities. The predictive performance was then evaluated based on the ability of each model to correctly predict the locality excluded from the training data set, using the 10th percentile training presence threshold (Pearson *et al.*, 2007). This approach is valid only for

small data sets (less than 25 calibration points: Pearson *et al.*, 2007), and was therefore applied to the analysis of reproduction.

To compare bioclimatic envelopes of presence points and of reproducing populations, we compared the response curves obtained using Maxent. Maxent curves provide only qualitative estimates of differences in niches, also because confidence intervals are not available. Nevertheless, they can provide useful insights into differences among distribution models (Martínez-Freiria *et al.*, 2008).

Finally, we used the four 2020 scenarios to project the predicted suitability to the future climatic conditions. Estimations of the future human footprint are not available. However, it is unlikely that human footprint in Europe will decrease in the near future, and slider turtles are positively associated with human footprint (see results). Therefore, models assuming a constant human footprint are conservative in respect of the future suitability.

RESULTS

Feral populations of slider turtle were present in 121 $10' \times 10'$ pixels, corresponding to 14% of the study area (Fig. 1). However, reproduction was observed only in a small subset of localities (16 pixels) (Fig. 1).

Bioclimatic features were different among pixels with and without observed reproduction. Pixels with reproduction had higher summer (unequal variance t -test: $t_{57} = 2.687$, $P = 0.009$) and winter temperature ($t_{50} = 2.686$, $P = 0.014$) and more annual radiation ($t_{21} = 2.462$, $P = 0.023$) than pixels where reproduction was not observed. We did not observe significant differences in annual precipitation and human footprint (both $P > 0.75$).

Suitability models

The variables most important to explain the presence of feral populations were summer temperature (61.1% of explained variation accounted), and human footprint (16% of variation); annual precipitation and solar radiation accounted for 11.2 and 10.5% of variation, respectively, while winter temperature explained only a minor portion of variance. The presence of feral populations of slider turtles was positively related to summer temperature, annual precipitation and human footprint, while the relationship with solar radiation showed a less clear, non-linear pattern (Fig. 2). The areas with the highest probability of containing feral populations were mostly in Northern Italy, close to the largest cities such as Milan, Turin and Venice, and in Central Italy around the cities of Rome and Florence (Fig. 3). The AUC of this model was 0.828, and was significantly higher than the null-model AUC (median = 0.603; 95% CI = 0.564–0.644). This indicates a good fit of the model.

The model describing the features of reproduction areas was quite different. The most important variable to explain the presence of reproducing populations was summer temperature (81.5% of variation). Annual radiation and precipitation explained 7.4% and 6.5% of variation, respectively, while human footprint and winter temperature explained only a minor

