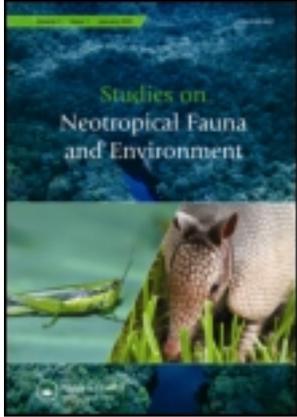


This article was downloaded by: [Universidad de Chile]

On: 20 January 2014, At: 06:00

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Studies on Neotropical Fauna and Environment

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/nnfe20>

Invasive African clawed frog *Xenopus laevis* in southern South America: key factors and predictions

Gabriel Lobos^{a b}, Pedro Cattán^{b c}, Cristian Estades^d & Fabian M. Jaksic^a

^a Center for Advanced Studies in Ecology & Biodiversity (CASEB), Pontificia Universidad Católica de Chile, Santiago, Chile

^b Centro de Estudios de Vida Silvestre (CEVIS), Facultad de Ciencias Veterinarias y Pecuarias, Universidad de Chile, Santiago, Chile

^c Departamento de Ciencias Biológicas, Facultad de Ciencias Veterinarias y Pecuarias, Universidad de Chile, Santiago, Chile

^d Laboratorio Ecología de Vida Silvestre, Facultad de Ciencias Forestales, Universidad de Chile, Santiago, Chile

Published online: 19 Feb 2013.

To cite this article: Gabriel Lobos, Pedro Cattán, Cristian Estades & Fabian M. Jaksic (2013) Invasive African clawed frog *Xenopus laevis* in southern South America: key factors and predictions, *Studies on Neotropical Fauna and Environment*, 48:1, 1-12, DOI: [10.1080/01650521.2012.746050](https://doi.org/10.1080/01650521.2012.746050)

To link to this article: <http://dx.doi.org/10.1080/01650521.2012.746050>

PLEASE SCROLL DOWN FOR ARTICLE

Taylor & Francis makes every effort to ensure the accuracy of all the information (the "Content") contained in the publications on our platform. However, Taylor & Francis, our agents, and our licensors make no representations or warranties whatsoever as to the accuracy, completeness, or suitability for any purpose of the Content. Any opinions and views expressed in this publication are the opinions and views of the authors, and are not the views of or endorsed by Taylor & Francis. The accuracy of the Content should not be relied upon and should be independently verified with primary sources of information. Taylor and Francis shall not be liable for any losses, actions, claims, proceedings, demands, costs, expenses, damages, and other liabilities whatsoever or howsoever caused arising directly or indirectly in connection with, in relation to or arising out of the use of the Content.

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden. Terms & Conditions of access and use can be found at <http://www.tandfonline.com/page/terms-and-conditions>

ORIGINAL ARTICLE

Invasive African clawed frog *Xenopus laevis* in southern South America: key factors and predictions

Gabriel Lobos^{a,b*}, Pedro Cattán^{b,c}, Cristian Estades^d & Fabian M. Jaksic^a

^aCenter for Advanced Studies in Ecology & Biodiversity (CASEB), Pontificia Universidad Católica de Chile, Santiago, Chile;

^bCentro de Estudios de Vida Silvestre (CEVIS), Facultad de Ciencias Veterinarias y Pecuarias, Universidad de Chile, Santiago, Chile; ^cDepartamento de Ciencias Biológicas, Facultad de Ciencias Veterinarias y Pecuarias, Universidad de Chile, Santiago, Chile; ^dLaboratorio Ecología de Vida Silvestre, Facultad de Ciencias Forestales, Universidad de Chile, Santiago, Chile

(Received 22 September 2011; accepted 25 October 2012)

The African clawed frog *Xenopus laevis* is one of the most widely distributed amphibians in the world. It has invaded an area of approximately 21,200 km² since its naturalization in Chile in the early 1980s. Currently, there is scant knowledge on the factors and processes underlying its distributional pattern. We constructed a bioclimatic niche model considering areas susceptible to be invaded (coarse model). At a local scale, we explored topographic, ecological, and anthropic variables, to identify which of these have the greatest predictive power for the expansion of this African species in southern South America. Not surprisingly, the projection of the distribution of *Xenopus laevis laevis* in southern Africa had the highest probabilities associated with the mediterranean area of the Cape region. From the habitat projection on southern South America, we predict high habitat suitability for this species in the mediterranean region of Chile. Nonetheless, the coastal desert of northern Chile, the Atlantic coasts of Argentina (32° to 54° S), Uruguay, southern Brazil, the north-central part of Argentina (22° to 35° S) and the central-southern region of Bolivia, are potentially suitable as well. At a local scale, we confirm that lentic aquatic environments, with slow drainage and murky waters, highly connected, human-disturbed, and part of an irrigation system of small streams and canals, account for the highest probabilities of successful establishment of *X. laevis* within the area of invasion. Based on our habitat suitability models, we expect the African clawed frog to invade farther north and farther south in Chile. We warn that the pet trade and subsequent release of African clawed frog to the wild pose a serious invasion risk to other countries of the southern cone of South America.

Keywords: invasion risk; niche modeling; *Xenopus laevis*; Argentina; Brazil; Chile; Uruguay

Introduction

A key aspect of biological invasions is our ability to predict habitat suitability of new areas at risk of being invaded (Kennedy et al. 2002). Thus, understanding the spatial dynamics of biological invasions is an important tool for preventing the invasion of new areas, monitoring the course of expansion, and for defining management priorities as a function of invasion risk (Ceréghino et al. 2005). Gido et al. (2004) have highlighted the importance of analyzing the patterns associated with bio-invasions over large scales such as watersheds or regions. However, the current lack of quantitative data imposes important impediments for the prediction of global distributions of invasive species. The recent development of methodologies that maximize the extraction of information from simple datasets, such as presence–absence, and then associate them with geographic information, has been a valuable contribution toward this aim (Bessa-Gomes & Petrucci-Fonseca 2003). Ecological Niche

Models are useful tools for predicting the potential distribution of invasive species (Peterson & Vieglais 2001; Peterson et al. 2003; Ficetola et al. 2008; Giovanelli et al. 2008). Climatic similarity between the native distribution range and potential areas of invasion has been considered a key factor in predicting the success of a biological invasion (Thuiller et al. 2004, 2005, 2007). Accordingly, information on the distribution in the native range of a species can be used to project its potential distribution in new areas (Ficetola et al. 2007). Nevertheless, at the local scale, factors such as propagule pressure, competition, predation and human activities also play a relevant role for the establishment of exotic species, but these factors cannot be accounted for in general predictive models, such as climate matching (Yiming et al. 2006; Ficetola et al. 2007).

The African clawed frog, *Xenopus laevis*, is one of the most widely distributed amphibian invaders in the world. It is native to a large part of sub-Saharan

*Corresponding author. Email: galobos@ug.uchile.cl

Africa, where six subspecies have been identified: *laevis*, *petersii*, *poweri*, *victorianus*, *sudanensis* and *bunyonensis* (Kobel et al. 1996). The African clawed frog has successfully invaded California (McCoid & Fritts 1980a, 1980b), and other states in the USA (Arizona, Colorado, Florida, Massachusetts, North Carolina, Texas, Utah, Virginia, Wisconsin and Wyoming; Crayon 2005; Krysko et al. 2011), South Wales in the UK (Measey 1998, 2001; Measey & Tinsley 1998), France (Fouquet & Measey 2006), Italy (Lillo et al. 2005, 2011), Portugal (Rebelo et al. 2010), Japan (Kobayashi & Hasegowa 2005; Arao & Kitano 2006; Kokuryo 2009), and Chile (Lobos et al. 1999; Lobos & Measey 2002; Lobos & Jaksic 2005). In spite of this wide distribution range, the African clawed frog has not been perceived as a species that causes impacts on biodiversity, in contrast to amphibians such as *Eleutherodactylus coqui*, *Lithobates catesbeianus* and *Rhinella marina* (Lowe et al. 2000). This perception is contradictory to the fact that this anuran has invaded extensive areas in several continents (Lillo et al. 2011), and to its importance as a vector of the fungus *Batrachochytrium dendrobatidis* (Weldon et al. 2004; Solís et al. 2010), which is the agent of chytridiomycosis, considered one of the main causes of global amphibian decline and extinction (Berger et al. 1998; Pounds et al. 2006). In addition, for the Chilean batrachofauna, *X. laevis* represents a large anuran in comparison to native ones, and thus constitutes a potential predator of their larvae as well as of native fishes (Lafferty & Page 1997).

