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Risk of invasion by frequently traded freshwater turtles

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Abstract Risk assessment allows the identification of non-native species most likely to become invasive and cause harm, and helps to set up preventive measures such as trade regulations. Freshwater turtles are among the most traded pets; an increasing number of species are easily available and frequently released by owners in natural wetlands. This study identified a pool of freshwater turtles frequently traded at cheap prices, and performed risk assessment at multiple steps of the invasion process. Establishment risk was assessed through species distribution models (MaxEnt and Boosted Regression Trees) based on global presence records and bioclimatic variables. We also analyzed ecological and life history traits favouring release, establishment and population growth. Besides the already invasive *Trachemys scripta*, at least 14 species are easily found in the pet market. For most of them, species distribution models identified areas with suitable climate outside the native range. Validation with independent data confirmed the reliability of the modelling approach. *Pelodiscus sinensis* and *Pelomedusa subrufa* had the broadest areas of suitable climate outside the native range. For all the species, possibility of coexistence with humans and reproductive traits suggest high risk of invasion, if introduced in areas with suitable climate. The availability of spatially explicit maps of risk allows to identify areas where preventive measures are urgently needed. In Europe, an expansion of trade regulations is needed to avoid that multiple freshwater turtles become invasive.

Keywords Body size · Ecological niche models · Fecundity · Human footprint · Invasive alien species · Risk assessment · Pet trade · Reptiles

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Introduction

Introduction of non-native species can occur through multiple pathways, and can be intentional or unintentional. However, non-native vertebrates are most frequently introduced intentionally, and especially through the pet trade. The pet trade is particularly important for amphibians and reptiles, as the majority of non-native species of herps are introduced through the pet trade; these animals can arrive into natural environments by escaping or (more frequently) because they are released by owners (Kraus 2009; van Wilgen et al. 2010).

Preventive measures, hampering the introduction of species that can establish invasive populations, are the

most effective approach to avoid biological invasions (Hulme 2006; Keller et al. 2007; Simberloff et al. 2011; see also the COP 6 Decision VI/23 of the Convention on Biological Diversity). The complete ban of trade of non-native reptiles is not a practicable option, because of the large economic income of the pet trade industry (Hulme 2009), but trade regulations can be effective, by limiting the trade to the species that are less likely to determine biological invasions. This approach would require the screening of currently traded species, and the identification of species for which the invasion risk and potential impact are highest (risk assessment). Such information is much required by authorities setting up animal trade regulations, but is not available for a large number of traded species.

Risk assessment can be performed using both qualitative (e.g., questionnaires) and quantitative approaches (e.g., probabilistic models). Both approaches have advantages, but quantitative or semi-quantitative risk assessments may allow a more objective quantification of the severity and of the uncertainty of the risk, and a better resolution (Leung et al. 2012). In principle, risk assessment should take into account the multiple steps of the invasion process: transport and release, establishment, increase of local density, spread and impact. However, most analyses performing quantitative risk assessment used mostly species distribution models (SDM) to assess the risk of establishment. The integration of SDM with other parameters affecting risk, such as propagule pressure and species traits, can be very useful to improve quantitative risk assessment (Leung et al. 2012).

Freshwater turtles are among the most traded reptiles. Until the 1990s, the trade of freshwater turtles focused mostly on the American red eared slider *Trachemys scripta elegans*. In the period 1989–1997, more than 52 million red eared sliders were exported from the US: this single subspecies represented 97 % of the whole US export of turtles (Telecky 2001). However, the European Union interrupted the import of *T. s. elegans* in 1997 (EU Regulation 338/1997; EU Regulation 349/2003) due to the high risk of biological invasion. As a consequence, turtle trade shifted to other subspecies of *T. scripta* (*T. s. scripta* and *T. s. troosti*), but also to a large number of other species of freshwater turtles (Ficetola et al. 2012; hereafter: *recently traded species*). Although risk assessment has provided key policy information, only limited analyses have evaluated the risk of invasion by these recently traded turtle species to date (but see Van Wilgen and Richardson 2012). Quantitative risk assessment usually requires the comparison of a large number of species. Statistical models are used to assess whether species having certain traits pose higher risk at a given step of the invasion process (Keller et al. 2011). Species traits associated with risk are then identified, and invasion risk may be projected to additional species within the same taxonomic group (Keller et al. 2011). However, this fully quantitative approach may be difficult to apply to freshwater turtles because, at the moment, only one species is considered as globally invasive (i.e., the most traded species, *T. scripta*).

In this study, we performed risk assessment for a number of recently traded species of freshwater turtles. Our assessment considered three major steps of biological invasions; for each step, we identified species trait that may affect risk. Additional references on the specific traits considered are provided in the methods section.

1. *Transport and release* We considered freshwater turtle species that are widely traded in Europe as pets; because species that are rare or very expensive are rarely released by owners (van Wilgen et al. 2010), we included only those that are commonly found in the pet market at cheap prices. This preliminary step identified the initial pool of candidate species for which a high propagule pressure is likely; we then applied the subsequent steps of assessment on this initial pool of species. In addition, we considered adult body size as a further parameter that can influence release, as large turtles are more often released (Teillac-Deschamps et al. 2009).
2. *Establishment* Climatic suitability is a major determinant of establishment success. We therefore used SDM to assess the climatic suitability for all the considered turtles at the global scale. We also used data from one species that already established non-native populations (*Pelodiscus sinensis*) to confirm the predictive ability of our approach. Additionally, we considered the ability of species to coexist with humans, as this may increase establishment success (Ficetola et al. 2007).
3. *Population growth and abundance* Freshwater turtles are long lived and are often massively released, therefore they may have very high

densities even in absence of quick demographic growth (Ficetola et al. 2012; Leung et al. 2012). Nevertheless, reproductive output and age at sexual maturity are key determinants of the growth of non-native populations, and may strongly influence their invasiveness. In our risk assessment, the life history features of recently traded species were then compared with those of *T. scripta*, which is the only freshwater turtle currently considered invasive at the global scale (Kraus 2009).

