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Ongoing invasions of the African clawed frog, *Xenopus laevis*: a global review

G. J. Measey · D. Rödder · S. L. Green ·
R. Kobayashi · F. Lillo · G. Lobos · R. Rebelo ·
J.-M. Thirion

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Abstract We conducted a literature review on the current status of all known extralimital populations of the African clawed frog, *Xenopus laevis*, to identify commonality in invasion pathways, lag between discovery and introduction, and whether old populations are in decline. Further, we investigated which locations are vulnerable to future establishment using geospatial data (1,075 native and 124 invasive records) in a Maxent model developed with data from the Worldclim database. We found introductions of *X. laevis* to be continuous over the last 50 years and invasions to be ongoing on four continents: Asia, Europe, North and South America. Invasion pathways were related to scientific use and the pet trade, with high rates of deliberate release followed by a lag of 2–25 years to first reports. No populations were found to be declining although some have been extirpated. Optimal uninvaded bioclimatic space was identified in

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G. J. Measey (✉)
School of Environmental Sciences and Development,
North-West University, Private Bag X6001,
Potchefstroom 2520, South Africa
e-mail: john@measey.com

D. Rödder
Section of Herpetology, Zoologisches Forschungsmuseum
Alexander Koenig (ZFMK), Adenauerallee 160,
53113 Bonn, Germany
e-mail: d.roedder.zfmk@uni-bonn.de

S. L. Green
Department of Comparative Medicine,
School of Medicine, Stanford University,
Stanford, CA, USA
e-mail: sherril@stanford.edu

R. Kobayashi
Center for Toki and Ecological Restoration (CTER),
Niigata University, 1101-1 Niibo-katagami,
Sado-City, Niigata 952-0103, Japan
e-mail: raita@cc.niigata-u.ac.jp

F. Lillo
Dipartimento di Biologia Ambientale e Biodiveristà,
Universita' di Palermo, Via Archirafi 18,
90123 Palermo, Italy
e-mail: francesco.lillo@gmail.com

G. Lobos
Centro de Vida Silvestre, Facultad de Ciencias
Veterinarias y Pecuarias, Universidad de Chile,
Casilla 2, Correo 15, La Granja, Santiago, Chile
e-mail: galobos@ug.uchile.cl

R. Rebelo
Departamento de Biologia Animal, Centro de Biologia
Ambiental, Faculdade de Ciencias da Universidade de
Lisboa, Campo Grande, 1749-016 Lisbon, Portugal
e-mail: rmrebelo@fc.ul.pt

J.-M. Thirion
Association Objectifs BIOdiversitéS (OBIOS), 22 rue du
docteur Gilbert, 17250 Pont-l'abbé-d'Arnoult, France
e-mail: thirion.jean-marc@sfr.fr

central Mexico and southern Australia, while larger suitable areas were found in southern South America and southwestern Europe. *Xenopus laevis* is a cryptic invasive species that is likely to increase its invasive distribution, through new introductions and by the spread of ongoing invasions. Many more invasive populations are likely to exist than are currently recognised and reducing invasive potential will largely rely on education of those involved with their captive care.

Keywords *Xenopus laevis* · Detection lag · Amphibians · Invasion pathways · Species distribution model · Chytridiomycosis

Introduction

The African clawed frog, *Xenopus laevis* (Daudin 1802), is best known as one of the most productive model organisms for studies in cell, molecular and developmental biology (Gurdon 1996). It has been the model amphibian, and together with the mouse, zebrafish, nematode and fruit fly, made up the most intensively studied organisms on earth. The use of this frog has resulted in important insights into gene regulation, cell-cycle control and signal transduction to name but a few. Many past and current studies centre on the relative ease of manipulating live embryos for developmental investigations. Today, laboratories with living colonies of *X. laevis* exist all over the world, such that it has been distributed more widely than any other amphibian species.