Although released to the wild in Chile in 1973, the first record of a naturalized population of *X. laevis* occurred at the beginning of the 1980s (Veloso & Navarro 1988). Since then, it has rapidly expanded, invading an area of about 21,000 km² in the mediterranean region with an estimated dispersal speed between 3.1 and 5.4 km year⁻¹ (Lobos & Jaksic 2005). At present, underlying processes of its dispersal are little explored, and we lack an estimation of the extent of Chilean territory threatened by this invasion. In this study, our goal is to create a predictive model of the areas in South America susceptible to invasion by *X. laevis*, for which we used information on its native distribution in South Africa and from the confirmed area of invasion in Chile. Further, we explored which topographic, ecological, and anthropic variables have the greatest predictive value at a local scale of establishment.

Material and methods

Bioclimatic model

Up to now, the taxonomic definition of *X. laevis* has been complex, with an open discussion on the

recognition of species and subspecies (Kobel et al. 1996; Measey & Channing 2003; Evans et al. 2011; Frost 2011). In this scenario, we built our bioclimatic model considering the data on the native distribution of the lineage which inhabits the mediterranean zone of the Cape Region of South Africa (Kobel et al. 1996; Measey & Channing 2003), based on the ideas of Measey et al. (2012), and due to the fact that this lineage includes the type locality for this species (Frost 2011) as well as historic records for its global trade. We first obtained 72 geo-referenced records of presence from Measey (2004a). In doing so we digitalized in a geographic information system (GIS) the distribution indicated for the mediterranean zone of the Cape Region of South Africa. Then we used the Animal Movement SA v.2.04 Beta (Arc-View 3.3) tool, in order to generate random points with a minimum distance of 1000 m between them (Arc-View 3.3). For South Africa we also considered records of the HerpNet database (2007) and our own direct collections (12 records). We additionally incorporated a total of 73 geo-referenced records from the invaded area in Chile (our own data, Appendix 1), as it is important to consider information from the invaded range, where the species can find environmental conditions differing from its original range (Steiner et al. 2008; Beaumont et al. 2009). Spatial autocorrelation represents a major problem in this type of study. Thus, in order to decrease its effects, we eliminated those data locations previously too close together (less than 1000 m) or duplicated in the database (Phillips et al. 2006).

We selected environmental parameters from a total of 19 bioclimatic variables and an altitudinal layer (Giovanelli et al. 2008), all with a resolution of 30 arc-seconds (Hijmans et al. 2005; available at <http://www.worldclim.org>). Several methods have been proposed for the selection of these variables; in our case we followed Marino et al. (2011). First, we summarized the information for each location by applying a principal component analysis (PCA), to identify the most representative variables of environmental conditions in our study area (Tognelli et al. 2009). The PCA was useful to identify a set of variables strongly associated with the first two axes of ordination (with positive and negative charges), which together accounted for 90% of the variation between locations (see Table 1). In order to reduce redundancy between any two variables, we proceeded to eliminate those that had high correlation (Pearson correlation values > 0.6). We ran models with combinations of minimally correlated variables (see Table 2).

Based on previous studies that demonstrate the high performance of the software MAXENT (Elith et al. 2006; Hernández et al. 2006; Tognelli et al. 2009), we used the version MAXENT 3.3.1 to model

Table 1. Results of principal component analysis (PCA) for *Xenopus laevis laevis* presence in localities.

Variables	PCA loadings			
	PC1	PC2	PC3	PC4
Annual mean temperature	-0.0082	0.0540	-0.0010	0.0174
Mean diurnal range	0.0289	0.0202	0.0262	0.0731
Isothermality	0.0002	0.0012	0.0078	0.0069
Temperature seasonality	0.8803	0.2912	-0.3638	0.0404
Maximum temperature of warmest month	0.0217	0.0627	0.0003	0.0295
Minimum temperature of coldest month	-0.0310	0.0314	-0.0190	-0.0872
Temperature annual range	0.0527	0.0314	0.0192	0.1167
Mean temperature of wettest quarter	-0.0108	0.0724	0.0329	0.2932
Mean temperature of driest quarter	-0.0053	0.0411	-0.0255	-0.1562
Mean temperature of warmest quarter	0.0022	0.0558	-0.0062	0.0206
Mean temperature of coolest quarter	-0.0203	0.0478	0.0009	0.0176
Annual precipitation	-0.1666	-0.3933	-0.6729	0.4086
Precipitation of wettest month	-0.0208	-0.0615	-0.1208	-0.0874
Precipitation of driest month	-0.0079	-0.0093	-0.0050	0.1123
Precipitation seasonality	0.0063	-0.0065	-0.0356	-0.2768
Precipitation of wettest quarter	-0.0605	-0.1833	-0.3556	-0.3219
Precipitation of driest quarter	-0.0225	-0.0355	-0.0181	0.3599
Precipitation of warmest quarter	-0.0217	-0.0337	-0.0180	0.4252
Precipitation of coolest quarter	-0.0639	-0.1866	-0.3624	-0.4261
Elevation	0.4271	-0.8150	0.3706	-0.0115
Proportion of variance	75.34	14.78	9.15	0.53
Cumulative proportion	75.34	90.12	99.27	99.80

Note: Values in bold indicate the higher loads associated with the first two PCA axes.

Table 2. Models of *Xenopus laevis laevis* habitat suitability.

Variables	Percentage contribution of variables				
	Model A	Model B	Model C	Model D	Model E
Temperature seasonality	53.2			39.1	
Maximum temperature of warmest month		19.5			18.2
Minimum temperature of coolest month		59		22.3	59.5
Temperature annual range			32.1		
Mean temperature of warmest quarter	26.4		41.2	28.2	
Annual precipitation				10.4	
Precipitation of coolest quarter	19.3	21.5	23.9		19.4
Elevation	1.1		2.8		2.8
Model performance					
Training AUC	0.993	0.985	0.985	0.996	0.990
Test AUC	0.990	0.976	0.975	0.995	0.985

Notes: In gray are highlighted the variables for each model that contained the most useful information alone and/or the information not present in other variables, according to the Jackknife test. Values in bold indicate the best model.

the habitat of *Xenopus* (Phillips et al. 2006). This algorithm estimates the geographic distribution of a species using its geo-referenced presence at well-defined localities and the values of their associated bioclimatic variables, generating a probability distribution with maximum entropy, subjected to the restrictions produced by the incomplete knowledge related to the distribution of that particular species (Phillips et al. 2006). The end product corresponds to a projection of habitat suitability values ranging from 0 (inadequate habitat) to 1 (optimum habitat). To develop the model we randomly selected 75% of the occurrence points, and used the remaining 25% to validate the

model. We evaluated the model performance using the receiver operating characteristics curve (ROC), which results from plotting the sensitivity values (the fraction of the true positives, against 1 minus the fraction of false positives, or specificity) for all thresholds of the model. Herein we applied the minimum training presence threshold; areas above this value are referred to as suitable (Measey et al. 2012). The area under the curve (AUC) of the ROC measures the ability of a model to discriminate between sites where a given species is present and sites where it is absent. Values of AUC less than 0.5 correspond to models with predictive discrimination abilities no better than random, while values

closer to 1 account for models with better predictive ability (Fielding & Bell 1997). We used a Jackknife test (MAXENT 3.3.1) to evaluate the importance of each environmental variable to explain the distribution. The model was re-run by excluding each environmental variable and then by using each variable in isolation (Ficetola et al. 2007).