Furthermore, Van Wilgen and Richardson (2012) recently developed a tool for risk assessment of amphibians and reptiles, and we used the results of our analyses to perform an additional risk assessment accordingly to their approach.

Methods

Selection of candidate species

The number of freshwater turtles traded is extremely high, but many species are present in extremely low numbers and sold in dedicated fairs only. We therefore considered retail price of the animals as a proxy of propagule pressure (van Wilgen et al. 2010). Freshwater turtles are mostly traded as hatchlings or juveniles (below 6 months of age). We considered as candidate species those with a retail price of juveniles ≤30 €. We obtained price lists for turtle hatchlings from the two largest exotic and pet animals wholesalers in Northern Italy: *Zoovarese* (Lombardy-based wholesaler) and *NaturaViva* (Veneto-based wholesaler). We also performed surveys of the online market in other European countries (see Kikillus et al. 2012 for a similar approach), which provided essentially the same list of species.

In our analysis we did not include two species that are very often traded: the slider turtle *T. scripta* and the snapping turtle *Chelydra serpentina*. These species are not analyzed because they are already recognised as being highly invasive, previous studies assessed their invasion risk and the threats to biodiversity, and some regulations are being set up (Kobayashi et al. 2006; Ficetola et al. 2009; Rödder et al. 2009; Kikillus et al. 2010; Ficetola et al. 2012). Furthermore, for *C. serpentina*, some countries (e.g., Italy, Germany) are already setting up trade ban because of the dangerousness of this large turtle. We remark that the invasion risk by *T. scripta* and *C. serpentina* should not be overlooked, and both these species should be considered in comprehensive regulations of turtle trade (see Ficetola et al. 2012).

In our study, *T. scripta* was used as an invasion benchmark/threshold to which the several traits (morphology, life history and ecological features; listed below) were compared.

Climatic suitability

We obtained occurrence data of each species from the Global Biodiversity Information Facility data portal (www.gbif.org) and from EMYSystem Global Turtle Database, which contains distribution records for most of turtle species of the world (Iverson et al. 2003). We considered only records within the native range of species; records outside the native range were considered only if the species is successfully established in a territory (following Kraus 2009). We excluded the GBIF data with spatial error of 10 arc-primes or more (Boitani et al. 2011), and multiple records within the same cell of 10 × 10 arc primes (i.e., 0.167°). Overall, we obtained between 32 and 532 records per species (Table 1).

As environmental predictors, we considered six bioclimatic variables that are expected to affect physiological tolerance, metabolism and thermoregulation of turtles, as well as water availability and productivity in ecosystems where they live. Variables were: minimum temperature of the coldest month, maximum temperature of the warmest month, summed precipitation in the driest season, summed precipitation in the wettest season (from Worldclim; Hijmans et al. 2005), annual solar radiation (Wh/m^2/day; New et al. 2002) and Normalized Difference Vegetation Index, a measure of primary productivity (Gutman et al. 1997). All variables were at the resolution of 10 × 10 arc primes.

We applied two widely used approaches to build SDM: maximum entropy modelling (MaxEnt; Elith et al. 2011) and boosted regression trees (BRT; Elith et al. 2008). Both approaches assess the suitability in a given cell on the basis of environmental features in that cell, and are considered among the most efficient approaches to SDM using presence-only data

Table 1 Distribution data available, and results of species distribution models

Species	*N*	AUC		*P*
		MaxEnt	BRT	
Apalone ferox[a]	95	0.983 ± 0.004	0.990 ± 0.010	<0.001
Apalone spinifera[a]	532	0.755 ± 0.023	0.845 ± 0.019	<0.001
Graptemys kohnii	220	0.899 ± 0.018	0.926 ± 0.023	<0.001
Pseudemys concinna[a]	181	0.893 ± 0.016	0.906 ± 0.032	<0.001
Pseudemys floridana[a]	96	0.977 ± 0.007	0.978 ± 0.018	<0.001
Pseudemys nelsoni	51	0.990 ± 0.001	0.993 ± 0.015	<0.001
Kinosternon baurii[a]	126	0.976 ± 0.005	0.984 ± 0.013	<0.001
Kinosternon subrubrum[a]	429	0.919 ± 0.008	0.961 ± 0.012	<0.001
Sternotherus carinatus	67	0.968 ± 0.001	0.969 ± 0.028	<0.001
Sternotherus odoratus[a]	248	0.861 ± 0.014	0.894 ± 0.026	<0.001
Pelomedusa subrufa[a]	316	0.769 ± 0.026	0.800 ± 0.030	<0.001
Pelodiscus sinensis[a]	167	0.902 ± 0.005	0.897 ± 0.032	<0.001
Mauremys reevesii[a]	76	0.907 ± 0.025	0.902 ± 0.049	<0.001
Mauremys sinensis	32	0.930 ± 0.072	0.932 ± 0.115	<0.001

AUC, area under the curve of the receiver-operator plot; values are ±SD; *P*, significance of prediction of presence in test data, calculated using a binomial test; *N*, number of records per species; BRT, boosted regression trees

[a] In the MaxEnt models, a regularization multiplier of 2.5 was used instead than the default value (Elith et al. 2010)

