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Prediction and validation of the potential global distribution of a problematic alien invasive species — the American bullfrog

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ABSTRACT

Predicting the probability of successful establishment and invasion of alien species at global scale, by matching climatic and land use data, is a priority for the risk assessment. Both large- and local-scale factors contribute to the outcome of invasions, and should be integrated to improve the predictions. At global scale, we used climatic and land use layers to evaluate the habitat suitability for the American bullfrog *Rana catesbeiana*, a major invasive species that is among the causes of amphibian decline. Environmental models were built by using Maxent, a machine learning method. Then, we integrated global data with information on richness of native communities and hunting pressure collected at the local scale. Global-scale data allowed us to delineate the areas with the highest suitability for this species. Predicted suitability was significantly related to the invasiveness observed for bullfrog populations historically introduced in Europe, but did not explain a large portion of variability in invasion success. The integration of data at the global and local scales greatly improved the performance of models, and explained > 57% of the variance in introduction success: bullfrogs were more invasive in areas with high suitability and low hunting pressure over frogs. Our study identified the climatic factors entailing the risk of invasion by bullfrogs, and stresses the importance of the integration of biotic and abiotic data collected at different spatial scales, to evaluate the areas where monitoring and management efforts need to be focused.

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INTRODUCTION

Alien invasive species (AIS) are one of the main causes of loss of biodiversity and extinction at global scale. A large number of studies are therefore investigating invasions, with the aim to help the management of invasive species and to eliminate or reduce their negative impacts.

When AIS are established, large efforts should be devoted to detect the negative impact of invaders, and to plan their eradication (Hulme, 2006). However, the removal of the whole invasive populations can be an impossible task, especially for species that are established over large areas (Myers *et al.*, 2000). The prevention of introduction and establishment of species with a high risk of becoming invasive is therefore considered the most cost-effective way of reducing future problems (Leung *et al.*, 2002). The essential role of prevention is stipulated in the Convention on Biological Diversity (http://www.biodiv.org/) and the Global Strategy of the Global Invasive Species Programme (McNeely *et al.*, 2001). Preventative measures are also required just after introduction to prevent establishment. The invasive potential of recently

introduced alien species needs to be reassessed regularly, since many alien species undergo a clear 'lag phase', sometimes for decades following introduction, before the species shows any signs of becoming invasive (Crooks & Soulé, 1999).

An important approach to prevention is predicting the potential outcome of introductions on the basis of knowledge of ecological requirements of potential invaders, and of factors influencing the likelihood of establishment. For instance, climatic similarity between native and target regions is considered a basic requirement for successful invasions (Panetta & Mitchell, 1991; Mack, 1996; Welk *et al.*, 2002; Robertson *et al.*, 2004; Thuiller *et al.*, 2005; Richardson & Thuiller, 2007). Climatic matching is definitely not the final answer, as biotic factors and other aspects play an important role (Stohlgren & Schnase, 2006; Thuiller *et al.*, 2006), but there is no doubt that climate matching is, in many cases, the most important single factor. It clearly has considerable potential for use in invasion ecology (Peterson & Vieglais, 2001; Thuiller *et al.*, 2006). Data on the native range of a species can be used to model their climatic niche, and projected at global scale to locate the areas where the likelihood of establishment will be
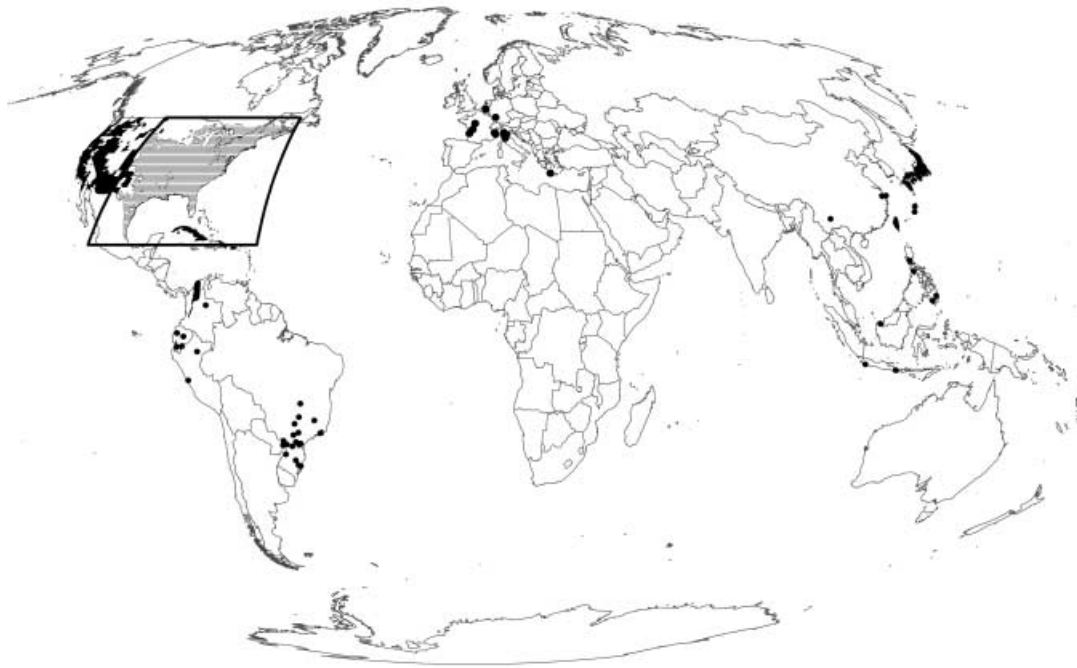
Figure 1 Distribution of native (barred) and non-native (black) populations of the American bullfrog. The inset represents the area of calibration of the suitability model. Distribution maps are from the Global Amphibian Assessment (Santos-Barrera *et al.*, 2004).