The rise of the use of *X. laevis* in the laboratory has a convoluted history that centres on its efficacy for human pregnancy diagnosis in the 1930s (Gurdon and Hopwood 2000). This led to exports of thousands of live animals from its native South African Cape to laboratories, first to the United Kingdom and eventually all over the world. The supply of large numbers of frogs to laboratories was followed in the 1960s and 70s by reports of invasive populations in California (Mahrdt and Knefler 1972; St. Amant and Hoover 1969; St. Amant et al. 1973). The first review of global invasions of *X. laevis* confirmed a single population in the UK and several in California, as well as some unsubstantiated reports from Chile and mainland Europe (Tinsley and McCoid 1996). A more recent review of USA invasions details 12 states where *X. laevis* has been found, although only populations in California and Arizona appear to persist (Crayon 2005). The last decade has also seen a rise in evidence of the negative impact of this invasive species on local populations of amphibians and fish (e.g. Crayon 2005; Lafferty and Page 1997; Lillo et al. 2011; Rebelo et al. 2010), as well as spread of disease (Robert et al. 2007), so that in some areas there have been serious questions about banning all trade (Garner et al. 2009; Vogel 2008).

Xenopus laevis has a number of morphological, physiological and behavioural traits that makes them all the more suitable for adoption to laboratory conditions. Firstly, they have impressive longevity in a totally aquatic environment (15 years: Flower 1936), such that typical laboratory rearing facilities provide no place for this anuran to come out of the water (Green 2010). Erroneously described as totally aquatic with surprising regularity, species in the genus are known to migrate overland (Eggert and Fouquet 2006; Hewitt and Power 1913; Loveridge 1953; Measey and Tinsley 1998), are capable of surviving drought by burrowing into drying mud (Alexander and Bellerby 1938; Balinsky et al. 1967; Lobos and Jaksic 2005), and can starve for up to 12 months (Hewitt and Power 1913; Tinsley et al. 1996). Each trait is backed by a suite of physiological adaptations (Hillman et al. 2009). For example, *X. laevis* is capable of becoming ureotelic when dehydrated (Balinsky et al. 1961), and can withstand exposure to hyperosmotic solutions (Bentley 1973). It has a high tolerance to salt water, as well as a high tolerance of anoxic conditions (Jokumsen and Weber 1980). Adults and larvae perform well over a wide range of temperatures, additionally larvae can metamorphose over a wide range of temperatures (Balinsky 1981; Miller 1982; Walsh et al. 2008).

Xenopus laevis, like other members of the family Pipidae, is distinguished by its lack of tongue, allowing inertial suction feeding (Carreno and Nishikawa 2010) of a wide variety of invertebrate prey from zooplankton to aquatic coleopterans (e.g. Measey 1998a). In addition, *X. laevis* has a set of toothed jaws with which to grip prey and a powerful overhead kick with clawed feet that can be used to reduce oversized prey (Avila and Frye 1978), so that vertebrates are also found in stomach contents (Crayon 2005; Lafferty and Page 1997; Lillo et al. 2011; Measey 1998a). Individuals are also capable of lunging out of the water to retrieve terrestrial prey, which is a frequent component of their diet (Measey 1998b). Taken together, these morphological, physiological and behavioural traits make *X. laevis* one of the most robust and versatile anurans known both inside and outside of the laboratory.