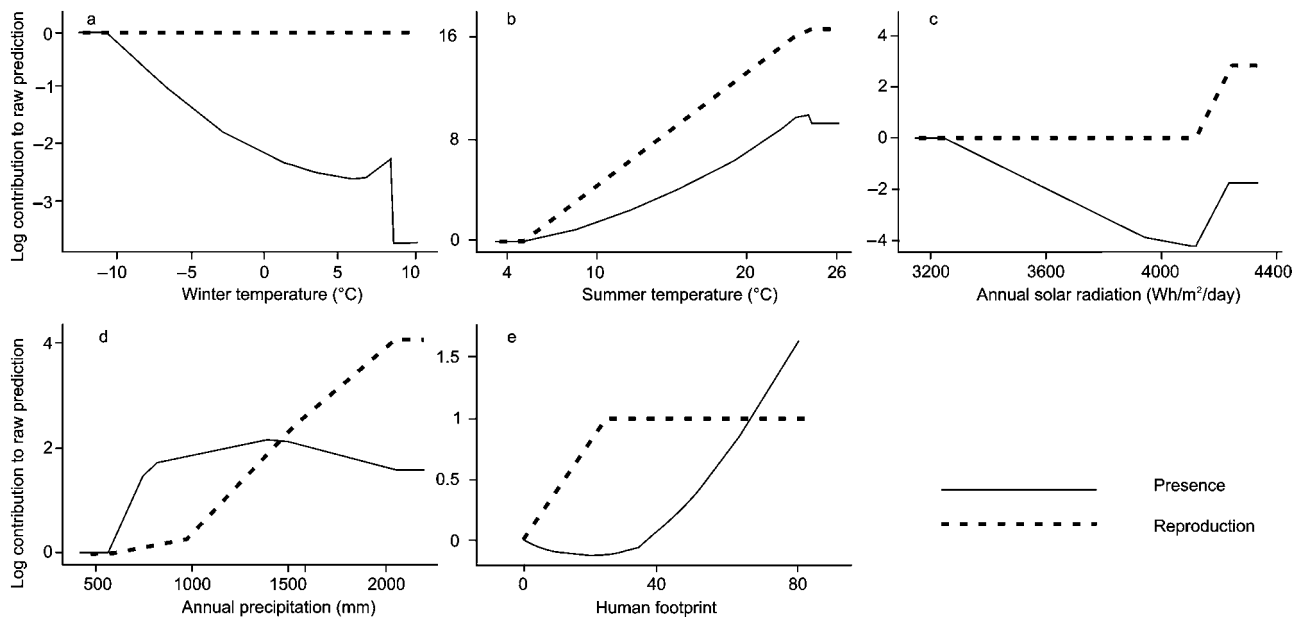


Figure 2 Results of environmental suitability models: relationships between environmental features and presence (continuous line) or reproduction (broken line) of *Trachemys scripta*.

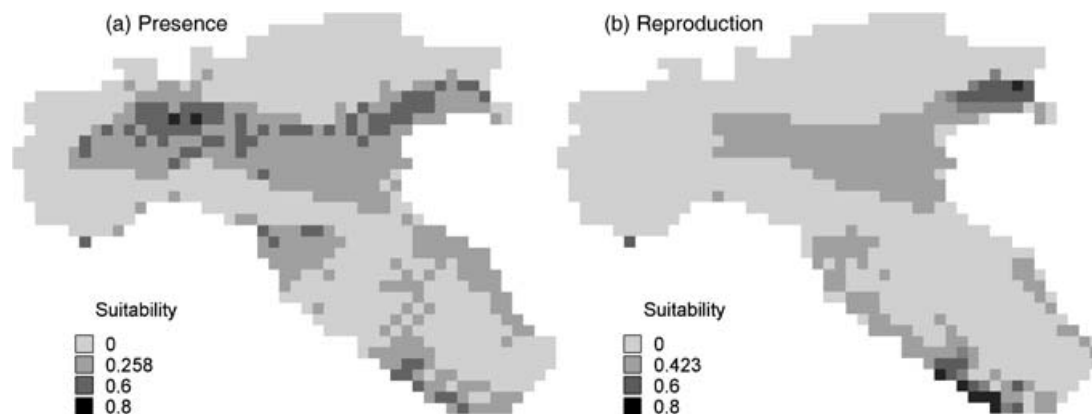


Figure 3 Results of environmental suitability models: predicted probability of (a) presence and (b) reproduction of *Trachemys scripta*. The different suitability thresholds (0.258 and 0.423) correspond to the 10th percentile training presence thresholds of the presence and reproduction models, respectively.

portion of variance. The reproduction of slider turtles was related to areas with high summer temperature, solar radiation and annual precipitation (Fig. 2). The AUC of this model was 0.868, and was significantly higher than the AUC of null-model (median = 0.725, 95% CI = 0.640–0.803). This indicates a good fit of the model. The jackknife procedure showed that the model had a good capacity to predict new localities of reproduction (predictive success = 0.75, average probability of success under randomness = 0.32, $P = 0.0005$).

The areas most suitable for reproduction did not correspond exactly to the areas where the probability of presence of feral populations is highest (Fig. 3). Probability of reproduction was highest in the Mediterranean and coastline areas. Using the 10th percentile training presence threshold, 42% of the study area was

suitable for the presence of slider turtles, while only 27% was suitable for reproduction (Fig. 3).

The comparison of response curves confirmed the differences between the bioclimatic niches obtained using presence and reproduction data (Fig. 2). Slider turtle reproduction showed a more positive relationship with solar radiation, summer and winter temperature than slider turtle presence.