higher. The availability of climatic and land use data sets at global scale, and new modelling techniques have boosted the potential for such studies to evaluate the risk of invasion (Thuiller *et al.*, 2005).

However, relying on these large-scale species distribution models can have important limitations (Guisan & Thuiller, 2005). First, the model performance can be highly variable in space, and it can be difficult to evaluate the predictive power in regions that are far from the source area, in a completely different biogeographical context, and therefore their utility has been questioned (Hulme, 2003, 2006). Independent data sets are necessary to validate the predictive power of such models, and therefore their applicability in the management context. The study of species that were repeatedly introduced in different localities can help resolve this issue, because the outcome of these introductions can be used to evaluate if climatic envelop models make correct predictions.

A second limitation is that many variables other than climate influence the likelihood of establishment and subsequent invasion (Stohlgren & Schnase, 2006; Thuiller *et al.*, 2006). Key factors are the number of individuals introduced (propagule pressure), the environmental features that are not captured by large-scale environmental layers, the interactions with native species, and human activities (Kolar & Lodge, 2001; Lockwood *et al.*, 2005; Yiming *et al.*, 2006). There is no doubt that macro-climate and local abiotic and biotic factors influence the outcome of an invasion, but it can be difficult to integrate them in a unique hierarchical model. The evaluation of their relative role is an issue that should be resolved.

The American bullfrog *Rana catesbeiana* Shaw, 1802 is native of eastern North America, but has been introduced in over 40 countries and four continents over the last century (Lever, 2003) (Fig. 1). In Europe, at least 25 independent introductions of *R. catesbeiana* occurred in eight countries; free-ranging populations are present in Belgium, France, Germany, Greece, and Italy (Lanza & Ferri, 1997; Ficetola *et al.*, 2007). Bullfrogs can have negative impacts on native amphibian populations. The large tadpoles of this species can outcompete the larvae of native species; moreover, adults are generalist predators and also prey on other amphibians (Blaustein & Kiesecker, 2002; Kats & Ferrer, 2003). Complex biotic interactions with native species are also possible. For example, when bullfrogs are present the tadpoles of native frogs can alter their use of microhabitat, therefore becoming more vulnerable to the predation by fish (Blaustein & Kiesecker, 2002). Furthermore, introduced bullfrogs can be carriers of *Batrachochytrium dendrobatidis*, a fungus that is the agent of chytridiomycosis (Garner *et al.*, 2006). Chytridiomycosis is an emerging infectious disease that is considered one of the main causes of global amphibian decline and extinctions (Berger *et al.*, 1998; Lips *et al.*, 2006; Pounds *et al.*, 2006), and bullfrogs are probably one of the vectors of the expansion of this disease (Garner *et al.*, 2006). For these reasons, bullfrogs are considered to be among the most harmful AIS around the world (Lowe *et al.*, 2000); plans to halt their expansion and/or new introductions are a priority for amphibian conservation and are carried out in several countries (e.g. Ficetola *et al.*, 2007).