Given the global distribution of laboratory colonies and the suite of robust traits, it was surprising that the known invasive populations detailed by Tinsley and McCoid (1996) were so few. Perhaps not surprisingly, since the publication of their review, reports of more invasive populations have emerged from North America (Crayon 2005), South America (Chile: Lobos and Jaksic 2005; Lobos and Measey 2002), Asia (Japan: Arao and Kitano 2006; Kobayashi and Hasegawa 2005; Kokuryo 2009) and Europe (France, Italy and Portugal: Fouquet 2001; Fouquet and Measey 2006; Lillo et al. 2005; Rebelo et al. 2010). More prominence has been given to invasive frogs as a result of concerns over emerging amphibian pathogens, including the fungal pathogen: *Batrachochytrium dendrobatidis*. Invasive populations of *X. laevis* are often implicated in having played a key role in the spread of this pathogen (e.g. Daszak et al. 2003; Duffus and Cunningham 2010; Garner et al. 2006; Peeler et al. 2011; Skerratt et al. 2007; Solis et al. 2011). The oldest known chytrid infected specimen was a *X. laevis* from the South African Cape collected in 1938 (Weldon et al. 2004), a period when large numbers of live animals were being exported (Gurdon and Hopwood 2000; but also see Soto-Azat et al. 2010). The speculation of a causal link between the emergence of this infectious disease and the dissemination of *X. laevis* into laboratories world-wide and eventually invasive populations has yet to be substantiated. Whether or not the global spread of chytridiomycosis is linked to exports of *X. laevis*, invasive populations could play a part in the spread of disease in situ, as this frog is an asymptomatic carrier (Cheng et al. 2011; Schmeller et al. 2011).

To date, *Xenopus* (*Silurana*) *tropicalis* is the only amphibian to have its whole genome sequenced (Hellsten et al. 2010), which demonstrates the more tractable genetics of this diploid species over the tetraploid *X. laevis*. Numbers of publications resulting from the study of *Xenopus laevis* show clear and significant signs of decreasing (ISI Web of Knowledge topic annual search results from 2000 for "*Xenopus laevis*" shows an annual reduction on average of 25.6 publications per year: $F_{1,\ 20} = 1{,}836$; $P < 0.001$), while those on *X. tropicalis* are increasing (Fig. 1). This model amphibian boasts not only a sequenced genome, but is smaller and matures in only 4 months. So what is the future of the very many remaining laboratory populations of *X. laevis*?

Here we review the history and current status of all known invasive populations of the African clawed frog, *X. laevis*, in order to identify invasion pathways. We ask whether the newly reported introductions are simply newly discovered invasive populations, and we determine whether old introductions are in decline (as has been suggested: Kats and Ferrer 2003). By using species distribution models (SDMs) we investigate

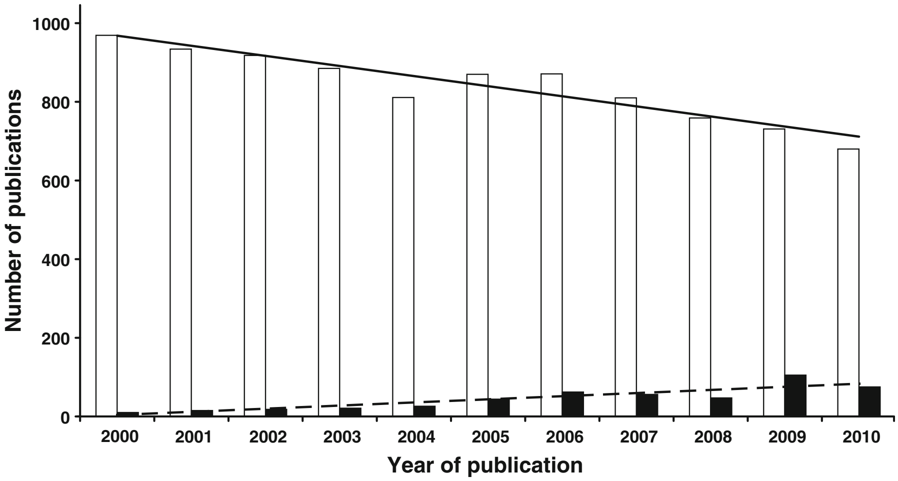

Fig. 1 Publication trend for *Xenopus laevis* (*light open bars*) and *X.* (*Silurana*) *tropicalis* (*closed bars*) show significant opposing trends. Data from Thompson ISI

whether current invasions have reached their full potential, and where new populations would likely prosper should propagules be released. Lastly, we determine whether the invasion potential of this species has been underestimated (Beaumont et al. 2009).