(Elith et al. 2006). MaxEnt models were ran using linear, quadratic and hinge features. We divided the dataset of each species in five groups, and ran the model five times. Each time we removed one group from the data (test data), we ran the model using the remaining data (training data), and tested model performance over the test data. For some species using the default regularization parameters in MaxEnt led to some degree of overfitting, as revealed by the presence of locally complex fit in the partial dependence plots (Elith et al. 2010). In these cases, we used a regularization multiplier of 2.5 (Table 1; Elith et al. 2010). BRT were built with a maximum of 3,000 trees, sampling the pseudo-absences in the same number than the collected presences. As no independent data exist for the evaluation (except for *P. sinensis*), models were built using 70 % of the data (selected with a random procedure) and tested on the remaining 30 % (Thuiller et al. 2009). This procedure was repeated 100 times for each species. MaxEnt models were ran using MaxEnt 3.3 (Phillips et al. 2006; Elith et al. 2011); BRT were ran using the BIOMOD package (Thuiller et al. 2009) in R 2.14.2 (R Development Core Team 2012).

All models were then projected at the global scale. Model predictions were converted to binary maps of predicted presence/absence using, for each model, the threshold that maximizes both sensitivity and specificity of prediction over the validation data. We then used committee averaging to estimate the global niche of the study species. Committee averaging is an ensemble forecasting method allowing the combination of results of different model algorithms (Gallien et al. 2012). Different algorithms can have different accuracy under different circumstances (Elith et al. 2006). In the committee averaging method the binary maps (or "voting maps"), coming from both MaxEnt and BRT methods, are averaged to obtain one single map of the final output (Gallien et al. 2012). The outcome of committee averaging is not a probability but rather a percentage of agreement on species presence between algorithms. For MaxEnt we built five cross-validated models (as this cross validation allows a good estimate of predictive performance; Nogués-Bravo 2009), while for BRT we built 100 replicated models [following suggestions in Barbet-Massin et al. (2012) for this method], therefore the number of potential BRT voting maps was 20 times larger than the number of MaxEnt voting maps. To ensure equal representation of the two methods, for each cell committee averaging was calculated as [*N* BRT voting maps + 20 × MaxEnt voting maps]/200 (Gallien et al. 2012).

We used two metrics of model performance. First, for each individual model we calculated the area under the curve (AUC) of the receiver-operator plot using test data. Furthermore, we used a binomial test to assess whether models can predict presence in cells with test data better than expected by chance.

In SDM, extrapolations beyond the training range may determine less reliable results. We therefore computed multidimensional environmental similarity surfaces, to identify areas where SDM extrapolated onto bioclimatic conditions that are outside those present within the training range (Elith et al. 2010; Measey et al. 2012).

The use of independent data is the most robust approach to assess the predictions of SDM. To confirm that our approach, based mostly on data from the native range, can actually predict the areas most at risk of invasion, we built SDM with native range data, we projected the model at the global scale, and assessed the suitability of localities with non-native populations. We then used a χ^2 test (1 *df*) to compare observed frequencies of correct and incorrect predictions of non-native populations, and therefore to evaluate if SDM can correctly predict distribution of invasive populations (Roura-Pascual et al. 2004). We assumed correct prediction if non-native records were present in areas with suitability >0.5. These data were available for only one species (*P. sinensis*), as most of study species have a short history of trade and introductions, therefore the evidence of established populations is limited (Kraus 2009). However, as the same SDM methods were used for all the species, the validation of *P. sinensis* predictions may provide a measure of the appropriateness of our overall approach to climate suitability modelling. Non-native records exist also for other species (see "Results"), but the low number of records hindered model validation.

Body size

Body size may affect both the release and the impact of alien turtles. Turtles are usually sold at a size of just a few centimetres, but can grow quickly, and adults are often released by owners because their adult size is not compatible with indoor aquaria and their domestic management becomes burdensome (Teillac-Deschamps et al. 2009). Therefore, species that can reach the largest size are also more likely to be released by owners. Large turtles may also have strong impact on ecosystems, because of their capability to capture larger preys or to outcompete smaller species of native turtles (Kolar and Lodge 2001; Ficetola et al. 2012). For each species, we obtained data on female adult body size from Bonin et al. (2006). For the majority of freshwater turtles, females are the larger sex (see Ceballos et al. 2013).

Coexistence with humans and invasion history

Releases often occur in sites nearby human settlements, therefore species that can coexist with humans can be favoured at the early stages of invasions. We used the human footprint dataset (Sanderson et al. 2002) to evaluate this issue. The human footprint is an index of human influence on global surface, combining data of population density, land transformation, human access, and presence of infrastructures; it ranges from 0 (no human influence) to 100 (maximum human influence; Sanderson et al. 2002). We extracted the human footprint values (resolution: 10 arc primes) for the localities with presence of each species. For *T. scripta*, we used GBIF and EMYSystem data, and we also considered the records by Kikillus et al. (2010). To assess whether turtle populations coexist with humans, we measured (1) the maximum human footprint of occupied cells; (2) the percentage of presence localities with human footprint ≥50 (i.e., the percentage of localities within human dominated landscapes). We also assessed invasion history (i.e., whether each species has already established non-native populations) on the basis of Kraus (2009).

