

Knowing the past to predict the future: land-use change and the distribution of invasive bullfrogs

GENTILE FRANCESCO FICETOLA*†, LUIGI MAIORANO‡§, ALESSANDRA FALCUCCI‡, NICOLAS DENDONCKER¶, LUIGI BOITANI‡, EMILIO PADOA-SCHIOPPA*, CLAUDE MIAUD† and WILFRIED THUILLER||

*Dipartimento di Scienze dell'Ambiente e del Territorio, Università di Milano-Bicocca, Piazza della Scienza 1, 20126 Milano, †Laboratoire d'Ecologie Alpine, UMR CNRS 5553, Université de Savoie, 73376 Le Bourget du Lac cedex, France, ‡Dipartimento di Biologia Animale e dell'Uomo, Sapienza Università di Roma, viale dell'Università 32, 00185 Roma, Italy, §Department of Ecology and Evolution, University of Lausanne, Biophore Building, CH-1015 Lausanne, Switzerland, ¶Centre for the Study of Environmental Change and Sustainability, University of Edinburgh, Drummond Street, EH89XP Edinburgh, UK, ||Laboratoire d'Ecologie Alpine, UMR CNRS 5553, Université Joseph Fourier, Grenoble Cedex 9, France

Abstract

Biological invasions and land-use changes are two major causes of the global modifications of biodiversity. Habitat suitability models are the tools of choice to predict potential distributions of invasive species. Although land-use is a key driver of alien species invasions, it is often assumed that land-use is constant in time. Here we combine historical and present day information, to evaluate whether land-use changes could explain the dynamic of invasion of the American bullfrog *Rana catesbeiana* (= *Lithobates catesbeianus*) in Northern Italy, from the 1950s to present-day. We used MAXENT to build habitat suitability models, on the basis of past (1960s, 1980s) and present-day data on land-uses and species distribution. For example, we used models built using the 1960s data to predict distribution in the 1980s, and so on. Furthermore, we used land-use scenarios to project suitability in the future. Habitat suitability models predicted well the spread of bullfrogs in the subsequent temporal step. Models considering land-use changes predicted invasion dynamics better than models assuming constant land-use over the last 50 years. Scenarios of future land-use suggest that suitability will remain similar in the next years. Habitat suitability models can help to understand and predict the dynamics of invasions; however, land-use is not constant in time: land-use modifications can strongly affect invasions; furthermore, both land management and the suitability of a given land-use class may vary in time. An integration of land-use changes in studies of biological invasions can help to improve management strategies.

Keywords: alien invasive species, amphibians, future scenarios, habitat suitability models, invasion dynamics, long term monitoring, *Rana catesbeiana*, temporal dynamics

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Introduction

Biological invasions are an unprecedented form of global change (Ricciardi, 2007), with alien invasive species (AIS) being a major issue for biodiversity conservation at the global scale (Sala *et al.*, 2000; Thuiller, 2007). AIS can negatively impact native species via

predation, competition and diffusion of diseases. Moreover, AIS can strongly affect the environment, for example by modifying ecosystem functioning and abiotic features (Strayer *et al.*, 2006; Ricciardi, 2007). Some AIS are now present in multiple continents, due to the interplay between human-assisted diffusion and natural dispersal ability. This is causing a global homogenization of faunas and floras, with important effects on biodiversity pattern at both local scales and worldwide (McKinney & Lockwood, 1999; Olden *et al.*, 2004, 2008; McKinney, 2006; Quian & Ricklefs, 2006).

Correspondence: Gentile Francesco Ficetola, Dipartimento di Scienze dell'Ambiente e del Territorio, Università di Milano-Bicocca, Piazza della Scienza 1, 20126 Milano, Italy, tel. +39 (0)2 64 48 29 45, fax 39 (0)2 64 48 29 96, e-mail: francesco.ficetola@unimi.it

The eradication of established AIS can be a difficult and expensive task (Hulme, 2006). If prevention was ineffective, the most effective option is often restricting the spread when the invasions are at their earlier stages. Much attention is therefore devoted to the understanding of the dynamic of invasions, to set up plans of biological screening and prevention in the areas that are most at risk of invasion (Hulme, 2006). Predictive models are therefore used to evaluate the areas most at risk of invasion based on environmental features recorded at both local and global scale, including climate, land cover and distribution of other species (Le Maitre *et al.*, 2008).