Our end product consisted of a projection (continuous map) of the habitat suitability for *X. laevis laevis* in southern South America. Values lower than the threshold were transformed to zero. In order to avoid spurious projections, we validated only areas within the range of the calibration area, using the clamping function available in MAXENT 3.3.1. Finally, we superimposed the prediction map on a map of the area currently invaded by the African clawed frog in Chile.

Evaluation of the determinant factors in the distribution of Xenopus laevis in Chile

We surveyed 128 sites (74 positive or presences and 54 negative or absences) within the area invaded in central Chile, between the years 2002 and 2009. Survey points were represented in a geographic information system in UTM coordinates, zone 19 South, datum WGS 84 (ArcGIS® 9.2). To determine the factors explaining the presence/absence of the species, we defined a buffer area of 500 and 3000 m around each site (models I and II, respectively), in order to measure a set of 14 topographical, ecological, and anthropic variables (see Table 3).

To explore which variables were correlated with the presence of *X. laevis*, we constructed a generalized linear model with a binomial distribution (multiple logistic regressions). The presence/absence data for the species were utilized as a response variable of the topographic, ecological, and anthropic variables (see Table 3). To find the best model at the two spatial scales (500 and 3000 m), we used a stepwise backward selection approach and applied Akaike's information criterion for selection of model (Harrel 2001). To develop the model we used the R package (R Development Core Team 2005).

Results

Prediction of the invasion area

We obtained a combination of five models, considering minimally correlated variables (Table 2). Three models retained elevation as a variable, although with a low contribution to them. Temperature seasonality was the main contributor in two models (A and D) and temperature of the coldest month in models B and E; variables related to rainfall had a low to medium contribution. All models indicated a good performance, although D provided the best model. We focus on model D, with the highest AUC, to describe the potential African clawed frog invasion in southern South America. To discriminate between sustainable and unsustainable areas, we use the lowest prediction for a place in the presence of the species

Table 3. Topographic, ecological, and anthropic variables utilized in the study.

Variables	Attributes
<i>Topographic</i>	
Altitude	Expressed in m asl, recorded in the field with GPS.
Slope	Classified as 1 = slight < 5°, 2 = moderate 5–15° and 3 = steep > 15° (LaRue & Nielsen 2008). Calculated from a digital elevation model and field estimation.
Density of water courses	Sum of the length of water channels (m) within each site, divided by the area of its polygon (km ²) (LaRue & Nielsen 2008). Maps are available at http://sigweb.sag.gob.cl/sagmaps/
<i>Ecological</i>	
Naturalness	Classified as a natural (lake, stream) or artificial (irrigation pond, irrigation canal, reservoir) environment.
Type of environment	Lentic (still water) or lotic (running water).
Permanence	With water seasonally or permanently.
Turbidity	Classified as 1 = transparent water, 2 = somewhat turbid, 3 = murky.
Water flow	1 = low velocity (lentic), 2 = medium velocity or 3 = high velocity.
Distance to source populations	Proximity measure expressed as the distance (through a water course, in m) to the nearest known infested neighbor. For isolated sites or those in a different basin, a value of 50 km was assigned. This variable was only incorporated in the large-scale model (3 km radius buffer).
<i>Anthropic</i>	
Road density	Sum of the length of roads (m) within each site divided by the area of the polygon (km ²) (LaRue & Nielsen 2008). Maps available at http://sigweb.sag.gob.cl/sagmaps/
Density of irrigation canals	Length of canals (m) in a site divided by the area of the polygon (km ²) (LaRue & Nielsen 2008). Maps available at http://sigweb.sag.gob.cl/sagmaps/
Distance to populated area	Distance (m) to the closest populated area. Maps available at http://sigweb.sag.gob.cl/sagmaps/
Human impact index	Mean value of the index of human impact of Sanderson et al. (2002) for each site.

as the minimum threshold of presence (Marino et al. 2011). For instance, some invaded localities in central Chile have a predictive value as low as 0.07.

The projection of the bioclimatic model in southern South America predicts high probability for the establishment of *X. laevis* in the mediterranean region of Chile (at present the only region invaded in the southern cone). Novel areas with potential to be invaded are along the desert coast of northern Chile, along the Atlantic Coast of Argentina (between 32° and 54° S, with a subarea of high probability between 43° and 47° S), the Atlantic coast of Uruguay and southern Brazil, as well as the north-central region of Argentina and Bolivia (between 18° and 31° S) (Figure 1).

Comparing all models, D was the most conservative (Figure 2), while the other larger models generated predictions for southern Brazil, Uruguay and the Atlantic coast of Argentina. Some models, such as A, B and C predict the spread over the Pacific coast of Peru; model A includes eastern Paraguay and B involves areas along the arid diagonal for much of South America.

For the region of southern South Africa, model D yielded highest probabilities of presence of *X. laevis*

associated with the mediterranean region of the Cape. The *Xenopus laevis laevis* range extends toward the northern region of South Africa, where it is replaced by other subspecies and by different *Xenopus* species.

The Jackknife test indicated seasonal temperature fluctuation as the variable with highest predictive power (39.1%), followed by mean temperature of the warmest quarter (28.2%), minimum temperature of coldest month (22.3%), and annual precipitation (10.4%).

Determinant factors in the distribution of *Xenopus laevis* in Chile

The presence/absence of the African clawed frog in Chile was influenced by different variables, depending on the scale of analysis. Table 4 shows the models best at explaining the presence of the species at a given site.

The two models incorporated the variability associated with qualitative variables such as water flow and type of environment (Table 2). Model II was more sensitive to geographic variables for predicting the presence of the African clawed frog in the invaded area. It showed a nearly significant positive effect of density of irrigation canals and a significant negative