The aim of this study was threefold. First, we used the native bullfrog distribution to build a model predicting which areas are

more susceptible to a successful invasion at the global scale. Second, we evaluated if the model correctly predicts the outcome of introductions, by using data on historical introduction attempts performed in Europe. Third, we evaluated if other factors can explain the variability in introduction success not captured by our global-scale model.

METHODS

Bullfrog distribution

We combined data from the Global Amphibian Assessment (Santos-Barrera *et al.*, 2004) with those in national and regional herpetological and wildlife atlas (see Appendix S1 in Supplementary Material) to obtain the distribution of bullfrogs within the native range; the species was present in 1424 10×10 min grid cells.

Reliable data on the distribution of non-native bullfrog populations are not available at the global scale, because of strong differences for data quality across countries and lack of information on failed introduction attempts. For this reason, we focused our analysis on non-native populations in Europe, for which extensive information exist (Ficetola *et al.*, 2007). Using a combination of field surveys, questionnaires, and literature review, we evaluated the outcome of each introduction (from the introduction year to 2006: see Ficetola *et al.*, 2007 for further details) as (1) invasive: a free-ranging population spread from the locality of introduction or (2) not invasive: the introduced population was extinct or, if established, did not expand its range from the locality of introduction (Kolar & Lodge, 2001). In three cases, eradication has been performed soon after the introduction, and the outcome of introduction was not be evaluated, therefore we analysed data from 22 introductions.

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). Two temperature variables described the availability of thermal energy and the species thermal tolerance: Tmax (maximum temperature of the hottest month); Tmin (minimum temperature of the coldest month). Two precipitation variables described the water availability during both summer and winter, since bullfrog tadpoles overwinter in water and therefore require permanent wetlands: Prec1202 (summed precipitation between December and February); Prec0608 (summed precipitation between June and August). To avoid the multicollinearity issue, we did not include other climatic variables (such as annual precipitation and average temperature) that were strongly correlated to linear combinations of the four variables used. Furthermore, we used the human footprint, 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 set including vector maps, satellite images, and census data (Sanderson *et al.*, 2002). Human footprint was used because some human modifications of land, such as agricultural practices and urbanization, may positively

influence bullfrog distribution (Rubbo & Kiesecker, 2005; Maret *et al.*, 2006).

Global-scale modelling

Environmental suitability at global scale was modelled using maximum entropy modelling (Maxent) (Phillips *et al.*, 2006). 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, can incorporate interactions between different variables, and deterministic algorithms have been developed that always converge to the optimal probability distribution (Phillips *et al.*, 2006). The suitability values provided by Maxent range from 0 (unsuitable habitat) to 100 (optimal habitat). In recent comparisons among several techniques of prediction of species distribution, Maxent resulted to be the most effective method using presence-only data, and showed sometimes a performance comparable to several traditional tools using presence/absence data, such as general linear models and general additive models (Elith *et al.*, 2006; Hernandez *et al.*, 2006).

The model was developed on the basis of distribution records within the native range (eastern part of USA, Canada, and Mexico), and run over the area represented by the inset in Fig. 1. Then, the model was projected to evaluate the environmental suitability of each grid cell at global scale. The area under the curve (AUC) of the receiver operator characteristic was used to test the agreement between observed species presence and projected distribution (Manel *et al.*, 2001). A jack-knife test was used to evaluate the importance of each environmental variable to explain the native distribution of the bullfrog. The model was re-run by excluding each environmental variable, and then by using each variable in isolation. The complete model was then compared with the jack-knifed ones.