However, biological invasions are a dynamic process in which the temporal dimension cannot be overlooked. Environmental features change in time, species can quickly evolve in the new environment and these modifications can influence the invasion dynamics (Urban *et al.*, 2008). Temporal change of climate is probably the dynamic feature most often integrated in models of biological invasions. Climate, in fact, is a major driver of environmental suitability for AIS, thus many recent studies used scenarios of future climate to project species distribution model and to predict the areas that might become suitable for AIS in the future (Roura-Pascual *et al.*, 2004; Beaumont *et al.*, 2009; Ficetola *et al.*, 2009).

Climatic suitability is a key tool to predict invasion risk at coarse spatial scales, i.e., from countrywide to global (Roura-Pascual *et al.*, 2004; Thuiller *et al.*, 2005). However, suitable areas identified using bioclimatic models are often very large, including entire regions or countries and making it difficult to implement conservation plans (Heller & Zavaleta, 2009). Climatic models should therefore be refined to identify smaller areas, with the integration of features recorded at finer scale (Ficetola *et al.*, 2007a).

At finer spatial scales, land-use plays a major role in the dispersal and distribution of AIS. Land-use is obviously not independent from the distribution of human population, and AIS often take advantage of human modified environments (McKinney, 2006). Land-use is not constant in time, and can change quickly in response to socioeconomic factors (Falcucci *et al.*, 2007). Common changes in land-use are the expansion of urban areas, conversion of natural vegetation to cropland and pasture or vice versa, and shift of agricultural practices to increase productivity (Leemans & Zuidema, 1995; Petit & Lambin, 2002; Hurtt *et al.*, 2006). Multiple changes in land-use observed at local scale clearly have a global effect (Leemans & Zuidema, 1995; Hurtt *et al.*, 2006), and the change of land-use is probably the force most strongly affecting biodiversity of terrestrial and freshwater ecosystems (Sala *et al.*, 2000) with important effects on conservation (Maiorano *et al.*, 2008). Unfortunately, it is often difficult to have

information on past land-use, and predicting future land-use can be challenging. In practice, most existing studies using models to predict the distribution of AIS implicitly assume a constant land-use in the past or in the future (Domenech *et al.*, 2005 being a noticeable exception).

In this study, we incorporate dynamic land-use in suitability models, to predict the distribution of a problematic AIS, the American bullfrog *Rana catesbeiana* Shaw, 1802 (= *Lithobates catesbeianus*) at a regional scale. Bullfrog is native of eastern North America, but has been introduced in over 40 countries and four continents during the 20th century (Lever, 2003). Bullfrog is considered among the most harmful invasive species, because it can outcompete and predate native species (Blaustein & Kiesecker, 2002; Kats & Ferrer, 2003), can interact with predatory fish which further increase their negative effect on native amphibians (Blaustein & Kiesecker, 2002), and it can spread diseases (Garner *et al.*, 2006). Moreover, only a handful of founders can originate populations invading large areas in a few generations, with a spreading ability that challenges the traditional management plans (Ficetola *et al.*, 2008). Plans are ongoing in several countries to prevent and control the spread of this species (Lever, 2003; Ficetola *et al.*, 2007b; Kraus, 2009). Predictive models showed that climatic features are major drivers of the distribution of invasive bullfrog populations at coarse spatial scale (Ficetola *et al.*, 2007a; Giovanelli *et al.*, 2008), but also human activities and land-use can affect the invasion success of bullfrogs (Yiming *et al.*, 2006; Ficetola *et al.*, 2007a).

The bullfrog invasion in Northern Italy is documented since the 1930s (Lanza, 1962; Albertini & Lanza, 1987). This represents a unique opportunity to evaluate the relationship between land-use changes and biological invasions. High quality distribution data cover 70 years of bullfrog expansion; furthermore, land-use information is available since the 1960s (Falcucci *et al.*, 2007). This study combined historical information on land-use and bullfrog distribution, to evaluate whether land-use can explain bullfrog spread in the investigated area. The historical information allowed us to test whether models correctly predict the expansion of this species. Moreover, we used scenarios of future land-uses (Rounsevell *et al.*, 2006) to identify the areas that can be most at risk of invasion in the near future.