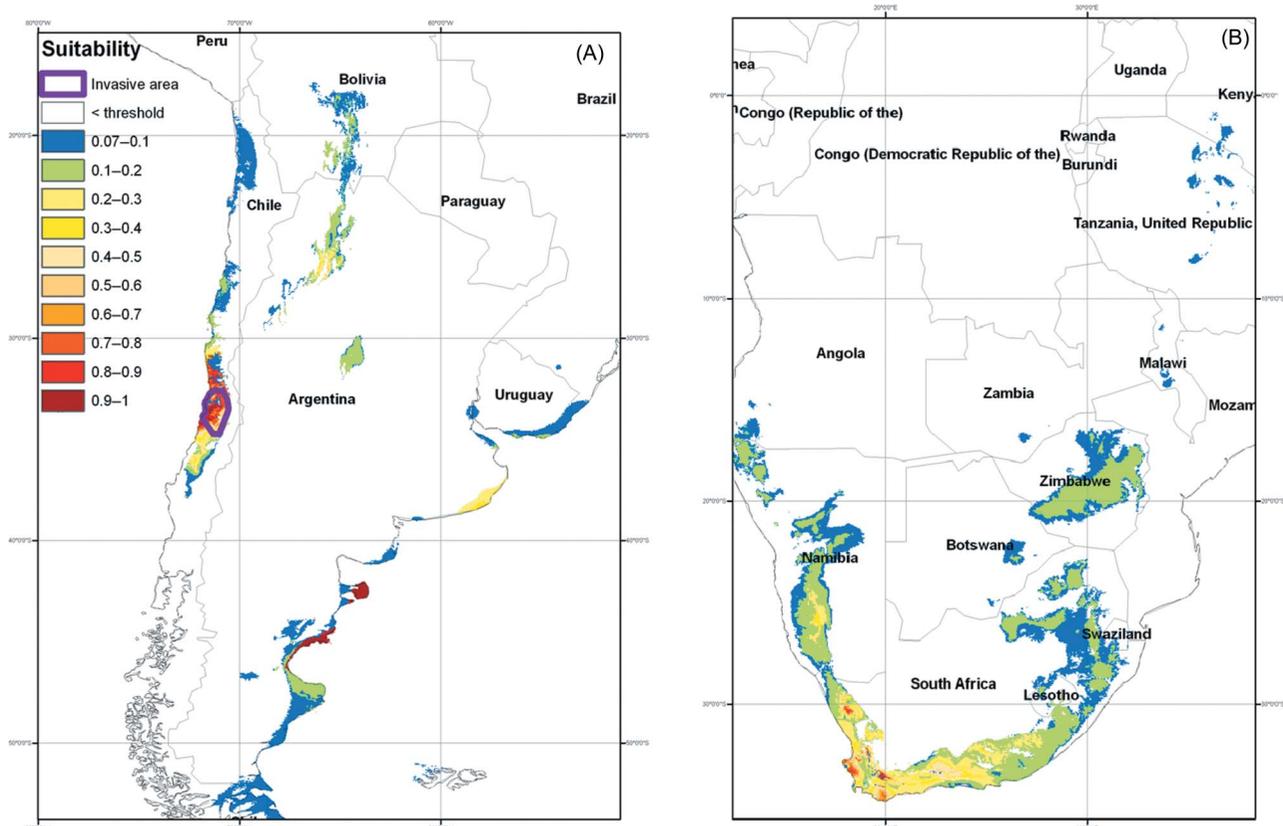


Figure 1. Modeling with MAXENT. Projection of the potential distribution of *Xenopus laevis* in (A) southern South America; (B) southern South Africa (native range). The colored area indicates the suitability of a given region for invasion.

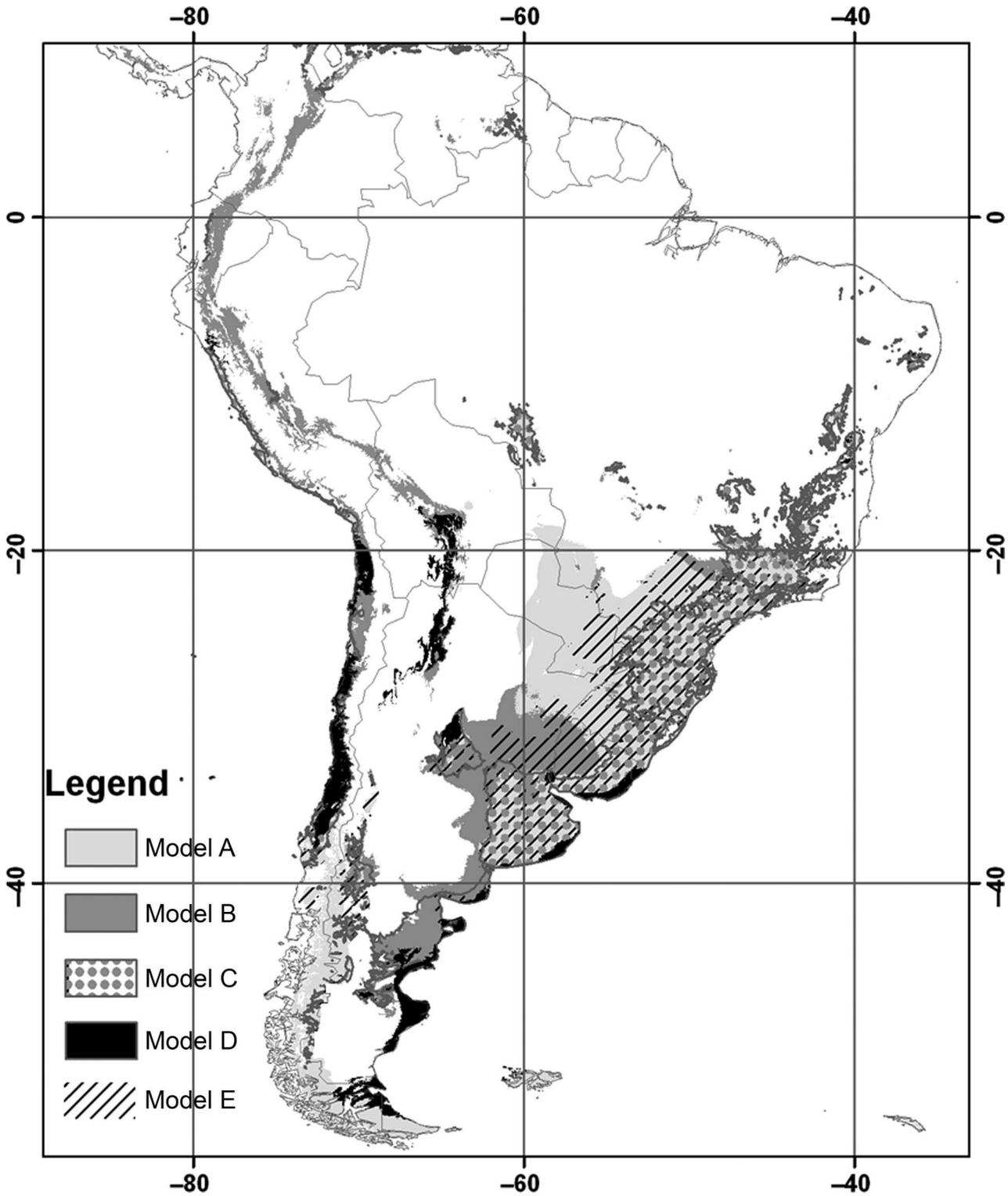


Figure 2. Modeling with MAXENT. Projection of the potential distribution of *Xenopus laevis* in southern South America according to five different models (A to E). Model D was the best in this study.

effect of slope and distance to the nearest population. Compared to model I, the main differences were that at the smaller scale, turbidity, naturalness and

a human impact index also had positive, highly significant effects on the presence of the invader. The distance to the nearest known population had a highly

Table 4. Stepwise logistic regression models for the evaluation of the determining factors of the presence/absence of *Xenopus laevis* in Chile's area of invasion.

Variables	B	Z	p	AIC
<i>Modeled with 500 m buffer</i>				
Distance to populated area	-6.684e - 05	-1.484	0.1379	106.65
Road density	-2.036e - 04	-1.456	0.1454	
Water flow	-1.725e + 00	-3.354	0.0007	
Index of human impact	5.989e - 02	1.927	0.0539	
Naturalness (natural)	1.877e + 00	2.354	0.0185	
Type of environment (lotic)	-2.285e + 00	-2.803	0.0050	
Turbidity	1.175e + 00	2.612	0.0090	
<i>Modeled with 3000 m buffer</i>				
Canal density	1.628e - 03	1.656	0.090	66.07
Water flow	-1.137	-1.834	0.056	
Distance to nearest population	1.371e - 04	4.703	0.001	
Naturalness (natural)	1.432	1.399	0.162	
Type of environment (lotic)	-3.169	-2.795	0.005	
Slope	-1.572	-2.113	0.034	

Notes: B is the coefficient of multiple regression, Z is the Z-test value, p is probability under the null hypothesis, and AIC is Akaike's information criterion. Only the best models for each spatial scale are shown.

significant negative effect, suggesting a contagious distribution.