Breeding parameters: fecundity and age at maturity

We considered two measures of fecundity: number of eggs per clutch (range), and number of clutches per year. We did not calculated annual fecundity as the product of *N* eggs per clutch × *N* clutches because, in species with multiple clutches, the first clutch often includes more eggs than the clutches laid later in years. Fecundity data for each species were obtained from the available literature (Mitchell 1985; Frazer et al. 1991; Ernst et al. 1994; Iverson and Moler 1997; Chen and Lue 1998; Wilson et al. 1999; Iverson 2002; Aresco 2004; Bonin et al. 2006; Boycott and Bourquin 2008; Ward and Jackson 2008; Lovich et al. 2011). Data on age at sexual maturity were retrieved from published databases (Ernst et al. 1998; de Magalhaes and Costa 2009; Van Wilgen and Richardson 2012) and from the literature (Avanzi and Millefanti 2003; Jackson 2008; Lindeman 2008; Lovich et al. 2011). We did not find information on age at maturity in *Pelomedusa subrufa*.

For scoring we assumed an age at maturity of 4 years, which is the median of all the considered species.

Assessment of invasion risk

We assessed invasion risk in two ways. First, we compared the species traits with those of *T. scripta*. All the candidate species are heavily traded, and the propagule pressure is potentially high. Therefore, species with more extreme traits, compared with *T. scripta*, are expected to show high invasiveness in areas where SDM indicate high suitability.

Furthermore, we applied the quantitative risk assessment of Van Wilgen and Richardson (2012) to the pool of candidate species. This approach combines information on life history (fecundity, age at maturity), habitat suitability (obtained from SDM) and phylogeny to derive estimates of invasion risk, ranging from very low to extreme. Invasion risk may be affected by the presence of related species in the recipient communities (Van Wilgen and Richardson 2012). We considered recipient communities hosting native turtles of the Emydinae subfamily (like wide areas of Europe), and communities hosting native turtles of both the subfamily Emydinae and of the family Geoemydidae (like the Iberian Peninsula, the south of the Balkan Peninsula and Turkey). We assumed introductions in areas with suitable climate (suitability $\geq$0.5 as assessed with SDM), and three potential rates of release into natural environments: 0.5, 1 and 2 events/year.

Results

Besides the already invasive *T. scripta* (which remains the most available species), we identified at least 14 species that are often found in the pet market at cheap prices (Table 2). These species accounted for nearly 70 % of freshwater turtles commonly traded by the surveyed stockists; the price of their juveniles was 10–30 €. Ten species were native of North America (*Apalone ferox*, *Apalone spinifera*, *Graptemys kohnii*, *Pseudemys concinna*, *Pseudemys floridana*, *Pseudemys nelsoni*, *Kinosternon baurii*, *Kinosternon subrubrum*, *Sternotherus carinatus*, *Sternotherus odoratus*), one was native of sub-Saharan Africa (*Pelomedusa subrufa*) and three were native of China and Eastern Asia (*Pelodiscus sinensis*, *Mauremys reevesii* and *Mauremys sinensis*).

Reliability of climatic suitability

For *P. sinensis*, we obtained records of likely naturalized populations from 13 cells in seven territories [Spain, Hawaii, Guam, Singapore, Thailand, Cambodia, southern Vietnam (outside the native range in Vietnam)]. Our model, built using native records only, correctly predicted suitability in all these cells. In all the naturalized cells, suitability was $\geq$0.51 (range 0.51–1; expected percentage of correct prediction: 35 %; observed correct prediction: 100 %; $\chi^2_1 = 23.6$, $P < 0.0001$). This supports the reliability of models built for the other species, which were based on native records only.

Models of climatic suitability

For the majority of species, SDM provided very good or excellent models (test AUC > 0.8) and, for all species, models predicted test points significantly better than expected by chance (Table 1), indicating a good predictive performance. Model performance was less good for *A. spinifera* and *P. subrufa* (AUC values between 0.7 and 0.8), still also for these species validation points were predicted better than expected by chance, and the AUC values indicates useful performance (Table 1).

For most of species, the models identified areas outside the native range with high climatic suitability (Fig. 1). *P. sinensis* and *P. subrufa* showed large suitable areas outside the native range in tropical, subtropical and temperate regions at the global scale. For *M. sinensis* suitable areas outside the native range were mostly in tropical regions, while for the majority of the other species there were suitable areas outside the native range particularly in subtropical and temperate regions (Fig. 1). The complete raster maps of predicted suitability are available upon request from the authors.

At the European level, suitability was high or very high over wide areas for at least five species (*A. spinifera*, *K. baurii*, *S. odoratus*, *P. subrufa* and *P. sinensis*; Table 2; Fig. 1, Fig. S1 in supplementary material). Furthermore, *P. floridana* showed areas with high suitability over >10 % of Portugal, and in some additional coastal areas of Europe (Fig. S1).

Table 2 Ecological features of traded species of turtle, and comparison with the invasive *T. scripta*

Species	Family	Human footprint		Body size (mm)	Invasion history	Fecundity[c]	Clutches/ year	Maturity (months)	Climate match in Europe
		Max[a]	% >50[b]						
A. ferox	Trion.	**93**	20	**600**		**9–38**	**Up to 6**	108	
A. spinifera	Trion.	**94**	11	**550**		**6–39**	2	**48**	**High[d]**
G. kohnii	Emyd.	**88**	9	250		2–8	2–3	84	
P. concinna	Emyd.	**94**	19	**430**		**7–24**	Up to 4 or more	**42**	
P. floridana	Emyd.	76	13	**400**		**4–23**	**6**	57	Medium[e]
P. nelsoni	Emyd.	**81**	15	**380**	Y	**8–30**	3–4	**36**	
K. baurii	Kinos.	**94**	16	120		1–6	3	**24**	**High[d]**
K. subrubrum	Kinos.	**88**	13	125		1–6	1–3	**48**	
S. carinatus	Kinos.	61	10	160		1–7	4	**48**	
S. odoratus	Kinos.	**88**	15	136		1–7	2	**48**	**High[d]**
P. subrufa	Pelom.	**100**	7	200		**10–42**	1	NA	**High[d]**
Pelodiscus sinesis	Trion.	**80**	**32**	**300**	Y	**10–35**	2–5	**48**	**High[d]**
M. reevesii	Geoe.	**79**	4	235	Y	4–9	3	72	
M. sinensis	Geoe.	**80**	**42**	240		**7–17**	1	60	
T. scripta	Emyd.	77	24	280	Y	2–15	Up to 5	48	High