Methods

Study area and distribution data

We analysed bullfrog distribution in the Eastern River Po basin, Northern Italy (Fig. 1). The study area is a lowland dominated by agriculture, with numerous wetlands, and crossed by a dense network of

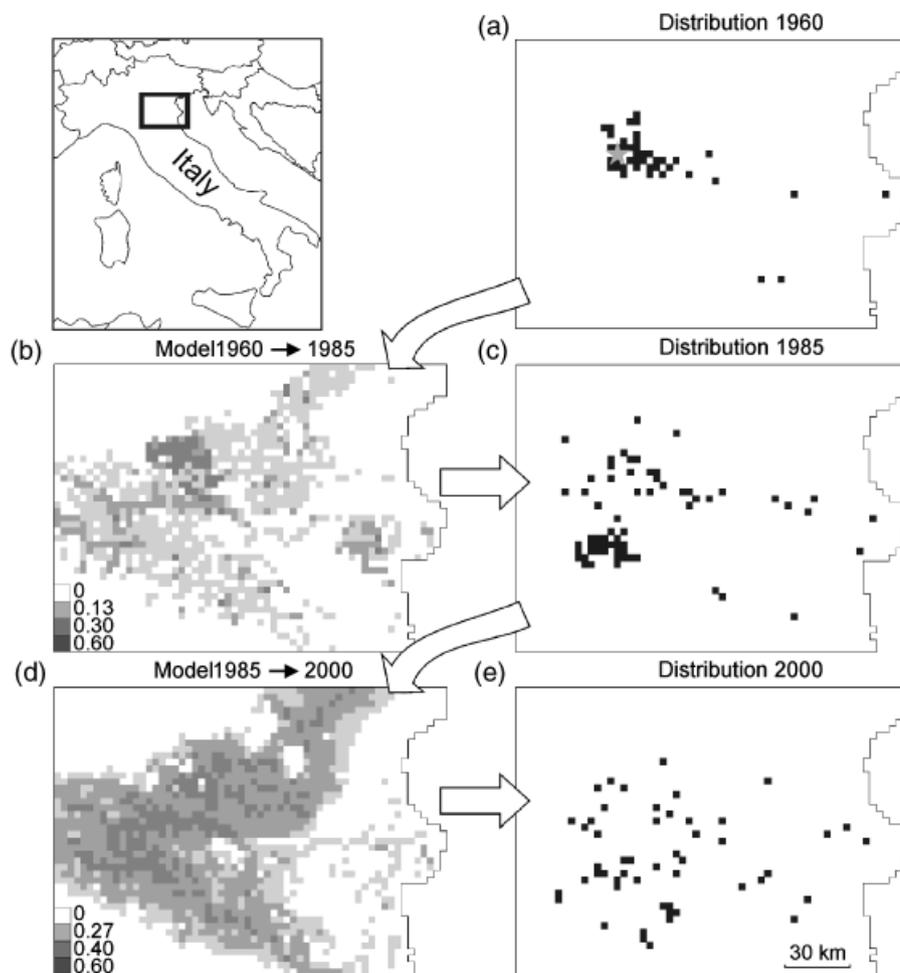


Fig. 1 (a, c, e): Observed distribution of bullfrogs in three temporal steps (1960, 1985 and 2000), and (b, d) suitability predicted using MAXENT models, based on the distribution observed in the previous temporal step, taking into account land-use change. The star in (a) represents the locality of first introduction. The different suitability thresholds (0.13 and 0.27) correspond to the 10th percentile training presence thresholds of models (Pearson *et al.*, 2007).

watercourses and irrigation channels. This is the region of Europe where bullfrogs are present over the largest area (Ficetola *et al.*, 2007b). Historical information indicates that a handful of bullfrogs have been first introduced in a single locality (Fig. 1a) in a single event, during the 1930s (between 1932 and 1937: Albertini, 1970); genetic analyses confirmed a single introduction of very few individuals (Ficetola *et al.*, 2008). For the period 1937–1986, we obtained point data on bullfrog distribution from the literature (Lanza, 1962; Albertini, 1970, 1983; Albertini & Lanza, 1987). These authors monitored the spread of bullfrogs using a combination of field surveys over the whole study area and interviews of local people. For the period 1986–2007, we used an updated version of the database of Ficetola *et al.* (2007a). We then divided the invasion in three temporal steps, corresponding to the time frames covered by the available land-use data: (1) 1937–1965 (98% of data

collected during 1952–1965), hereafter: Distrib1960; (2) 1967–1985 (the majority of data collected during the 1980s), thereafter: Distrib1985; (3) 1987–2007 (95% of data collected after 1990), thereafter: Distrib2000. Modifications of the temporal windows by 2–3 years would produce identical distributions.