Discussion

Biological invasions pose a serious threat to biodiversity (Gamradt & Kats 1996; Hecnar & M'Closkey 1997; Kupferberg 1997; Lawler et al. 1999; Kats & Ferrer 2003). The ability to predict the potential area of distribution of a given exotic species, and the factors that facilitate its naturalization, are important pieces of information for establishing monitoring programs for early detection of invasive species, and for improving subsequent eradication efforts (Ficetola et al. 2008). Thus, the development of predictive models and the identification of key factors that account for the distribution of *Xenopus* in South America should contribute to future control actions. To date, in South America the introduction of the bullfrog (*L. catasbeianus*), which has invaded a large area of Brazil, Uruguay, and Argentina, has received more attention (Laufer et al. 2008) than that of *X. laevis*, which has been in a rapid expansion process since at least 1980 (Lobos & Jaksic 2005).

Prediction of the area of invasion in South America and South Africa

Since the first report of naturalized populations of *X. laevis* near Santiago in the 1980s, the species has quickly spread throughout the mediterranean region of central Chile (Velooso & Navarro 1988). Currently, it has invaded an area of approximately 21,200 km² (Lobos & Jaksic 2005). However, we

cannot discriminate between sites where introductions have occurred, but *X. laevis* has failed to establish, and those where it has not been introduced yet, but which are potentially susceptible to invasion. Thus, our prediction that the African clawed frog has invaded only 12% of its potential range in Chile has to be taken with caution. For example, it is interesting to note that an isolated population of this species has persisted since 2003 at a site about 250 km north of the more continuous area of invasion, in the watershed of the Limarí River (Lobos & Jaksic 2005). Our model assigned 20% probability to finding the species in that specific region. Genetic information (Lobos, personal observation) indicates that those frogs possess the haplotype dominant in central Chile; thus we suspect that the translocation of frogs by humans represents an invasion risk within the areas of greater suitability (above 7% according to what has been recorded in Chile). North of the Chilean mediterranean region, our model predicted the presence of areas susceptible to invasion near the coast in the Atacama Desert up to 19° S (bordering Peru). In the rivers and watering places of this area, threatened and endemic amphibians such as *R. atacamensis* occur (Correa et al. 2008). Toward the south of the predicted distribution, the African clawed frog could invade the surroundings of the city of Concepción (38° S). Interestingly, the species is maintained routinely in laboratories in the latter city, so an inadvertent escape of specimens from those centers could accelerate the expansion of the species range in the south.

For the Atlantic coast of South America, the model predicts suitable areas along a stretch that includes southern Brazil, Uruguay and Argentina

from 32° to 54° S. It also predicts a suitable region in north-central Argentina and southern-central Bolivia. Interestingly, naturalized populations of the African clawed frog have not yet been reported in these countries, although the species is commercialized there (X Congreso Argentino de Herpetología, Salta, Argentina 2009). Indeed, Brazil only recently banned the cultivation of *X. laevis* in its southern territory (bordering Uruguay), which caused concern in the latter country, given the high risk of escapes or release of such animals, similar to the case of the bullfrog invasion (Gabriel Laufer 2011, personal communication). The presence of suitable environments at low latitudes on the Atlantic coast of Argentina (38° to 54° S) is a novel prediction for the invasion of *X. laevis* in South America. One example of this potential can be seen in the establishment of this species in the UK (up to 53° N) at least since 1962 (Measey 1998, 2001; Measey & Tinsley 1998), where our model also recognized suitable invasion areas (data not shown).

For southern Africa, it is interesting to note that the model predicts the presence of *X. laevis* up to the northern part of the Republic of South Africa, where it is thought to be replaced by other subspecies and other species of the same genus. Indeed, in recent years *X. laevis laevis* has invaded these areas, probably facilitated by the construction of a network of canals and dams for the irrigation of vineyards and the operation of grape arbors (Measey 2004a).

Keeping in mind the plasticity shown by *X. laevis*, which has invaded non-mediterranean environments such as the UK, even areas with low probability of invasion by this species should be considered at risk.

Determining local-scale factors in the distribution of *Xenopus laevis* in Chile

Xenopus laevis laevis has invaded a wide area of the Chilean mediterranean region, according to the prediction of our bioclimatic niche model. However, not all of the predicted area has been currently invaded. This could simply be due to the ongoing status of this invasion, which started only 30 years ago. However, it could also be accounted for by local factors, which may not be adequately addressed by large-scale predictions (Kolar & Lodge 2001; Yiming et al. 2006). Such local factors could be crucial in determining the spatial pattern of an invasion, involving the presence of geographical barriers, landscape connectivity, suitable microhabitats, edible prey, and the operation of predation and competition by other native species.

Based on results of the local-scale model, we predict that lentic aquatic environments with slow current, turbid water and high human impact that form part of a network of streams and irrigation canals are the most likely to be invaded by the African

clawed frog. Some of these variables closely resemble the conditions that *X. laevis laevis* faces in its native range, thus explaining why this species has naturalized in central Chile. The distance to the nearest infested neighbor population and the density of canals reflects the importance of these as conduits for dispersal, a fact recognized both in Chile (Lobos & Measey 2002; Lobos & Jaksic 2005) and South Africa (Measey 2004b), which is associated with the development of orchards, vineyards and other crops. A positive correlation with the Index of Human Impact (Sanderson et al. 2002) has also been widely recognized among invasive species, due to the role of humans as dispersing and facilitating agents (Paul & Meyer 2001; Riley et al. 2005; McKinney 2006; Ficetola et al. 2008).

Naturalness of the environment (natural: rivers, streams, small lakes versus artificial: irrigation ponds and canals, reservoirs) had a positive effect on the presence of *X. laevis*. This outcome seems surprising considering that, initially, the invasion was restricted mainly to anthropic aquatic environments (Lobos et al. 1999; Lobos 2002). Our observations in central Chile indicate that this invasion has extended quickly to more natural environments (Lobos, personal observation). This represents a serious threat for the natural ecosystems of Chile's mediterranean region with its endemic and threatened amphibians (Veloso & Navarro 1988), because *X. laevis* has recently been recognized as a vector of the fungal disease chytridiomycosis in Chile (Solís et al. 2010).

Our study contributes to the knowledge of the ongoing invasion of the African clawed frog, and complements similar studies performed on other exotic amphibians in South America, such as *L. catesbeianus* (Ficetola et al. 2008; Giovanelli et al. 2008). It also represents the first approach to predicting the area at risk of being invaded by *X. laevis*, and offers a valuable baseline for surveillance and control of this species outside its current range of invasion. A recent modeling of the global distribution of *X. laevis* indicated a high vulnerability of the mediterranean zones of the world (Measey et al. 2012). In this context, studies performed on a smaller scale are important to validate those models, to identify local mechanisms underlying the invasion and to estimate the risk the invasion represents to neighboring countries.

Acknowledgments

We are grateful for a doctoral fellowship granted to GA Lobos by the Comisión Nacional de Investigación Científica y Tecnológica de Chile, CONICYT. This work was supported by FONDECYT/FONDAP 1501-0001 and 1707-0004. Petra Wallem helped with cogent criticisms. The authors also appreciate the critical comments of anonymous reviewers.