A drawback of Maxent is that it uses an exponential model for probability, therefore probability does not have an upper limit. This can produce very large predicted values when environmental conditions are outside the range present in the area where the model is calibrated (Phillips *et al.*, 2006). For this reason, we projected the results of Maxent only in the areas of the world where environmental conditions fall within the range of calibration area (42% of grid cells) to avoid spurious projections (Thuiller *et al.*, 2004).

Evaluation of introduction success

The environmental suitability predicted using Maxent was projected to known European localities of introduction (Ficetola *et al.*, 2007). We then evaluated the relationship between environmental

suitability and outcome of introduction in these particular sites (invasive vs. not invasive) using logistic regression. Clearly, other factors such as biotic interactions with the native communities, human influence, and ability to disperse could influence the outcome of invasion at the local scale. We thus compared the model including only environmental suitability with models including other factors that were not captured by our global-scale environmental layers, recorded at the locality of introduction. The richest communities are sometimes believed to be more difficult to invade [Kennedy et al., 2002; Shea & Chesson, 2002; but see also Stohlgren et al. (2003, 2006) and Richardson et al. (2005) for an opposite pattern]. We tested if the number of amphibian species recorded in the same mesh was a good predictor of outcome of invasion (Gasc et al., 1997). Human hunting could be a further factor influencing the outcome of invasion (Yiming et al., 2006). We used interviews to local people (at least one field herpetologist per introduction area) or our direct knowledge to assess whether frogs are captured for alimentary reasons. A further key factor on the outcome of invasions is propagule pressure (Kolar & Lodge, 2001). However, reliable data were available only for a few introduction sites (Ficetola et al., unpublished manuscript) and could not be included in this analysis. Hunting pressure and native community act at a more proximal scale than climate, since they have effect only where climatic suitability allows bullfrog establishment. Therefore, we analysed the different factors in a hierarchical framework, keeping into account the effects of climate.

We used Akaike's Information Criterion, corrected for small sample size (AIC_C), to compare the relative performance of logistic regression models including three possible predictors: suitability predicted using Maxent, hunting pressure, and richness of native community (Burnham & Anderson, 2002). For this task, we con-sidered as potential candidates the models including only significant variables. Models including not significant variables were not considered, because the use of AIC as unique criterion for selection can lead to models overfitting the data (Maggini et al., 2006).

The significance of variables was tested by using a likelihood ratio test; we used the Nagelkerke's r^2 (r_N^2), which measures the proportion of variance explained by the model, as a measure of the fit of our models (Nagelkerke, 1991). Following Cushman & McGarigal (2002), we also performed variance partitioning to calculate the percentage of variation explained by each independent variable. Variance partitioning allowed us to decompose the independent and the joint effect of variables, and to rank them according to their explanatory power. As above, the AUC was used to test the agreement between observed outcome of introductions and the predictions of logistic regressions (Manel et al., 2001).