Past land-use

We used three land-use/land-cover maps covering the study area and spanning the time frame 1960–2000. The oldest map (geographic scale 1:200 000; legend of 22 classes) was produced by the National Research Council using cadastral datasets collected during the period 1956–1968. We will refer to this map as the 'Map1960'. The 1985 and the 2000 land-use maps (hereafter: Corine1985 and Corine2000) are part of the Corine Land Cover program started in 1985 by the European

Community to generate digital land-use/land-cover maps covering the European continent. These two maps, produced using satellite images taken during late 1980s and 1999–2001, respectively (Buttner *et al.*, 2004), have a legend of 44 classes and a spatial detail comparable to that of a paper map on a scale of 1:100 000. The map obtained using images taken during late 1980s is usually referred to as Corine1990. However, in this study we name it Corine1985 for consistency with the available distribution data. A more detailed description of the three maps can be obtained from Falcucci *et al.* (2007). To obtain a common legend (thematic generalization: Petit & Lambin, 2002), we reclassified the three maps simplifying the legend already proposed by Falcucci *et al.* (2007) and considering five classes: crops (except rice fields), rice fields, forests, artificial areas, inland water. Moreover, to obtain three spatially homogeneous layers, we used a Block Statistics function in ARCGIS 9.2 (ESRI[®], Redlands, CA, USA), producing three raster maps (3 km cell size) indicating for each pixel the percentage occupied by each land-use/land-cover class.

Future land-use

Scenarios of future (2020) land-use change were developed by previous studies (Rounsevell *et al.*, 2006) on the basis of an interpretation of five alternative storylines of the ALARM project (Spangenberg, 2007), representing different assumptions about demographic changes, technological and socioeconomic development (Nakicenovic & Swart, 2000). The five scenarios were: GRAS, a future world orientated towards economic growth approximating the scenario A1F1 of International Panel on Climate Change special report on emission scenarios (SRES); BAMBU (= A2 SRES), a continuation into the future of currently known socioeconomic and policy strategies; BAMBU-SEL, the same as BAMBU plus shock in energy price level; BAMBU-CANE, the same as BAMBU plus contagious natural epidemic; SEDG (= B1 SRES), a scenario focused on the achievement of sustainable development. The scenarios were down-scaled at the spatial resolution of Corine2000 (250 m) using a mix of spatial multinomial logistic regression and Bayesian statistics (Dendoncker *et al.*, 2006). Further details are described elsewhere (Dendoncker *et al.*, 2006; Rounsevell *et al.*, 2006). For the purpose of this study, future land-uses were aggregated to 3 km resolution raster maps, as described for the past land-uses.

Data analysis

We modelled environmental suitability using MAXENT 3.2.1 (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, 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. MAXENT requires presence-only data, and can calculate the relative importance of different environmental features (Phillips *et al.*, 2006). We used a logistic output of MAXENT, with suitability values ranging from 0 (unsuitable) to 1 (optimal habitat) (Phillips & Dudík, 2008). In recent comparisons, MAXENT was among the most effective methods of species distribution modelling, and showed high quality performance with both small and large sample sizes (Elith *et al.*, 2006; Wisz *et al.*, 2008). The reliability of MAXENT has been confirmed by its capacity to predict the outcome of introductions of invasive species outside the native range (Ficetola *et al.*, 2007a) and novel presence localities for poorly known species (Pearson *et al.*, 2007).

We used the following procedure to evaluate the role of land-use in the bullfrog invasion. First, for each temporal step, we used MAXENT to build a model relating species distribution to land-use (per pixel: cropland%, rice field%, forest%, artificial areas%, inland water%) and altitude (average altitude obtained from a digital terrain model with 20 m cell size). We did not include climatic features, since coarse scale models showed that the whole study area has very high climatic suitability (Ficetola *et al.*, 2007a); models including scenarios of climate change suggest that climatic suitability within the study area will remain high in the future (G. F. Ficetola, unpublished results). We did not include water bodies distribution because the small wetlands used by bullfrogs (e.g., ditches, ponds) are not recorded at the resolution of the historical and future land-uses; small water bodies used for irrigation are present at high density in the areas with rice fields or croplands. We included altitude as it can influence frog dispersal and the features of water bodies (e.g., slow stream ditches are only present in lowlands). We developed each model using linear, quadratic and hinge functions (Phillips & Dudík, 2008). Then, we used the land-use of the subsequent temporal step to predict the new bullfrog distribution (See Table 1). Therefore, we built suitability model for Distrib1960 using the Map1960 (Model1960); then we used Corine1985 to project suitability in the subsequent temporal step (Model1960 → 85) (Table 1, Fig. 1a and b). Similarly, we built the model for Distrib1985 using Corine1985 (Model1985); then we used Corine2000 to project