References

- Arao K, Kitano T. 2006. *Xenopus laevis* from Hamamatsu City, Shizuoka Prefecture, Japan. Bull Herpetol Soc Japan. 2006(1): 17–19.
- Beaumont LJ, Gallagher RV, Thuiller W, Downey PO, Leishman MR, Hughes L. 2009. Different climatic envelopes among invasive populations may lead to underestimations of current and future biological invasions. Diversity Distrib. 15(3):409–420.
- Berger L, Speare R, Daszak P, Green DE, Cunningham AA, Goggin CL, Slocombe R, Ragan MA, Hyatt AD, McDonald KR, et al. 1998. Chytridiomycosis causes amphibian mortality associated with population declines in the rain forest of Australia and Central America. PNAS. 95(15):9031–9036.
- Bessa-Gomes C, Petrucci-Fonseca F. 2003. Using artificial neural networks to assess wolf distribution patterns in Portugal. Anim Conserv. 6(3):221–229.
- Ceréghino R, Santoul F, Compin A, Mastrorillo S. 2005. Using self-organizing maps to investigate spatial patterns of non-native species. Biol Conserv. 125(4):459–465.
- Correa C, Sallaberry M, Jara-Arancio P, Lobos G, Soto E, Méndez MA. 2008. Amphibia, Anura, Bufonidae, *Rhinella atacamensis*: altitudinal distribution extension, new records and geographic distribution map. CheckList. 4(4):478–484.
- Crayon JJ. 2005. Species account: *Xenopus laevis*. In: Lannoo MJ, editor. Amphibian declines: the conservation status of United States species. Berkeley (CA): University of California Press. p. 522–525.
- Elith J, Graham CH, Anderson RP, Dudik M, Ferrier S, Guisan A, Moritz C, Nakamura M, Nakazawa Y, Overton JMcC, et al. 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography. 29(2):129–151.
- Evans BJ, Greenbaum E, Kusamba C, Carter TF, Tobias ML, Mendel SA, Kelley DB. 2011. Description of a new octoploid frog species (Anura: Pipidae: *Xenopus*) from the Democratic Republic of the Congo, with a discussion of the biogeography of African clawed frogs in the Albertine Rift. J Zool. 283(4):276–290.
- Ficetola GF, Bonin A, Miaud C. 2008. Population genetics reveals origin and number of founders in a biological invasion. Mol Ecol. 17(3):773–782.
- Ficetola GF, Thuiller W, Miaud C. 2007. Prediction and validation of the potential global distribution of a problematic alien invasive species – the American bullfrog. Divers Distrib. 13(4):476–485.
- Fielding AH, Bell JF. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ Conserv. 24(1):38–49.
- Fouquet A, Measey GJ. 2006. Plotting the course of an African clawed frog invasion in western France. Anim Biol. 56(1):95–102.
- Frost DR. 2011. Amphibian species of the world: an online reference [Electronic Database]. Version 5.5 (31 Jan 2011); [cited 2011 Sep]. Available from: <http://research.amnh.org/vz/herpetology/amphibian>
- Gamradt SC, Kats LB. 1996. Effect of introduced crayfish and mosquitofish on California newts. Conserv Biol. 10(4):1155–1162.
- Gido KB, Schaefer JF, Pigg J. 2004. Patterns of fish invasions in the Great Plains of North America. Biol Conserv. 118(2):121–131.
- Giovannelli JGR, Haddad CFB, Alexandrino J. 2008. Predicting the potential distribution of the alien invasive American bullfrog (*Lithobates catesbeianus*) in Brazil. Biol Invasions. 10(5):585–590.
- Harrell FE. 2001. Regression modeling strategies: with applications to linear models, logistic regression and survival analysis. New York (NY): Springer-Verlag.
- Hecnar SJ, M'Closkey RT. 1997. The effects of predatory fish on amphibian species richness and distribution. Biol Conserv. 79(2–3):123–131.
- Hernandez PA, Graham CH, Master LL, Albert DL. 2006. The effect of sample size and species distribution modeling methods. Ecography. 29(5):773–785.
- HerpNet [Internet]. 2007. Specimens searching portal; [cited 2009 May 20]. Available from: <http://www.herpNet.org>
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. 2005. Very high resolution interpolated climate surfaces for global land areas. Int J Climat. 25(15):1965–1978.
- Kats LB, Ferrer RP. 2003. Alien predators and amphibian declines: review of two decades of science and the transition to conservation. Divers Distrib. 9(2):99–110.
- Kennedy TA, Naeem S, Howe KM, Knops JM, Tilman D, Reich P. 2002. Biodiversity as a barrier to ecological invasion. Nature. 417(6889):636–638.
- Kobayashi R, Hasegawa M. 2005. Can the African clawed frog *Xenopus laevis* become established in Japan? An inference from recent distribution records in the Kanto plain. Bull Herpetol Soc Japan. 2005(2):169–173.
- Kobel HR, Loumont C, Tinsley RC. 1996. The extant species. In: Tinsley RC, Kobel HR, editors. The Biology of *Xenopus*. Oxford (UK): Oxford University Press. p. 9–33.
- Kokuryo Y. 2009. A survey of feral populations of African clawed toad in Shizuoka Prefecture. Bull Herpetol Soc Japan. 2009(2):103–106.
- Kolar CS, Lodge DM. 2001. Progress in invasion biology: predicting invaders. Trends Ecol Evol. 16(4):199–204.
- Krysko KL, Burgess JP, Rochford MR, Gillette CR, Cueva D, Enge KM, Somma LA, Stabile JL, Smith DC, Wasilewski JA, et al. 2011. Verified non-indigenous amphibians and reptiles in Florida from 1863 through 2010: outlining the invasion process and identifying invasion pathways and stages. Zootaxa. 3028:1–64.
- Kupferberg S. 1997. Bullfrog (*Rana catesbeiana*) invasion of a California river: the role of larval competition. Ecology. 78(6):1736–1751.
- Lafferty KD, Page CJ. 1997. Predation on the endangered tidewater goby, *Euicyclogobius newberryi*, by the introduced African clawed frog, *Xenopus laevis*, with notes on the frog's parasites. Copeia. 1997(3):589–592.
- LaRue MA, Nielsen CK. 2008. Modelling potential dispersal corridors for cougars in midwestern North America using least-cost path methods. Ecol Model. 212(3):372–381.
- Laufer G, Canavero A, Nuñez D, Maneyro R. 2008. Bullfrog (*Lithobates catesbeianus*) invasion in Uruguay. Biol Invasions. 10(7):1183–1189.
- Lawler SP, Dritz D, Strange T, Holyoak M. 1999. Effects of introduced mosquitofish and bullfrog on the threatened California redlegged frog. Conserv Biol. 13(3):613–622.
- Lillo F, Faraone FP, Lo Valvo M. 2011. Can the introduction of *Xenopus laevis* affect native amphibian populations? Reduction of reproductive occurrence in presence of the invasive species. Biol Invasions. 13(7):1533–1541.
- Lillo F, Marrone F, Sicilia A, Castelli G, Zava B. 2005. An invasive population of *Xenopus laevis* (Daudin, 1802) in Italy. Herpetozoa. 18:63–64.
- Lobos G. 2002. Antecedentes sobre la distribución del sapo africano *Xenopus laevis* en Chile. Not Mens Mus Nac Hist Nat Chile. 347:3–8.
- Lobos G, Cattán P, López M. 1999. Antecedentes de la ecología trófica del sapo africano *Xenopus laevis* en la zona central de Chile. Bol Mus Nac Hist Nat Chile. 48:7–18.
- Lobos G, Jaksic FM. 2005. The ongoing invasion of African clawed frog (*Xenopus laevis*) in Chile: causes of concern. Biodivers Conserv. 14(2):429–439.
- Lobos G, Measey GJ. 2002. Invasive populations of *Xenopus laevis* (Daudin) in Chile. Herpetol J. 12(4):163–168.