RESULTS

Prediction at global scale

Maxent observed a positive relationship between probability of occurrence of bullfrogs and four variables: Prec1202; Prec0608, Tmax, and Human Footprint. Moreover, probability of occurrence was maximum for Tmin ranging between –20 and +13 °C (Fig. 2a–e). Areas having high precipitations during both summer and winter, high maximum temperature, high human pressure, and intermediate minimum annual temperature were those with the highest predicted suitability for bullfrogs. The jack-knife procedure suggested that winter precipitation was the variable having most predictive power, while maximum temperature was the least important (Fig. 2f). The AUC of model for the calibration area was 0.759.
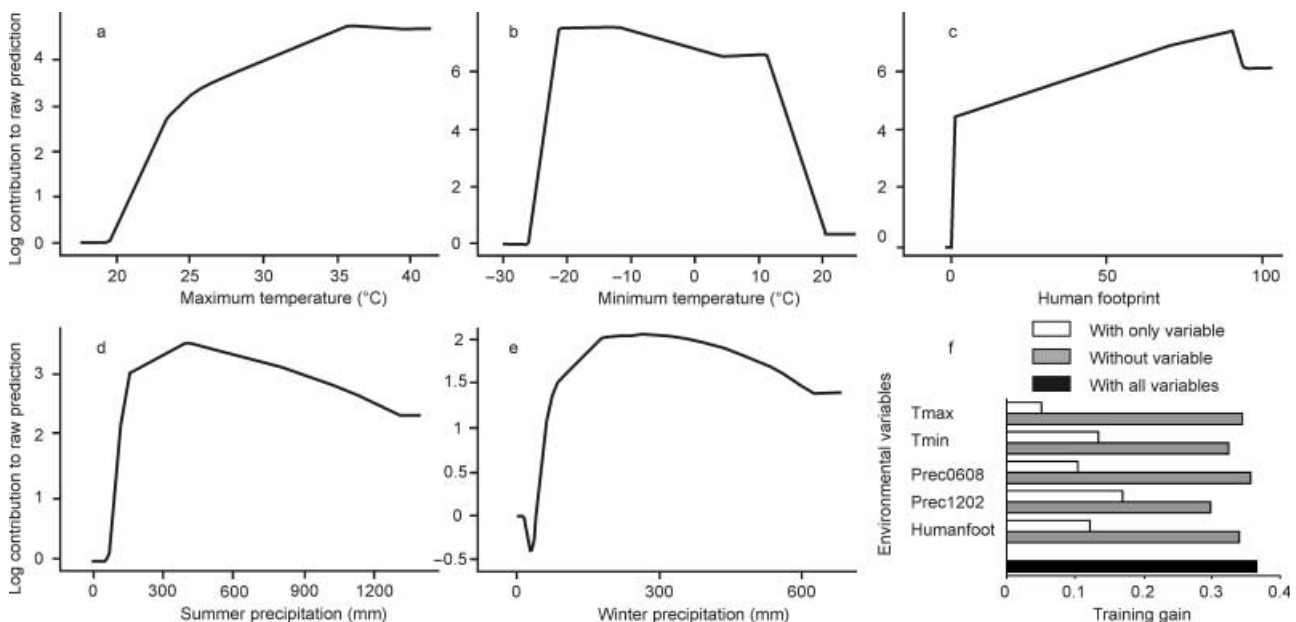

Figure 2 Results of environmental suitability model. (a–e) Relationships between environmental features and suitability for bullfrogs. (f) Results of jack-knife evaluation of relative importance of predictors.
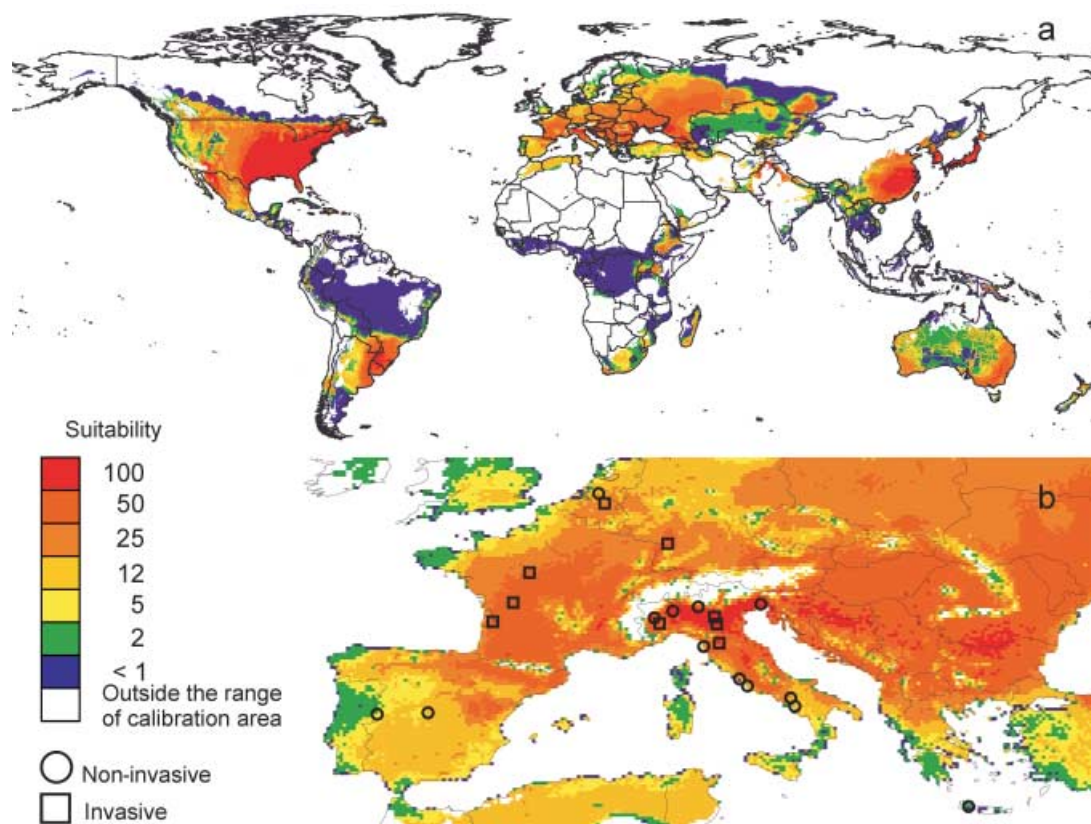
Figure 3 (a) Worldwide projection for the environmental suitability for bullfrogs. (b) Projected suitability in the areas of Europe where bullfrog introductions occurred. Squares: invasive populations; circles: non-invasive populations.