Table 1 Distribution data and environmental layers used to build the models predicting bullfrog expansion

Model	Input data	Environmental layers	
		For model calibration	For model projection
Model1960	Distrib1960	Map1960	Map1960
Model1960 → 1985	Distrib1960	Map1960	Corine1985
Model1985	Distrib1985	Corine1985	Corine1985
Model1985 → 2000	Distrib1985	Corine1985	Corine2000
Model2000	Distrib2000	Corine2000	Corine2000
Model2000 → 2020	Distrib1985	Corine2000	5 future scenarios

See the text for the acronyms.

suitability (Model1985 → 2000) (Table 1, Fig. 1c and d). Finally, we built the model for Distrib2000 using Corine2000 (Model2000) and we projected the suitability into the future using the five 2020 scenarios (Table 1). Rice fields were a category not available in the future scenarios, therefore for Model2000 we pooled rice fields with other croplands. Pooling rice fields with croplands did not affect these models, because the models based on Corine2000, pooling or not pooling rice fields with croplands, were identical (results not shown). In each model, we assumed that a cell was suitable for bullfrog presence if its suitability score was greater than the 10th percentile of training presence points (Pearson *et al.*, 2007). We then examined the omission and commission error of models to evaluate their predictive performance (Jiménez-Valverde *et al.*, 2008).

We restricted our analysis to an area of high bioclimatic suitability (180 km × 132 km) individuated by Ficetola *et al.* (2007a), surrounding the introduction point. Genetic data showed that bullfrog dispersion can occur at this spatial scale (Austin *et al.*, 2004). As there are no major barriers for dispersion (e.g., mountains), we assume that the whole area can be potentially colonized in a few generations.

We used two methods to evaluate the ability of our models to predict the bullfrog spread. First, we used a χ^2 test (1 df) to compare observed frequencies of correct and incorrect predictions, and therefore to evaluate if our models predict distribution in the subsequent temporal step significantly better than expected under random expectations (Roura-Pascual *et al.*, 2004). Second, we built logistic regression models relating the observed bullfrog distribution in a temporal step to the suitability predicted on the basis of the two models built for the previous step (e.g., we predicted Distrib1985 on the basis of either Model1960 and Model1960 → 85). We assessed significance of the logistic regression using likelihood ratio. We then used an information-theory approach, based on Akaike Information Criterion (AIC) to compare the relative ability of models (Burnham & Anderson, 2002), and therefore to evaluate if taking into

account land-use changes actually improves model predictions. This analysis assumes pseudo-absences in cells where bullfrogs have not been observed. Despite that pseudo-absences are not always reliable (Engler *et al.*, 2004), we used this approach to compare the performance of different models on the same distribution data, therefore the bias caused by pseudo-absences was constant between models compared.

Results

During the period 1937–1965, bullfrogs were recorded in 43 pixels (3 km × 3 km) (Fig. 1a); most of presence localities were clumped close to the introduction locality. During the period 1966–1986, bullfrogs' distribution was less clumped and the species was present in 64 pixels. During the period 1987–2007, bullfrog presence has been recorded in 51 pixels.

Predicting the past invasion

The model built for 1960s showed that bullfrog presence was associated to high rice fields%, low elevation, intermediate/high cropland%, and intermediate levels of forest%; rice field% was the variable with the largest contribution (56% of explained variation) (Table 2). Model1960 → 85 predicted an expansion of areas suitable for bullfrogs, mostly south-east to the area of introduction. The observed bullfrog expansion followed the same overall pattern predicted by the model (Fig. 1b and c).