- Lowe S, Browne M, Boudjelas S, De Poorter M 2000. 100 of the world's worst invasive alien species a selection from the global invasive species database. Gland (Switzerland): Invasive Species Specialist Group (ISSG). The World Conservation Union (IUCN) technical report. 12 p.
- Marino J, Bennett M, Cossios D, Iriarte A, Lucherini M, Pliscoff P, Sillero-Zubiri C, Villalba L, Walker S. 2011. Bioclimatic constraints to Andean cat distribution: a modelling application for rare species. *Diversity Distrib.* 17(2):311–322.
- McCoid MJ, Fritts TH. 1980a. Observations of feral populations of *Xenopus laevis* (Pipidae) in southern California. *Bull South Calif Acad Sci.* 79:82–86.
- McCoid MJ, Fritts TH. 1980b. Notes on the diet of a feral population of *Xenopus laevis* (Pipidae) in California. *Southwest Nat.* 25:272–275.
- McKinney ML. 2006. Urbanization as a major cause of biotic homogenization. *Biol Conserv.* 127(3):247–260.
- Measey GJ. 1998. Diet of feral *Xenopus laevis* in South Wales, UK. *J Zool (Lond).* 246(3):287–298.
- Measey GJ. 2001. Growth and ageing of *Xenopus laevis* (Daudin) in South Wales, UK. *J Zool (Lond).* 246:287–298.
- Measey GJ. 2004a. *Xenopus laevis* (Daudin). In: Minter LR, Burger M, Harrison JA, Braack HH, Bishop PJ, Kloepfer D, editors. Atlas and Red Data Book of the frogs of South Africa, Lesotho and Swaziland. Washington (DC): Smithsonian Institution. p. 264–266.
- Measey GJ. 2004b. *Xenopus laevis*: una perspectiva sobre invasiones globales. In: Solis R, Lobos G, Iriarte A, editors. Antecedentes sobre la biología de *Xenopus laevis* y su introducción en Chile. Servicio Agrícola y Ganadero de Chile. Santiago (Chile): Universidad de Chile. p. 3–8.
- Measey GJ, Channing A. 2003. Phylogeography of the genus *Xenopus* in southern Africa. *Amphibia-Reptilia.* 24:321–330.
- Measey GJ, Rödder D, Green SL, Kobayashi R, Lillo F, Lobos G, Rebelo R, Thirion JM. 2012. Ongoing invasions of the African clawed frog, *Xenopus laevis*: a global review. *Biol Invasions.* 14(11):2255–2270.
- Measey GJ, Tinsley RC. 1998. Feral *Xenopus laevis* in South Wales. *Herpetol J.* 8:23–27.
- Paul MJ, Meyer JL. 2001. Streams in the urban landscape. *Annu Rev of Ecol Syst.* 32:333–365.
- Peterson AT, Scachetti-Pereira R, Kluza DA. 2003. Assessment of invasive potential of *Homalodisca coagulata* in western North America and South America. *Biota Neotrop.* 3:1–7.
- Peterson AT, Vieglais DA. 2001. Predicting species invasions using ecological niche modeling: new approaches from bioinformatics attack a pressing problem. *BioScience.* 51(5):363–371.
- Phillips SJ, Anderson RP, Schapire RE. 2006. Maximum entropy modeling of species geographic distributions. *Ecol Model.* 190(3–4):231–259.
- Pounds JA, Bustamante MR, Coloma LA, Consuegra JA, Fogden MPL, Foster PN, La Marca E, Masters KL, Merino-Viteri A, Puschendorf R, et al. 2006. Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature.* 439(7073):161–167.
- R Development Core Team. 2005. Royal: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing; [cited 2011 Sep]. Available from: <http://www.R-project.org>
- Rebelo R, Amaral P, Bernardes M, Oliveira J, Pinheiro P, Leitão D. 2010. *Xenopus laevis* (Daudin 1802), a new exotic amphibian in Portugal. *Biol Invasions.* 12(10):3383–3387.
- Riley SPD, Busteed GT, Kats LB, Vandergon TL, Lee LFS, Dagit RG, Kerby JL, Fisher RN, Sauvajot RM. 2005. Effects of urbanization on the distribution and abundance of amphibians and invasive species in southern California streams. *Conserv Biol.* 19(6):1894–1907.
- Sanderson EW, Jaiteh M, Levy MA, Redford KN, Wannebo AV, Woolmer G. 2002. The human footprint and the last of the wild. *BioScience.* 52(10):891–904.
- Solis R, Lobos G, Walker SF, Fisher M, Bosch J. 2010. Presence of *Batrachochytrium dendrobatidis* in feral populations of *Xenopus laevis* in Chile. *Biol Invasions.* 12(6):1641–1646.
- Steiner FM, Schlick-Steiner BC, VanDerWal J, Reuther KD, Erhard C, Stauffer C, Suarez AV, Williams SE, Crozier RH. 2008. Combined modelling of distribution and niche in invasion biology: a case study of two invasive *Tetramorium* ant species. *Diversity Distrib.* 14(3):538–545.
- Thuiller W, Brotons L, Araujo MB, Lavorel S. 2004. Effects of restricting environmental range of data to project current and future species distributions. *Ecography.* 27(2):165–172.
- Thuiller W, Richardson DM, Midgley GF. 2007. Will climate change promote alien plant invasions? In: Nentwig W, editor. *Biological Invasions.* Berlin (Germany): Springer. p. 197–211.
- Thuiller W, Richardson DM, Pysek P, Midgley GF, Hughes GO, Rouget M. 2005. Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. *Glob Chang Biol.* 11(12):2234–2250.
- Tognelli MF, Roig-Juñent SA, Marvaldi A, Flores GE, Lobo JM. 2009. An evaluation of methods for modelling distribution of Patagonian insects. *Rev Chil Hist Nat.* 82(3):347–360.
- Veloso A, Navarro J. 1988. Systematic list and geographic distribution of amphibians and reptiles from Chile. *Mus Reg Sci Nat Torino.* 6:481–540.
- Weldon C, Du Preez LH, Hyatt AD, Muller R, Speare R. 2004. Origin of the amphibian Chytrid fungus. *Emerg Infect Dis.* 10(12):2100–2105.
- Yiming L, Zhengjun W, Duncan RP. 2006. Why islands are easier to invade: human influences on bullfrog invasion in the Zhoushan archipelago and neighboring mainland China. *Oecologia.* 148(1):129–136.

Appendix 1. Geographic information.