In bold, features with scores equal or higher than those of *T. scripta*

NA data not available

Trion Trionychidae, *Emyd* Emydidae, *Kinos* Kinosternidae, *Pelom* Pelomedusidae, *Geoe* Geoemydidae

[a] Maximum human footprint of cells with presence of the species within the native range

[b] Percentage of cells within the native range with human footprint >50

[c] *N* eggs per clutch

[d] Climate match >0.5 in at least 10 % of at least two EU countries

[e] Climate match >0.5 in at least 10 % of one EU country

Ability to live in disturbed areas and invasion history

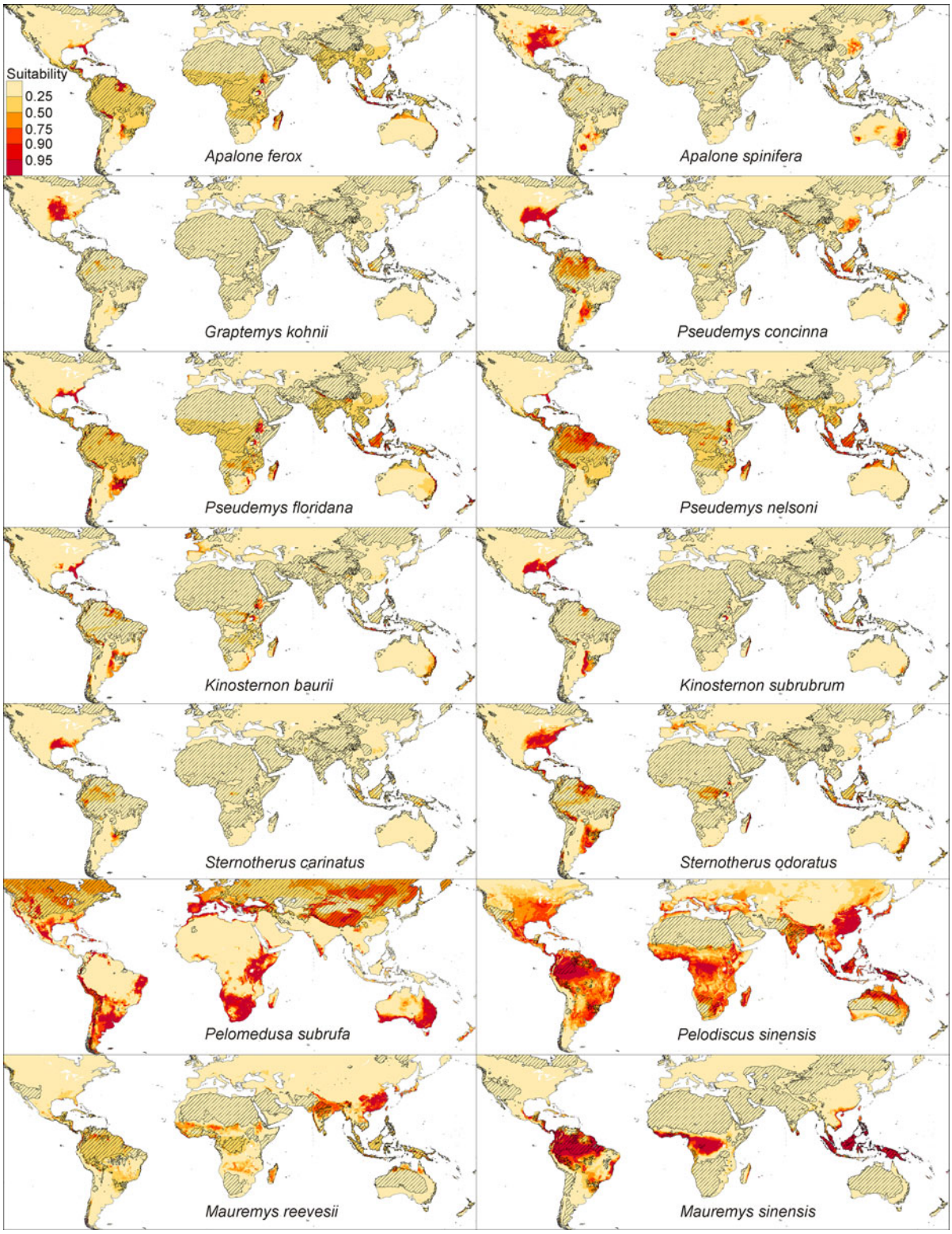
For all the species considered, ≥7 % of presence localities were in human dominated areas (human footprint ≥50 %; Table 2). The species with the highest frequency of populations in human dominated areas were *M. sinensis*, *M. reevesii*, and *P. sinensis*. Populations of some species (e.g., *A. ferox*, *A. spinifera*, *K. baurii*, *P. subrufa*, *P. concinna*) were also found in areas with extreme human footprint. At least three species (*M. reevesii*, *P. sinensis* and *P. nelsoni*) have already established non-native populations.