Methods and materials

A working taxonomic definition for *X. laevis*

The last review of the taxonomy of the genus *Xenopus* listed six subspecies of *X. laevis*, although at the time the authors acknowledged that many were likely to be full species (Kobel et al. 1996). Since that time, some authors have considered each subspecies to be a full species with the exception of *Xenopus bunyonensis* and *Xenopus poweri* (Frost 2011). Further, molecular studies of mitochondrial DNA suggest a distinct difference between *X. l. laevis* and *X. l. petersii*, and that *X. l. laevis* from the winter rainfall region of the Cape is distinct from those that are found in the summer rainfall region of South Africa up to Malawi (Du Preez et al. 2009; Evans et al. 2004; Measey and Channing 2003). All lineages are discussed in detail by Evans et al. (2011). We agree with previous workers that a thorough revision of this species complex is overdue. However, in this study we have opted to take a sensu stricto definition for *X. laevis* and confine the data in our study to a single lineage of the species from the southwestern Cape of South Africa (Evans et al. 2011; Measey and Channing 2003). Firstly, this includes the type locality for the species and genus (Frost 2011). Secondly, animals for experimentation almost exclusively originate from this same Cape lineage (Gurdon and Hopwood 2000; Weldon et al. 2007). Lastly, a sensu lato definition of *X. laevis* (Kobel et al. 1996) would be unlikely to represent a true climatic envelope in order to characterise the potential of invasive populations to establish.

Ongoing invasive populations of *X. laevis*

We reviewed the scientific and grey literature, interviewed colleagues and conservation workers on invasive populations of *X. laevis* in order to determine the most likely dates of introductions, and compare this to the dates discovered and/or when the first investigations were undertaken. In other studies, the invasion pathways of anurans have been shown to consist of unintentional introductions through the horticultural and aquacultural trade (e.g. Christy et al. 2007), while the majority of taxa are moved via intentional pathways (Kraus 2009). In the case of *X. laevis*, large numbers of animals are specifically exported from South Africa and are in general circulation in laboratories and the pet trade. Thus, we wanted to discover from which source specimens are released into the environment, and specifically whether this is an accidental or deliberate release.

Species distribution modelling

In order to assess the minimum invasion potential of *X. laevis* via species distribution modelling (SDM), we compiled a set of 1,075 native, and 124 invasive records. Bioclimatic data (Beaumont et al. 2005; Busby 1991) with a spatial resolution of 2.5 arcmin was obtained from the Worldclim database (Hijmans et al. 2005). The original data set comprised 19 bioclimatic variables, of which many may be inter-correlated hampering SDM development and transferability through geographic space (Heikkinen et al. 2006). Therefore, we assessed the degree of inter-correlation by computing pair-wise Pearson's correlation coefficient and subsequently chose only the putatively biologically most relevant predictor from each group of inter-correlated variables with $R^2 > 0.75$. The final set of bioclimatic predictors comprised 'isothermality' (bio3), 'min temperature of coldest month' (bio6), 'temperature annual range' (bio7), 'mean temperature of wettest quarter' (bio8), 'mean temperature of driest quarter' (bio9), 'mean temperature of warmest quarter' (bio10), 'precipitation seasonality' (bio15), 'precipitation of wettest quarter' (bio16), 'precipitation of driest quarter' (bio17), and 'precipitation of coldest quarter' (bio19).