The model built using Distrib1985 showed that bullfrogs were associated to intermediate/high cropland% and low elevation (Table 2). In this model, rice fields and forest% explained only a minor percentage of variation (3% or less). Model1985 → 2000 predicted an expansion of areas suitable for bullfrogs, mostly in the southern and in the northern part of the study area (Fig. 1d and e). Distrib2000 only slightly expanded the area of occurrence observed in Distrib1985. Nevertheless, it should be noted that the localities with new

Table 2 Predictive performance of models, evaluated by examining omission and commission errors

Model	Environmental variables*	test N	Omission error		Commission error		χ^2	P
			Pres. correct	Pres. incorrect	Abs. correct	Abs. incorrect		
Model1960	Rice fields, elevation, cropland, forest	43	39 (11)	4 (32)	1837 (1809)	581 (609)	99.6	<0.001
Model1960 → 1985		64	47 (20)	17 (44)	1660 (1633)	737 (764)	52.3	<0.001
Model1985	Elevation, cropland	64	58 (34)	6 (30)	1146 (1122)	1251 (1275)	37.0	<0.001
Model1985 → 2000		51	42 (27)	9 (24)	1158 (1142)	1252 (1267)	18.5	<0.001
Model2000	Elevation, cropland	51	45 (26)	6 (25)	1190 (1171)	1220 (1238)	28.3	<0.001

The table reports the correct and incorrect predictions of presence and absence, and Pearson’s χ^2 with 1 df (Roura-Pascual *et al.*, 2004). Suitability of each cell was based on the 10th percentile of training presence points (Pearson *et al.*, 2007). In parenthesis, the values under random expectations.

*Variables accounting for >5% of explained variation. The variables with the largest independent contributions are first in the lists.

Table 3 Relative performance of GLMs, based on MAXENT models, in predicting bullfrog expansion, evaluated using Akaike’s Information Criterion (AIC)

Distribution to be predicted	Includes temporal change?	Model	AIC
Distrib1985	Yes	Model1960 → 1985	549.6
	No	Model1960	571.5
Distrib2000	Yes	Model1985 → 2000	480.06
	No	Model1985	480.81

The two models including temporal changes in environmental variables (Model1960 → 1985, Model1985 → 2000) are compared against models not including the temporal changes (Model1960, Model1985).

records are within the high probability areas predicted by Model1985 → 2000 (Fig. 1d and e).

All models tended to predict well observed presence localities (Table 2). Conversely, all models tended to overpredict suitable areas, i.e., predicted suitability in a large number of pixels where bullfrog presence has not been recorded yet (Fig. 1, Table 2).

Using logistic regression, Model1960 → 1985 predicted Distrib1985 significantly better than random expectations (likelihood ratio test, $\chi^2_1 = 47.845$, $P < 0.001$). Its performance was much better than the one of the model not taking into account temporal change in environmental variables (difference in AIC, $\Delta AIC = 21.9$) (Table 3). Similarly, Model1985 → 2000 predicted Distrib2000 significantly better than random expectations ($\chi^2_1 = 20.280$, $P < 0.001$). Its performance was better than that of the model not taking into account changes in environmental variables, but the difference was limited ($\Delta AIC = 0.75$) (Table 3). The small difference between the two models probably occurred because land-use and consequently suitability

did not change considerably between 1980s and 2000 (Falcucci *et al.*, 2007). For instance, the suitability predicted by Model1985 was very similar to that predicted by Model1985 → 2000 ($r = 0.97$). Conversely, land-use strongly changed from 1960 to 1985 (as described in Falcucci *et al.*, 2007), and the correlation between Model1960 → 1985 and Model1960 was weaker ($r = 0.54$).

Scenarios of future invasion

Model2000 was very similar to Model1985 (Figs 1 and 2, Table 2), and showed that bullfrogs were associated to intermediate and high cropland percentage and low elevation. As the previous models, Model2000 predicted presence with high accuracy, but predicted suitability in many pixels without bullfrog records (Table 2).

The projection using the 2020 scenarios did not show strong changes in suitability. The results were extremely similar among the five alternative scenarios, with only minor differences (Fig. 2). These results were essentially linked to the high stability in land-use projection predicted for our study area for the timeframe considered, where intensive agriculture is and will continue to be the dominant land-use class.