Breeding parameters

The largest clutch size was observed in the large Trionychidae (*A. ferox*, *A. spinifera* and *P. sinensis*) and in *P. subrufa* (Table 2). Most of species are able to lay multiple clutches per year, with a maximum of six clutches in *A. ferox* and *P. floridana* (Table 2). Differences in maturity among species were limited. For the majority of species, sexual maturity is attained at 4 years or later (Table 2).

Risk assessment according to Van Wilgen and Richardson (2012)

According to the Van Wilgen and Richardson (2012) procedure, all the candidate species have a high or extreme risk of invasion, if two or more introductions per year are performed into areas with suitable climate (Table 3). Several species (*K. baurii*, *P. sinensis*, *P. subrufa*, *S. carinatus* and *S. odoratus*) might have a high invasion risk in regions with suitable climate even if the rate of introduction is low (Table 3). Out of


Suitability
0.25
0.50
0.75
0.90
0.95
Apalone ferox
Apalone spinifera
Graptemys kohnii
Pseudemys concinna
Pseudemys floridana
Pseudemys nelsoni
Kinosternon baurii
Kinosternon subrubrum
Sternotherus carinatus
Sternotherus odoratus
Pelomedusa subrufa
Pelodiscus sinensis
Mauremys reevesii
Mauremys sinensis

◀ **Fig. 1** Predicted global suitability for 14 species of frequently traded freshwater turtles. *Maps* represent the committee averaging of BRT and MaxEnt models (proportion of models indicating suitability in a given cell). Areas with bioclimatic conditions exceeding those in the training areas and requiring model extrapolation (MESS) are indicated by *diagonal fill*

these species, *K. baurii*, *P. sinensis*, *P. subrufa* and *S. odoratus* are identified as posing a high risk in Europe due to climate matching, coexistence with humans, high fecundity and human tolerance (Table 2; Fig. 2).

Discussion

An increasing number of species of freshwater turtles are available in pet market, constituting a pool of species that may be released in freshwater environments. We have detected at least 14 turtles that are easily available at cheap prices (Table 1). The set of species considered does not purport to be complete, as the number of turtle species traded is increasing, and the identity of species can change in response to supply and demand. Many more turtles can be available in the pet market [see e.g., Arena et al. (2012) for European data]; here we considered those that are more frequently traded at the lowest prices, as cheap species have the highest risk of being released, i.e., the highest potential propagule pressure (van Wilgen et al. 2010; see also Kikillus et al. 2012). This analysis allows the first broad screening of traded turtles, identifying a number of species that may have a high invasion risk in the near future. Similar approaches can be applied to the other species that are available in pet market. Our study has a special focus on Europe, which is one of the continents receiving the largest number of reptile introductions (Kraus 2009), but our results can be used to assess invasion risk in any territory in which these species are traded, as we provide global maps of climatic suitability (Fig. 1).

Risk assessment: climatic suitability

Lack of suitability in SDM does not ensure that a species will never establish in areas where it is heavily introduced, because species might be able to exploit environmental conditions that are not available in the native ranges, and evolutionary processes sometimes

Table 3 Invasion risk according to Van Wilgen and Richardson (2012)

Species	Presence of Emydinae			Presence of Emydinae *and* Geoemydidae		
	Introductions/year			Introductions/year		
	0.5	1	2	0.5	1	2
A. ferox	3.9 (M)	5.7 (H)	6.9 (E)	3.9 (M)	5.7 (H)	6.9 (E)
A. spinifera	3.9 (M)	5.7 (H)	6.9 (E)	3.9 (M)	5.7 (H)	6.9 (E)
G. kohnii	2.7 (M)	4.5 (H)	5.7 (E)	3.6 (M)	4.8 (H)	6.0 (E)
P. concinna	3.6 (M)	5.4 (H)	6.6 (E)	3.6 (M)	5.4 (H)	6.6 (E)
P. floridana	3.4 (M)	5.2 (H)	6.4 (E)	3.4 (M)	5.2 (H)	6.4 (E)
P. nelsoni	3.8 (M)	5.6 (H)	6.8 (E)	3.8 (M)	5.6 (H)	6.8 (E)
K. baurii	5.2 (H)	7.0 (E)	8.2 (E)	5.2 (H)	7.0 (E)	8.2 (E)
K. subrubrum	4.5 (H)	6.3 (E)	7.5 (E)	4.5 (H)	6.3 (E)	7.5 (E)
S. carinatus	4.7 (H)	6.5 (E)	7.7 (E)	4.7 (H)	6.5 (E)	7.7 (E)
S. odoratus	4.3 (H)	6.1 (E)	7.3 (E)	4.3 (H)	6.1 (E)	7.3 (E)
P. subrufa	4.3 (H)	6.1 (E)	7.3 (E)	4.3 (H)	6.1 (E)	7.3 (E)
Pelodiscus sinesis	4.8 (H)	6.6 (E)	7.8 (E)	4.8 (H)	6.6 (E)	7.8 (E)
M. reevesii	3.5 (M)	5.4 (H)	6.6 (E)	2.5 (L)	4.3 (H)	5.5 (H)
M. sinensis	3.4 (M)	5.2 (H)	6.4 (E)	2.3 (L)	4.1 (H)	5.3 (H)

For each species, we considered climatic suitability = 0.50, a range of introductions per year, and a) presence of native freshwater turtles of the family Emydidae, subfamily Emydinae; b) presence of both Emydinae and Geoemydidae. In bold: species for which climatic suitability is >0.5 in at least 10 % of at least one EU country

L, invasion risk low; M, invasion risk moderate; H, invasion risk high; E, invasion risk extreme