Future suitability

The projection of suitability for reproduction using the bioclimatic features of the 2020 scenarios showed a clear increase of suitable areas (Fig. 4, see Appendix S1 in Supporting Information). Despite minor differences among the four 2020 scenarios (Fig. 4,

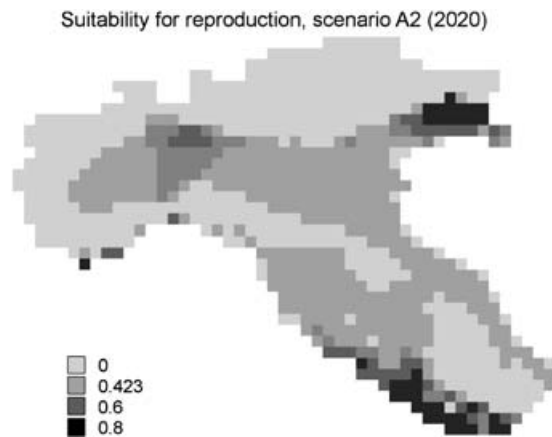


Figure 4 Projected suitability for reproducing populations of *Trachemys scripta* under future climatic conditions (2020, scenario A2). Results of projections using different scenarios (A1, B1 and B2) are extremely similar and are shown in Appendix S1.

Appendix S1), all of them predicted an expansion of suitable areas far from the coastline, in the Northern regions and in most of areas where feral populations are currently present (compare with Fig. 1). For example, following the A2 scenario, 87% of the 121 pixels where feral populations are currently present will be suitable for reproduction in 2020.

DISCUSSION

Under present-day environmental conditions, the bioclimatic envelope entailed by the presence of feral populations of slider turtle is markedly different from the envelope of populations where reproduction actually occurs. This indicates that most of the feral populations are introduced and survive in suboptimal environment, where bioclimatic conditions currently are not suitable for reproduction. However, lack of reproduction in many feral populations (Luiselli *et al.*, 1997; Bringsøe, 2001; Prévot-Julliard *et al.*, 2007) does not mean that the slider turtle will quickly become extinct before establishment. These long-lived species can persist for decades and thus influence the native species even in absence of actual reproduction. Our analysis clearly shows that the environmental features required for reproduction are currently present in several areas of Mediterranean Europe (Fig. 3), and that ongoing climate change will likely expand the areas of suitability in the near future (Fig. 4, Appendix S1).

The distribution of reproductive populations delineates a bioclimatic envelope corresponding to areas with high summer temperature, intense solar radiation and rather high annual precipitation (Fig. 2). The identification of a clear envelope, distinct from the one of non-reproductive populations, shows that reproduction does not occur in a random subset of presence localities, but is instead related to well-defined environmental parameters. The association with high temperature and solar radiation likely describes physiological limitations and the large amount of thermal energy required for embryo development.

For example, the optimum temperature for slider activity is 25–26 °C, and the optimum temperature for embryo development is above 25 °C (Cagle, 1950; Morreale & Gibbons, 1986; Cadi *et al.*, 2004). Our model describes very well these requirements, and maximum suitability for both presence and reproduction was at about 26 °C (Fig. 2b). Moreover, embryos require a wet substrate for correct development (Tucker & Paukstis, 2000). Therefore, the most arid Mediterranean areas are not suitable for reproduction, which explains the positive relationship with annual precipitation. High precipitation can be also associated to the presence of wetlands, with obvious positive effects on populations of a freshwater turtle. Precipitation, temperature and solar radiation are key drivers of the energy/water balance in ectotherms, and can therefore be important also for other invaders (e.g. reptiles, amphibians and crustaceans).

Human footprint was only positively correlated to species presence but not to species reproduction. This is intuitive, as species introduction into the environment occurs through pet release or escape and pets are most likely to be kept in human-modified areas, but human modifications of landscape do not have a positive effect on turtle reproduction.

The smallest predicted range for reproduction (compare Fig. 3a,b) suggests that adult sliders can survive under a wide range of environmental conditions, but they have more stringent requirements for critical phases of life history, such as reproduction. The AUC of models of reproductive populations (0.868) was higher than the AUC of localities of presence (0.828). This further confirms that reproductive populations have a small but well-defined niche, because distribution models of generalist species often have lower AUC (Brotons *et al.*, 2004; Allouche *et al.*, 2006). Species distribution models usually rely on occurrence data, without any knowledge of the actual fitness of the population in those areas. However, a more complete modelling of ecological niche should define the environmental conditions where the fitness of individuals is greater than one (Guisan & Thuiller, 2005; Kearney, 2006). Simply considering distribution records does not allow full delineation of a species fundamental niche (Kearney, 2006), and can predict suitability into too large areas. Moreover, the projection of bioclimatic models in the future, or into new geographical areas, is a critical phase of the application of bioclimatic models to conservation (Guisan & Thuiller, 2005). The differences between the suitability obtained using presence records, and the one obtained using fitness measures could be amplified when bioclimatic niches are projected to new conditions.