Latitude	Longitude	Area	Source
18.050	-33.026	South Africa	Measey (2004a)
18.301	-33.100	South Africa	Measey (2004a)
18.138	-30.546	South Africa	Measey (2004a)
17.766	-30.316	South Africa	Measey (2004a)
18.635	-31.313	South Africa	Measey (2004a)
18.962	-32.021	South Africa	Measey (2004a)
18.816	-31.923	South Africa	Measey (2004a)
18.122	-31.541	South Africa	Measey (2004a)
19.367	-32.201	South Africa	Measey (2004a)
19.363	-32.434	South Africa	Measey (2004a)
19.402	-32.616	South Africa	Measey (2004a)
18.861	-32.594	South Africa	Measey (2004a)
19.226	-32.701	South Africa	Measey (2004a)
19.377	-33.074	South Africa	Measey (2004a)
19.113	-33.079	South Africa	Measey (2004a)
19.595	-33.094	South Africa	Measey (2004a)
19.331	-33.058	South Africa	Measey (2004a)
19.169	-33.047	South Africa	Measey (2004a)
19.064	-33.046	South Africa	Measey (2004a)
18.809	-33.038	South Africa	Measey (2004a)
18.582	-33.190	South Africa	Measey (2004a)
18.296	-33.166	South Africa	Measey (2004a)
18.131	-33.178	South Africa	Measey (2004a)
21.925	-32.982	South Africa	Measey (2004a)
21.697	-33.705	South Africa	Measey (2004a)
21.393	-33.713	South Africa	Measey (2004a)
21.723	-33.963	South Africa	Measey (2004a)
21.605	-33.993	South Africa	Measey (2004a)
21.246	-33.986	South Africa	Measey (2004a)
20.823	-33.964	South Africa	Measey (2004a)
20.408	-33.985	South Africa	Measey (2004a)
20.059	-34.016	South Africa	Measey (2004a)
19.825	-34.081	South Africa	Measey (2004a)
19.527	-34.042	South Africa	Measey (2004a)
19.277	-34.066	South Africa	Measey (2004a)
18.822	-34.024	South Africa	Measey (2004a)
18.750	-34.022	South Africa	Measey (2004a)
18.620	-34.026	South Africa	Measey (2004a)
18.421	-34.095	South Africa	Measey (2004a)
18.416	-34.180	South Africa	Measey (2004a)
18.858	-34.188	South Africa	Measey (2004a)
18.842	-34.216	South Africa	Measey (2004a)
18.967	-34.217	South Africa	Measey (2004a)
19.001	-34.242	South Africa	Measey (2004a)
19.476	-34.646	South Africa	Measey (2004a)
19.560	-34.696	South Africa	Measey (2004a)
19.994	-34.825	South Africa	Measey (2004a)
20.022	-34.803	South Africa	Measey (2004a)
20.744	-34.434	South Africa	Measey (2004a)
21.169	-34.349	South Africa	Measey (2004a)
21.600	-34.342	South Africa	Measey (2004a)
22.326	-33.953	South Africa	Measey (2004a)
22.751	-33.996	South Africa	Measey (2004a)
21.986	-33.915	South Africa	Measey (2004a)
21.979	-33.719	South Africa	Measey (2004a)
21.428	-33.685	South Africa	Measey (2004a)
21.945	-33.074	South Africa	Measey (2004a)
18.909	-34.357	South Africa	Measey (2004a)
19.528	-34.670	South Africa	Measey (2004a)
20.029	-34.533	South Africa	Measey (2004a)
19.097	-31.377	South Africa	Measey (2004a)
18.477	-33.927	South Africa	Measey (2004a)

(Continued)

Appendix 1. (Continued).

Latitude	Longitude	Area	Source
18.910	-33.955	South Africa	Measey (2004a)
18.904	-33.934	South Africa	Measey (2004a)
18.992	-34.002	South Africa	Measey (2004a)
18.481	-33.904	South Africa	Measey (2004a)
18.850	-33.933	South Africa	Measey (2004a)
24.968	-32.718	South Africa	Measey (2004a)
18.633	-33.925	South Africa	Measey (2004a)
18.850	-33.933	South Africa	Measey (2004a)
16.450	-28.692	South Africa	Measey (2004a)
18.417	-33.910	South Africa	Measey (2004a)
20.700	-33.900	South Africa	HerpNet (2007)
26.500	-33.300	South Africa	HerpNet (2007)
18.850	-33.900	South Africa	HerpNet (2007)
18.410	-33.910	South Africa	HerpNet (2007)
25.580	-33.960	South Africa	HerpNet (2007)
23.700	-31.950	South Africa	HerpNet (2007)
16.500	-28.630	South Africa	HerpNet (2007)
26.500	-31.250	South Africa	HerpNet (2007)
25.600	-33.960	South Africa	HerpNet (2007)
18.950	-33.930	South Africa	own collection
18.850	-33.970	South Africa	own collection
18.860	-33.910	South Africa	own collection
19.160	-34.050	South Africa	own collection
18.770	-34.050	South Africa	own collection
18.700	-33.830	South Africa	own collection
18.620	-33.800	South Africa	own collection
18.550	-33.790	South Africa	own collection
18.490	-33.830	South Africa	own collection
18.480	-33.880	South Africa	own collection
18.370	-34.200	South Africa	own collection
18.440	-34.310	South Africa	own collection
-71.140	-33.670	Chile	own collection
-70.830	-33.500	Chile	own collection
-71.330	-33.450	Chile	own collection
-70.770	-33.580	Chile	own collection
-70.830	-33.390	Chile	own collection
-71.060	-33.820	Chile	own collection
-71.220	-33.730	Chile	own collection
-70.820	-33.280	Chile	own collection
-70.680	-33.750	Chile	own collection
-71.250	-34.070	Chile	own collection
-71.070	-34.620	Chile	own collection
-71.380	-34.520	Chile	own collection
-71.380	-34.120	Chile	own collection
-71.470	-34.180	Chile	own collection
-71.260	-34.350	Chile	own collection
-71.360	-34.600	Chile	own collection
-71.470	-34.570	Chile	own collection
-71.080	-32.430	Chile	own collection
-71.180	-32.880	Chile	own collection
-71.110	-32.890	Chile	own collection
-71.110	-32.900	Chile	own collection
-71.090	-32.900	Chile	own collection
-70.880	-32.850	Chile	own collection
-70.900	-32.870	Chile	own collection
-71.090	-32.900	Chile	own collection
-70.850	-32.870	Chile	own collection
-71.430	-32.930	Chile	own collection
-71.520	-30.670	Chile	own collection
-71.700	-33.800	Chile	own collection
-71.610	-33.510	Chile	own collection
-71.700	-30.730	Chile	own collection

(Continued)

Appendix 1. (Continued).

Latitude	Longitude	Area	Source
-71.500	-33.050	Chile	own collection
-71.500	-33.040	Chile	own collection
-71.650	-33.430	Chile	own collection
-71.520	-30.680	Chile	own collection
-71.500	-33.620	Chile	own collection
-71.540	-33.630	Chile	own collection
-71.650	-33.270	Chile	own collection
-71.560	-33.580	Chile	own collection
-71.620	-33.600	Chile	own collection
-71.610	-33.640	Chile	own collection
-71.590	-33.510	Chile	own collection
-71.700	-33.760	Chile	own collection
-71.610	-33.500	Chile	own collection
-71.740	-33.810	Chile	own collection
-71.740	-33.810	Chile	own collection
-71.600	-33.530	Chile	own collection
-71.620	-33.610	Chile	own collection
-71.680	-33.760	Chile	own collection
-71.720	-33.800	Chile	own collection
-71.620	-33.610	Chile	own collection
-71.620	-33.600	Chile	own collection
-71.630	-33.620	Chile	own collection

(Continued)

Appendix 1. (Continued).

Latitude	Longitude	Area	Source
-71.610	-33.290	Chile	own collection
-71.520	-33.680	Chile	own collection
-71.610	-33.610	Chile	own collection
-70.810	-33.050	Chile	own collection
-70.870	-33.180	Chile	own collection
-70.830	-33.500	Chile	own collection
-70.610	-33.520	Chile	own collection
-70.840	-33.970	Chile	own collection
-70.680	-33.440	Chile	own collection
-71.010	-33.710	Chile	own collection
-70.680	-33.190	Chile	own collection
-70.640	-33.180	Chile	own collection
-70.630	-33.380	Chile	own collection
-70.630	-33.570	Chile	own collection
-70.910	-33.610	Chile	own collection
-70.630	-33.570	Chile	own collection
-70.840	-33.430	Chile	own collection
-70.930	-33.850	Chile	own collection
-70.790	-33.200	Chile	own collection
-70.900	-33.840	Chile	own collection
-70.900	-33.010	Chile	own collection