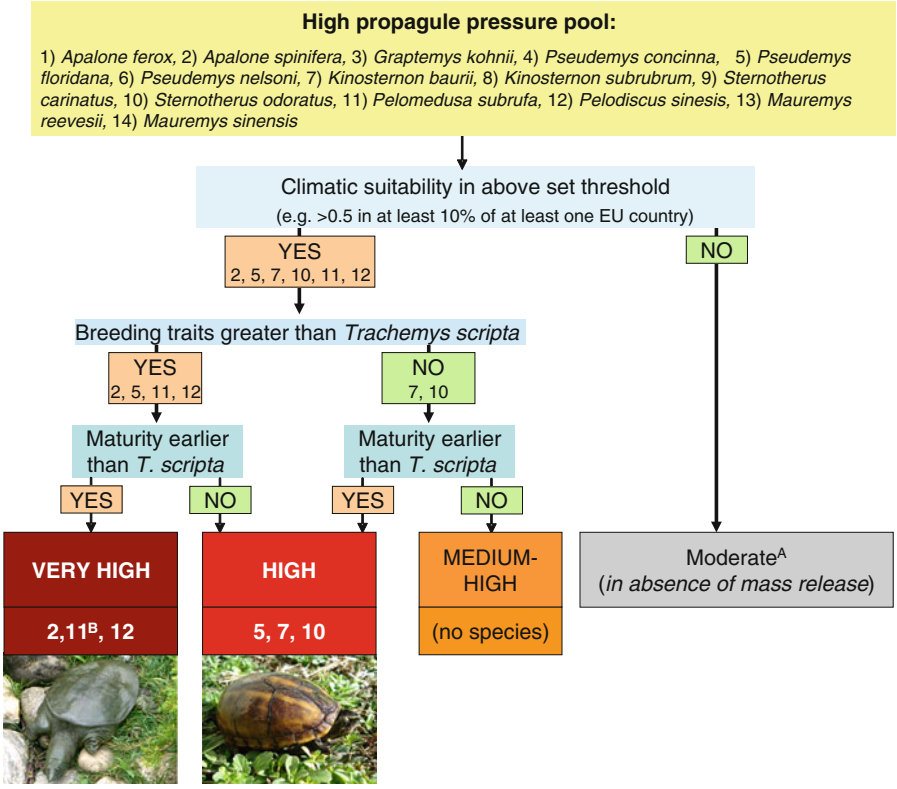


Fig. 2 Diagram of the combined use of information on climate and life history to identify freshwater turtles with the highest risk of invasion. All the species considered have high scores of coexistence with humans (Table 2). Species are identified by their respective number. *Left picture P. sinensis*, photo by R. Colombo; *right picture K. baurii*, photo by R. Bonacci. [A] Lack of suitability in SDM does not ensure that a species will never establish if it is heavily introduced, because species might exploit conditions that are not available within native ranges, and adaptation to novel climates is possible. [B] For *P. subrufa* no data on age at maturity were available

occur during invasions, allowing adaptations to novel climates (Lockwood et al. 2005; Broennimann et al. 2007). Nevertheless, the majority of invasive populations exploit climatic niches that are similar to those found in the native range, supporting the usefulness of SDM for risk assessment (Petitpierre et al. 2012). Actually, several tests using independent validation datasets have shown that SDM can be able to accurately predict the localities where introduced species will establish and become invasive (Ficetola et al. 2007; Reshetnikov and Ficetola 2011). The ability of correctly predicting localities of likely naturalization was confirmed for *P. sinensis*, which was the only species for which several non-native records were available. This corroborates the robustness of our results.

According to our SDM, for most species bioclimatic suitability is high in multiple areas outside the native range (Fig. 1). *P. sinensis* and *P. subrufa* are the turtles with the largest suitable areas outside the native range in all the continents (Fig. 1). For the majority of the other turtles there are suitable areas outside the native range, particularly in regions with Mediterranean and temperate climate, while *M. sinensis* is the only species for which suitable areas were mostly tropical (Fig. 1). For some turtles (e.g., *P. concinna*, *K. baurii*, *S. odoratus*) highly suitable areas are found in the Eastern North America, in the area between Southern Brazil and Argentina, in Eastern Asia, in Eastern Australia and in Europe. This global pattern of invasion risk is similar to the one observed for other freshwater invaders living in temperate or subtropical climates (e.g., the bullfrog *Lithobates catesbeianus*, the crayfish *Procambarus clarkii* and the turtle *T. scripta*; see Ficetola et al. 2007; Rödder et al. 2009; Capinha et al. 2011). For at least five species

(*A. spinifera*, *K. baurii*, *S. odoratus*, *P. subrufa* and *P. sinensis*) wide areas of Europe have high or very high suitability (Fig. 1, Fig. S1), particularly in the Iberian Peninsula, Southern France, Italy, in coastal areas of the Balkan Peninsula and in Greece. For all the considered species, the life history traits indicate some invasive potential in regions with suitable climate (Tables 2, 3; see below for "Discussion"), suggesting that preventive measures may be urgently needed in areas with high climatic suitability.

For most of species, the performance of SDM was very good (Table 1). Model performance was slightly lower for *A. spinifera* and *P. subrufa*. This might occur because, for presence-only SDM, the maximum achievable AUC is below 1, and tends to be lower in species with broad geographic distribution (Phillips et al. 2006; Lobo et al. 2008). Furthermore, both *P. subrufa* and *A. spinifera* show deep genetic structure (McGaugh et al. 2008; Vargas-Ramirez et al. 2010); genetically distant lineages might have distinct niches, reducing the effectiveness of a model considering records from the whole species range (Pearman et al. 2010).