For these reasons, using fitness measures when available instead of occurrence data can lead to great improvement in the quality of species distribution models. The improvement can be particularly valuable for alien species, for species with high vagility that are often observed in suboptimal environments, and for species with strong source-sink dynamics. The availability of modelling techniques having good performance even with a few presence localities, such as Maxent (Hernandez *et al.*, 2006), can be particularly useful, because collecting data on species presence/absence is clearly more cost-effective than comparing fitness among localities.

From introduction to establishment: conservation implications

Only a subset of feral populations is currently breeding, and their reproductive success is probably not very high. Nevertheless, the small number of localities where reproduction has been ascertained should not be used to underestimate the risk of establishment of slider turtle populations. First, detecting reproduction of freshwater turtles can be difficult, because juveniles are less detectable than adults (Zuffi, 2000) and small turtles are still released in natural wetlands by unconcerned people. The actual number of reproductive populations is probably larger than that reported here (see also Cadi *et al.*, 2004). Second, some peculiar features of introduced sliders may increase their recruitment potential. Turtles sold as pets are reared in farms with artificially high temperature, to accelerate the development rate. As sex determination in the slider is temperature dependent, the sex ratio of introduced turtles is unbalanced, with a prevalence of females (Cadi *et al.*, 2004). If environmental conditions are suitable, this high proportion of females may increase the number of recruits of introduced populations (see Girondot *et al.*, 1998).

Most importantly, ongoing global climate change will probably boost the fitness of introduced individuals in the near future. Long lived animals can survive decades in suboptimal habitats. As the longevity of sliders in nature is at least 30 years (Gibbons & Semlitsch, 1982), the individuals that are released now can survive for 20 years or so in suboptimal areas, where bioclimatic features are currently unsuitable for reproduction. These feral individuals may successfully reproduce during particularly warm years, or in the near future, when suitability will increase (compare Figs 1 and 4 and the Appendix S1). The successful reproduction of these populations corresponds to the transition from introduced individuals to established alien populations. In many cases, alien species became invasive and problematic after lag phases that may last decades, and then suddenly explode (Crooks & Soulé, 1999). Climate change can be a key factor triggering this process.

This is therefore a case where species distribution models have direct and practical implications for the management. Immediate management actions (such as the eradication of feral individuals) have high probability of success. Currently, many non-native populations of the slider are non-reproductive. These feral sliders can have negative effects on native biodiversity (Cadi & Joly, 2003, 2004; Teillac-Deschamps & Prevot-Julliard, 2006), but their eradication can be successful even with moderate effort, since current recruitment is zero, and trapping techniques have a high success rate on adult freshwater turtles (Fowler & Avery, 1994). However, if the species becomes naturalized, eradication will be much more difficult and costly. Management efforts should first focus on the areas where suitability for reproduction is highest (Fig. 3b), because these areas are sources of biological invasion. It is also important to act promptly, to remove individuals from areas where suitability is predicted to increase in the near future. Of course, these management actions will be successful only if education programs will help

stopping the release of new turtles in natural environments (Ficetola *et al.*, 2007a).

It is widely accepted that the ongoing global climate change can exacerbate the issues of biological invasions, but we are far from a full understanding of the mechanisms facilitating the response of AIS to the change (Thuiller *et al.*, 2007; Richardson & Pysek, 2008). Differences in fitness among areas of the introduced ranges can strongly interact with climatic change, complicating the invasion dynamics, and should be considered in models trying to predict the future of invasions.

ACKNOWLEDGEMENTS

We thank all field herpetologists providing unpublished observations, particularly A. Romano, L. Lapini and U. Fusini. G. F. Ficetola was founded by a grant of EVK2-CNR on biodiversity conservation. W. Thuiller was partly funded by the EU FP6 MACIS specific targeted project (Minimization of and adaptation to climate change: impacts on biodiversity no. 044399) and EU FP6 ECOCHANGE integrated project (Challenges in assessing and forecasting biodiversity and ecosystem changes in Europe). The comments of M. Burgman, J. Ott and two anonymous reviewers improved an earlier version of the manuscript.

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Editor: Mark Burgman

SUPPORTING INFORMATION

The following Supporting Information is available for this article:

Appendix S1 Projected suitability for reproducing populations of *Trachemys scripta* under future climatic conditions (2020, scenarios A1, B1, B2).

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