Discussion

Suitability models, based on land-use and distribution data, predicted the invasion of bullfrogs in Northern Italy relatively well. Our analysis used information collected in three subsequent temporal steps: we predicted bullfrog distribution in the 1980s using data collected during the 1960s; similarly, we predicted present-day distribution using the 1980s data. This approach is a true validation of the models; our results therefore provide a measure of the effectiveness of

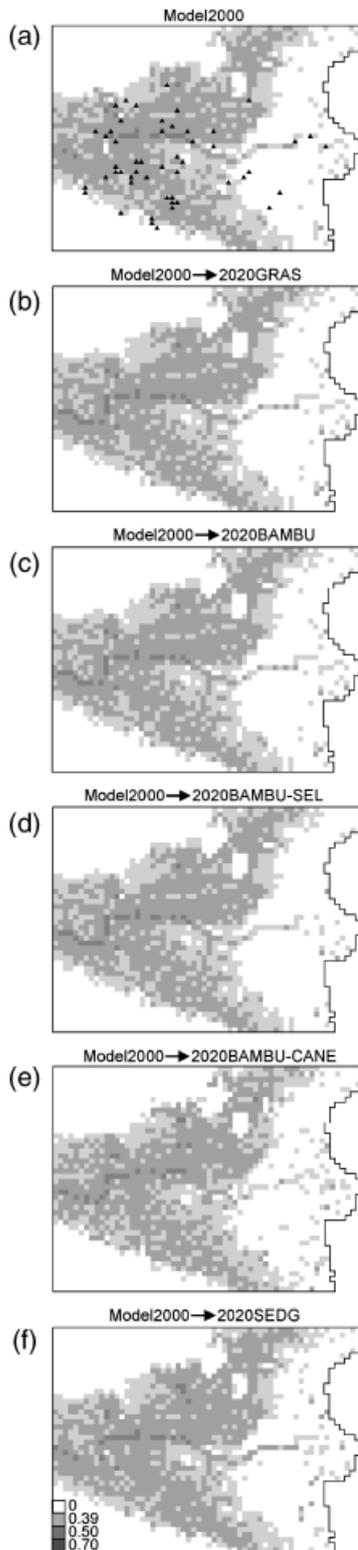


Fig. 2 (a) Observed distribution of bullfrog for the temporal step 2000, and environmental suitability of Model2000. (b–e): projected suitability in the future (2020) using five scenarios of land-use change.

suitability models trying to predict the spread of invasive species. Habitat suitability models are often used for this task, with applications in risk assessment or in control strategies (e.g., Ward, 2007; Evangelista *et al.*, 2008; Nielsen *et al.*, 2008; Ficetola *et al.*, 2009). However, long term historical data are seldom available (Loo *et al.*, 2007; Vallecio *et al.*, 2009), and it is therefore difficult to evaluate whether model predictions correspond to the actual invasion dynamics. Our analysis suggests that suitability models have a good performance in predicting invasions. Nevertheless, the comparison of predictions with the actual invasion dynamics reveals important points. First, the match between predicted suitability and invasion data was not perfect, highlighting potential issues. Second, the most important variables to explain the bullfrogs' distribution were not the same in the three temporal steps, confirming the complexity of extrapolating model results in time (Guisan & Thuiller, 2005). Most importantly, despite altitude does not change in time, other environmental variables (land-use) are not constant in time; the incorporation of environmental changes in suitability models can be essential to correctly understand invasion dynamics.

Models and real invasion: reliability and discrepancies

The predictions of our models showed high sensitivity, i.e., most of presence records corresponded to high suitability pixels, on the basis of models developed in the previous temporal step (Table 2). Bullfrogs were strongly associated to lowland agricultural areas; for the 1960s model, rice fields were the land-use with the highest suitability (Table 2). Water bodies are particularly important for bullfrogs: tadpoles usually require 2 years for metamorphosis, and the adults are strongly dependent on waterbodies (Graves & Anderson, 1987). In the study area, agriculture is associated to a dense network of ditches and reservoirs: bullfrogs can take advantage of the increased availability of permanent wetlands used for irrigation (Maret *et al.*, 2006). Climatic suitability models have been deemed to predict suitability at a too coarse spatial scale, with the delineation of too large areas having limited usefulness for conservation actions (Heller & Zavaleta, 2009). For example, based on climatic data, the whole study area had a high suitability for bullfrogs (Ficetola *et al.*, 2007a). The integration of climatic data with land-use or other data recorded at finer scale can help to refine predictive models, and to focus on the areas where invasion risk is high at a spatial scale more appropriate for conservation.