Risk assessment

Assessment of the invasion risk by non-native species is a complex task, that should take into account the different steps of the invasion process. Leung et al. (2012) proposed to examine the risk by invasive species in five steps: (1) transport and introduction, (2) establishment, (3) abundance and local density in the non-native range, (4) subsequent spread and (5) impact. This framework can be followed using both quantitative and qualitative approaches. Our analysis considered species for which the increase of trade was recent, and the history of introduction is limited, therefore we mostly focused on the first steps of invasions (transport and introduction, establishment, and abundance). In absence of complete quantitative information, we combined quantitative results (particularly SDM) with qualitative comparisons with other invasive freshwater turtles.

Transport and introduction

The species considered in the analysis are widely traded at cheap prices, therefore propagule pressure is potentially high (Fig. 2). Actually, several of them are already released into natural environments (Kraus 2009). The three species of Trionychidae quickly reach large body size (Table 2), therefore they may have a large risk of release by owners that do not intend to maintain them in large aquaria. Conversely, Kinosternidae have rather small size, and this might reduce their release (Table 2).

Establishment

For the majority of species, there are wide areas with high climatic suitability outside the native range, indicating high risk of establishment (see above for "Discussion"). Native populations of all the candidate species can be found in human dominated landscapes, suggesting that they may get established even if introduced nearby human settlements.

Abundance and population growth

Freshwater turtles may be massively released, therefore they can reach very high abundance even in absence of fast population growth (Ficetola et al. 2012; Leung et al. 2012). Nevertheless, certain breeding parameters can boost the growth of populations, enhancing the invasion risk for some species. Differences for age at maturity among species were limited (Table 2), while fecundity showed much larger variation among species. Kinosternidae present the lowest annual fecundity, while large Trionychidae and Emydidae can have fecundity higher than *Trachemys scripta*, and are therefore those with the highest potential of quick population growth (Table 2; Fig. 2).

Risk assessment following Van Wilgen and Richardson (2012)

For all the study species invasion risk may be high, even with limited introductions (Table 3). The number of introductions per year considered (0.5–2) is rather low, if compared to the values observed for heavily traded freshwater turtles (Teillac-Deschamps et al. 2009; Ficetola et al. 2012; Kikillus et al. 2012). Nevertheless, it should be remarked that these values have been obtained using the introductions as recorded in Kraus (2009), and should not be considered as the literal number of releases. The Van Wilgen and Richardson (2012) approach suggests some differences in output depending on the native freshwater

turtle species, with the risk of establishment by Geoemydidae slightly lower in regions where inhabited by native species of the same family (see Table 3), still differences are minor and invasion risk remains always high, particularly if individuals are intensively released. This probably occurs because differences among species for other parameters are small and do not determine strong differences in invasion outcome, if species are introduced into suitable climates.

Conclusion

Multiple studies have identified propagule pressure and climatic suitability as the major determinants of invasion risk (Lockwood et al. 2005; Colautti et al. 2006; Richardson and Thuiller 2007; Bomford et al. 2010). Our analysis agrees with these findings: most of the study species, if introduced in regions with suitable climate, might become invasive (as suggested when parameters such as fecundity or coexistence with humans are considered; Tables 2, 3). Freshwater turtles are among the most frequent pets, and all these species are traded in large numbers and at cheap price, thus all of them might be introduced many times, resulting in a high propagule pressure. Overall, climate matching is expected to be the major determinant of invasion risk in a given region. Nearly all the study species have some suitable area outside their native range; distinct species have high invasion risk in different regions of the world, and in all the temperate or tropical regions the climate is suitable for at least one traded turtle (Fig. 1). In other words, there are no species showing global invasion risk, but each area of the world has its own set of risky species. Establishment risk may be particularly high for *P. sinensis* and *P. subrufa*, which are among the species with largest suitable areas, and show breeding traits greater than *T. scripta* (Fig. 2). Release rate and population growth may be particularly high for the Trionychidae, as they quickly reach large size, have high fecundity and often coexist with humans (Table 2).

The availability of spatially explicit maps of risk of establishment (Figs. 1, 2, Fig. S1) may allow to set up specific preventive measures in different regions, like trade regulation or appropriate communication campaigns. In Europe, regulations for potentially invasive species have often banned the import at the continental scale, while overlooking the trade among EU countries. However, due to the strong differences in climatic suitability (see e.g., Fig. S1), each country might set up specific trade regulations, targeting those turtles showing the highest risk in their territory. Setting up effective regulations may be challenging. For instance, regulations banning the trade of the subspecies *T. scripta elegans* has determined trade shift toward other subspecies of *T. scripta* and toward other species of freshwater turtles, and even attempts to disguise the head diagnostic colours of specimens have been made to smuggle them (Scalera 2007). Nevertheless, regulations based on quantitative or semi-quantitative risk assessments have a greater potential to limit propagule pressure for the species posing the highest risk. Environmental education can also play an important role to increase public awareness and avoid introductions of turtles by owners. Effective campaigns should include communication targeted to explain the problems caused by introduced turtles (e.g., exhibitions in public parks, communication to schoolboys), but also a more general communication, encouraging people to change their perception toward nature and support biodiversity conservation. Large scale education campaigns have a great potential to limit the establishment of non-native populations (Teillac-Deschamps et al. 2009; Ficetola et al. 2012). Even if they can require substantial resources, in the long term they may be more cost-effective than the eradication of invasive populations. Our research provides baseline information to predict potential invasiveness, as recommended by European strategy on invasive alien species (Genovesi and Shine 2004), and identifies six species (*A. spinifera*, *P. floridana*, *K. baurii*, *S. odoratus*, *P. subrufa* and *P. sinensis*; Fig. 2) requiring regulation changes and public education in European countries.

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