Table 1 Logistic regression models relating the outcome of the introduction of American bullfrog in Europe (invasive vs. not invasive) to the suitability predicted on the basis of global-scale model, and to local-scale factors (richness of amphibian communities, hunting pressure over frogs). Significant models are ranked according to the Akaike's Information Criterion (AIC$_C$). B: multiple regression coefficient; r_N^2: Nagelkerke's r^2; AUC: area under the curve of the receiver operator characteristic.

Model rank	Variables	B	χ_1^2	P	AIC$_C$	r_N^2	AUC
1	Suitability	+0.130	11.553	<0.001	24.157	0.573	0.872
	Hunting	−4.708	7.111	0.008			
2	Suitability	+0.049	5.070	0.024	28.697	0.278	0.769
Non-significant models							
3	Suitability	+0.125	8.846	0.003			
	Hunting	−4.299	3.851	0.050			
4	Community richness	0.102	0.137	0.711			
	Suitability	+0.029	5.016	0.025			
	Community richness	0.402	3.397	0.065			

The projection at global scale identified four areas outside the native range having very high suitability for bullfrogs: the western North America, mainly close to the Mexico–USA and Canada — USA borders; the area between Southern Brazil and Argentina; the eastern Asia (eastern China, South Korea, and Japan); and several areas of Europe. There was a striking correspondence between these areas and the areas where introduced bullfrogs are present (Figs 1 and 3a).

Validating the prediction of introduction success in Europe

Of the 22 introductions considered in Europe, nine (41%) resulted in invasive populations. Of the 13 not invasive populations, 11 disappeared after the introduction, and two persisted only in a single wetland or in a very small number of wetlands. There was a significant, positive relationship between

success of introduction and suitability calculated on the basis of climatic and land use data (Table 1). Introductions performed in areas having predicted suitability of < 20 never resulted in invasive populations; most of these introductions were performed in the Mediterranean areas of Europe (Spain, coastal Italy, and Greece). However, the logistic regression including only projected habitat suitability did not capture a large portion of variance in introduction success (Table 1), since several introductions performed in apparently suitable areas failed (Fig. 3b). The AUC of logistic regression for Europe was 0.769, almost identical to those obtained for the calibration area.

We therefore tested logistic regressions combining environmental suitability and other factors, namely richness of local amphibian community and hunting pressure, to predict the outcome of historical introductions. The best logistic regression was those including suitability and hunting pressure: invasive populations were strongly related to areas with high suitability and lack of hunting. This model explained > 57% of the variance in introduction success; the AUC was 0.872 (Table 1). Out of the explained deviance, 41.6% was explained by the pure effect of climatic suitability, 5.2% by the pure effect of hunting, and 53% by the joint effect of these two variables.

DISCUSSION

We developed a model to predict the risk of invasion of American bullfrogs at global scale on the basis of large-scale environmental data, and we observed a strong concordance at both global and European scale between predicted suitability and distribution of non-native bullfrogs. The integration of large-scale environmental layers with local data on hunting allowed a striking increase in the predictive ability of model, suggesting that the integration of data collected at different spatial scale can greatly improve the performance of predictions.