While our models showed high sensitivity, they all tended to overpredict suitability: bullfrogs have never

been recorded in large areas, which are predicted as suitable (Table 2, Fig. 1). These commission errors may have occurred for several reasons. First, the knowledge of bullfrog distribution is imperfect, because fine scale monitoring has not been performed over the whole study area. Efforts to improve our knowledge are currently ongoing (Ficetola *et al.*, 2007b; Societas Herpetologica Italica, 2008), but several years will be needed for a complete knowledge of bullfrog distribution. Moreover, a model can fail because of the lack of key predictors affecting distribution, including the presence of predators/competitors. Our models were limited by the unavailability of some environmental variables in maps of past and future land-use. Furthermore, invasive species can be absent from suitable areas where they have not been introduced, or where they have not been able to disperse. In principle, bullfrogs might colonize the whole study area in a few generations, given their known dispersal ability (Austin *et al.*, 2004). However, animal movements are strongly influenced by landscape features (Bélisle, 2005; Fahrig, 2007). Amphibians are particularly susceptible to fragmentation and to the presence of barriers (Cushman, 2006): the study area is strongly modified by humans, and elements such as roads and urbanization may have precluded colonization (Ficetola *et al.*, 2007c).

Finally, the models developed for the three temporal steps were not identical. Two variables were consistently important in all models (i.e., elevation and cropland presence; Table 2). Conversely, rice fields were the most important variable in the 1960s, while they were unimportant in the subsequent temporal steps. The change of the explanatory power of rice field is probably related to strong modifications in agricultural practices. In Italy, rice cultivation traditionally requires the flooding of fields, and the presence of associated water reservoirs. Until the 1960s, the permanence of deep water within rice fields allowed farmers to perform aquaculture within the rice fields; bullfrogs and other amphibians took advantages of this environment (Albertini, 1970; Lupotto, 2005). In the last decades, agricultural practices strongly changed and the new technologies have modified the suitability of given land-use classes for many species. In fact, new rice cultivars require less water, with fields and irrigation network retaining water for shorter times and at lower depths, thus strongly reducing the ecological value of rice fields for amphibians (Lupotto, 2005). As a consequence, the simple presence of a land-use category (rice field in our case) can be a misleading indicator of habitat suitability, because key ecological attributes related to land management have been changed. This is a further example of the complexities and pitfalls linked to extrapolating model predictions in time.

Integrating temporal variations of the environment

The models including temporal changes of land-use showed a better prediction of the invasion dynamics and of the changes in distribution occurring through time. The global environment is changing at an unprecedented rate, and land-use changes have major impacts on biodiversity distribution (Sala *et al.*, 2000). To date, most attention has been devoted on the effect of land-use change on native biodiversity. However, land-use is also important for the establishment and the spread of AIS. Land-use modifications have therefore important implications for the study and management of AIS.

First, land-use modifications can strongly affect the dynamics of invasive species. For example, in Model1960 bullfrogs were strongly associated to rice fields, and the model predicted high suitability in the East of the study area, where rice field density was high (Fig. 1b). However, the abundance of rice fields declined in the study area in the last decades of the 20th century, and this probably reduced the eastward bullfrog expansion. Both the land cover (i.e., the abundance of rice fields) and the land management practices (i.e., the way rice fields are cultivated) are not constant in time, and are subjected to the constraints of regional planning. Therefore, an integration of control strategies with the planning of land-use can have an important role for the management of invasive species, and to reduce their spread. Furthermore, ecological models are often used to predict invasion dynamics, with important applications in conservation strategies. However, species distribution models usually assume a static land-use. When these data are available, taking into account environmental modification can greatly improve model performance. Similarly, the combination of models with scenarios of future environmental changes can provide important insights that can be used to drive conservation strategies and regional planning. Our results therefore call for an increased consideration of temporal change of environmental variables when modelling distribution and suitability.

Our future land-uses do not constitute a 'prediction', but are the outcomes that can arise under different assumptions, and with a degree of coherence in the trends of future development (Rounsevell *et al.*, 2006). Our models showed good performance in predicting historical changes of bullfrog distribution (Fig. 1), and our results were stable under various future scenarios (Fig. 2), suggesting that our conclusion on are robust. Nevertheless, projection of suitability models outside the area of calibration are always challenging (Guisan & Thuiller, 2005), and should be considered with cautions. For example, the dynamic of the study area can be altered by unpredicted factors: human-related, climatic or biotic.

Despite being human dominated, the study region is adjacent to some of the areas of Italy with the highest biodiversity irreplaceability values (Maiorano *et al.*, 2007), particularly for freshwaters. These unique freshwater communities are threatened by the joint effects of land modifications and invasive species (Gherardi *et al.*, 2008). As the spread of AIS is strongly related to land-use changes, an appropriate planning, with coordination between conservation and development policies, can help to achieve the management targets, with optimization of resources.

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