Global-scale environmental features

Bullfrog is one of the most common and studied species of North American amphibians. Although several authors have investigated its ecology at both local and regional scale, we are not aware of studies describing its climatic requirement using data from the whole range. Bullfrog presence seems to be positively related to both winter and summer precipitation; the jack-knife procedure suggests that winter precipitation is the most important climatic feature (Fig. 2). The availability of water and the presence of permanent wetlands for breeding are commonly recorded environmental features needed for the presence of bullfrogs (Graves & Anderson, 1987; Skelly et al., 1999; Maret et al., 2006). In most of the range, the tadpoles of bullfrogs require more than 1 year for metamorphosis, and overwinter in water (Ryan, 1953; Willis et al., 1956; Govindarajulu et al., 2006). This species therefore requires water permanence for reproduction. We also observed a positive relationship between bullfrog distribution and maximum temperature, with the species predicted to be present in areas having maximum temperature > 20 °C (Fig. 2a). Bullfrog is considered a 'warm-adapted species' (Bachmann,

1969) since below 15 °C, adults are generally inactive, eggs will not hatch, and larvae will not develop (Viparina & Just, 1975; Harding, 1997). High temperatures during summer (above 26 °C) are preferred by the adults, and are considered a key determinant of suitability for bullfrogs (Lillywhite, 1970; Graves & Anderson, 1987). We observed a bell-shaped relationship between minimum temperature and bullfrog distribution, and suitable areas had minimum temperature ranging between –20 °C and +14 °C. That is, bullfrogs are not present in areas with very cold winters, but some degree of seasonality is present over the whole range. Finally, the positive association between bullfrogs and human footprint corroborates the observations that bullfrogs can take advantage from human modifications of land and from the increase of permanent ponds created, for example, for agricultural and recreational purposes (Rubbo & Kiesecker, 2005; Maret et al., 2006).

It should be noted that the trends of plots produced by Maxent are sometime not monotonous. For example, the suitability greatly increased when winter precipitation increased from 0 to about 300 mm, and slightly decreased for higher values of precipitation. Maxent does not produce confidence intervals, therefore these plot should be carefully evaluated. The inclusion of confidence intervals in the response curves would constitute an important improvement of this technique (Elith et al., 2006; Hartley et al., 2006).

Predicting the risk of invasion

Our model identified four areas having maximum suitability for bullfrogs, entailing a maximum risk of successful invasion (Fig. 3). Bullfrogs have already been introduced in these areas, and in some of them invasion is ongoing (Fig. 1, Lever, 2003). This observation stresses the importance of implementation of an early detection and eradication plan of this AIS within the areas having high suitability.

The simple individuation of 'climate matching' between native and non-native areas is only a first step for the evaluation of the risk of invasion, and has several limitations that cannot be overlooked. The predictions obtained from climatic model are based on the 'realized niche' of the species within their range (Kearney, 2006). However, biotic and abiotic interactions can modify the dimensions of the realized niche (Broennimann et al., 2007), therefore the niche projected outside from the native range should be considered as a coarse approximation. For instance, the model tended to predict low invasion success in tropical areas where non-native bullfrogs are present, such as Cuba. These tropical areas exhibit combination of environmental conditions that do not exist within the native range, making extrapolation of suitability to these non-native areas likely to be not robust (Hartley et al., 2006). Moreover, the low suitability of some areas of the world does not mean that bullfrogs can be introduced without any risk of invasion. Another hypothesis to explain the low suitability in these islands might be the poor accuracy of the climatic variables in these somewhat small areas.

The approach we presented here can be used to focus the preventive monitoring on the areas that are more at risk.

Indeed, being a correlative method, this approach does not consider directly the effects of biotic interactions that are known to be fundamentally important for the recruitment, establishment, and spread of introduced species.

The pixel resolution of environmental data ($10 \times 10'$) may also cloud some finer-scale variations in the species' ecological requirements that are not detectable at the spatial scale of our analysis. Because the influence of each environmental variable in determining the species' niche is scale dependent, different degrees of ecological niche variation can arise among populations, depending on the spatial resolution of analyses (Wiens, 1989). Finally, the ongoing climatic changes at global scale can modify the suitability of some area; for example, global warming can cause an expansion of suitable areas towards higher latitude (Roura-Pascual *et al.*, 2004; Thuiller *et al.*, 2007).

The integration of local environmental data greatly increased the performance of models. This suggests that integrating information collected at different spatial scales can boost the performance of models evaluating the risk of invasion. These local-scale factors act *a posteriori* and can have meaningful effects only in areas where climate is suitable. It is therefore important to evaluate their role within a hierarchical framework.

Climate matching can help to locate the areas with high suitability at broad (i.e. global) scale, but these areas are frequently very large, sometime including entire countries or large portions of continents and biogeographical provinces (e.g. (Roura-Pascual *et al.*, 2004; Hartley *et al.*, 2006). Extensive areas are also delineated because AIS frequently have broad niche. The monitoring and the management of the whole suitable area (such as the south-eastern China or large areas of Europe) can be impossible for logistic and financial constraints. The integration of information collected at multiple spatial scales has been proven important to understand the dynamics driving species distribution and to improve habitat suitability models for threatened species (Fischer *et al.*, 2004; Radford & Bennett, 2004; Guisan & Thuiller, 2005; Resetarits, 2005; Brambilla *et al.*, 2006), and should be included in the analysis of suitability for AIS, to obtain a quantitative measure of suitability of target regions and focus the efforts for more effective prevention and management.

We observed a strong relationship between effect of hunting and invasion success, while the species richness of the native community did not show a significant effect. It is remarkable that hunting pressure is strongly related to introduction success both in Europe and in a study performed at small spatial scale in China (Yiming *et al.*, 2006), confirming the generality of its importance. This might suggest promoting hunting as a non-expensive tool for controlling this invasive species. However, most introductions of bullfrogs have been performed by people considering this species as a source of food (Lever, 2003) and promoting bullfrog hunting might cause the introduction in new localities. Several other taxa, such as fish and crayfishes, are introduced and expand their range by people spreading them as a source of food (e.g. Cambray, 2003; Magalhaes *et al.*, 2005). Moreover, the promotion of hunting over frogs might mean an increased pressure over native species.

For these reasons, we strongly discourage the promotion of hunting over frogs as a tool to limit their invasion; indeed, the eradication plan ongoing in western France includes education programmes discouraging these human predations, to contain new introductions.

Variance partitioning suggested that the pure effect of hunting pressure was limited, and most of explanatory power of our model was due to the joint effect of hunting and climatic suitability. This is not surprising, because the effect of hunting is somewhat subordinated to climatic suitability: in areas where climate is unsuitable, introductions are always unsuccessful, independently from hunting. The large importance of the joint effect of climate and hunting further stresses the importance of integrating information from different sources.

Conversely, we did not find a significant effect of richness of native amphibian communities. A reduced probability of invasion of species rich communities is frequently expected, yet the presence of extrinsic factors influencing both native and non-native species can masque this relationship and cause the non-detection of such a pattern (Shea & Chesson, 2002; but see also Stohlgren *et al.*, 2006). For example, climate and landscape alteration influence both bullfrogs and native amphibians (Ficetola & De Bernardi, 2004; Araujo *et al.*, 2006; Maret *et al.*, 2006). Moreover, bullfrogs are much larger than any native European amphibian; therefore native species might be more important as source of food than as competitors. Finally, for this analysis we used data from herpetological atlas because field data were not available for all the localities of introduction. Some of the native species only partially share the breeding wetlands with bullfrogs, and this might reduce the potential for interaction.

Our study shows that the integration of large-scale environmental layers with data collected at a more local scale, and the combination of climatic data with information on human activities, can greatly improve the prediction of invasion risk. In the areas that are most at risk, education should be performed to limit new introductions; a strict monitoring should be performed for early detection of new introduced populations, followed if necessary by immediate eradication.

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SUPPLEMENARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 List of data sources for bullfrog distribution within the native range.

This material is available as part of the online article from:
http://www.blackwell-synergy.com/doi/abs/10.1111/
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