Maxent 3.3.3e (Phillips et al. 2006; Phillips and Dudík 2008) was used for SDM computation. Following previous suggestions (Broennimann and Guisan 2008), we pooled records from native and introduced ranges in order to incorporate as much information on the realised bioclimatic niche of *X. laevis*. Maxent used pseudo-absence data to characterize the general environmental conditions available for the target species. Selection of appropriate background data is a crucial step during model building (VanDerWal et al. 2009). Therefore, we restricted the background data to a radius of 250 km around the records. SDM performance was evaluated using the area under the receiver operating characteristic curve (Swets 1988) by randomly splitting the records into 70 % used for model training, and the remaining records for model testing. This procedure was repeated 100 times, and subsequently the average logistic prediction per grid cell was used for further processing. As the logistic output format of Maxent provides a continuous probability surface ranging from 0 (unsuitable) to 1 (optimal), it is often useful to transform it into presence/absence maps, wherein a variety of different thresholds were proposed for this task (Liu et al. 2005). Herein, we applied two of them; the minimum training presence and the 10 % training omission thresholds. Areas above the minimum training presence threshold are referred to as 'suitable', while areas above the 10 % training omission are termed 'optimal'.

Extrapolations beyond the training range of an SDM may be less reliable (Fitzpatrick and Hargrove 2009). Therefore, we computed multidimensional environmental similarity surfaces in order to identify those areas where SDMs may need to extrapolate onto bioclimatic conditions exceeding the training range (Elith et al. 2010).

Based on the Maxent output, areas with probabilities above suitable (minimum training presence) and optimal (10 % training omission) thresholds in which current invasions occur were separately measured using ArcMap 10. In addition, minimum convex hull polygons based on all available species records within each invaded area were calculated to determine current areas of invasions if more than one record was available. Notes were made where these continuous areas failed to include known invaded localities.

Results

Modelling

Our SDM has a good discrimination ability between bioclimatic conditions at the presence of *X. laevis*, and random background conditions ($\mathrm{AUC}_{\mathrm{trainng}} = 0.955$; $\mathrm{AUC}_{\mathrm{test}} = 0.936$). 'Isothermality' had the highest contribution to the final SDM (27.4 %), followed by the 'min temperature of coldest month' (19.8 %), 'precipitation of coldest quarter' (11.7 %), 'mean temperature of warmest quarter' (10.4 %), 'mean temperature of wettest quarter' (8.8 %), 'temperature annual range' (6.7 %) and 'precipitation of wettest quarter' (6.6 %), wherein all other variables contributed less than 5 %. The minimum training presence was 0.0159 and the 10 % training omission threshold 0.3485. Major extrapolation areas are situated in the centre of continents (compare crosshatched areas in Fig. 2; Electronic Supplementary Material).

Our SDM for the range of *X. laevis* sensu stricto in South Africa highlights the winter rainfall area of the Cape as environmentally most suitable (Fig. 2; and Electronic Supplementary Material). Applying the stricter optimal presence/absence threshold, assuming 10 % errors in training sites, mostly excludes localities in the Ceres Karoo and near Beaufort West. These were included in the training data-set following the genetic results of Du Preez et al. (2009), although it should be noted that haplotypes of this lineage were found in a minority.

For colonised regions of Europe, the model suggests very few areas with optimal Maxent scores, above the 10 % training omission threshold (Fig. 2; Table 1; Electronic Supplementary Material). These are restricted to isolated parts of Portugal and France, and coastal northern Morocco (where no current *X. laevis* invasions are known). Areas where populations occur in Portugal and France demonstrate a large suitable climatic potential for this species to invade over one million square kilometres (Table 1). This includes relatively high scores for most of southern Portugal and adjoining Spain, as well as central and southern France, and mainland Italy. Interestingly, few suitable areas are found in the United Kingdom outside southern coastal areas. Most of southwestern Europe and coastal North Africa is predicted to be suitable for invasion by this species.

Much of coastal California is predicted to have an optimal climate with the core areas already invaded by *X. laevis* (Fig. 2 and Electronic Supplementary Material), as has been previously documented (van Wilgen et al. 2009). Populations in Arizona and Imperial County, California, occupy climates just above the minimum training threshold, as might be expected from their climatic confinement at modified sites (see below). Some of the oldest established populations, in the Santa Ana River catchment of California, appear to have become established outside of the species' climatic

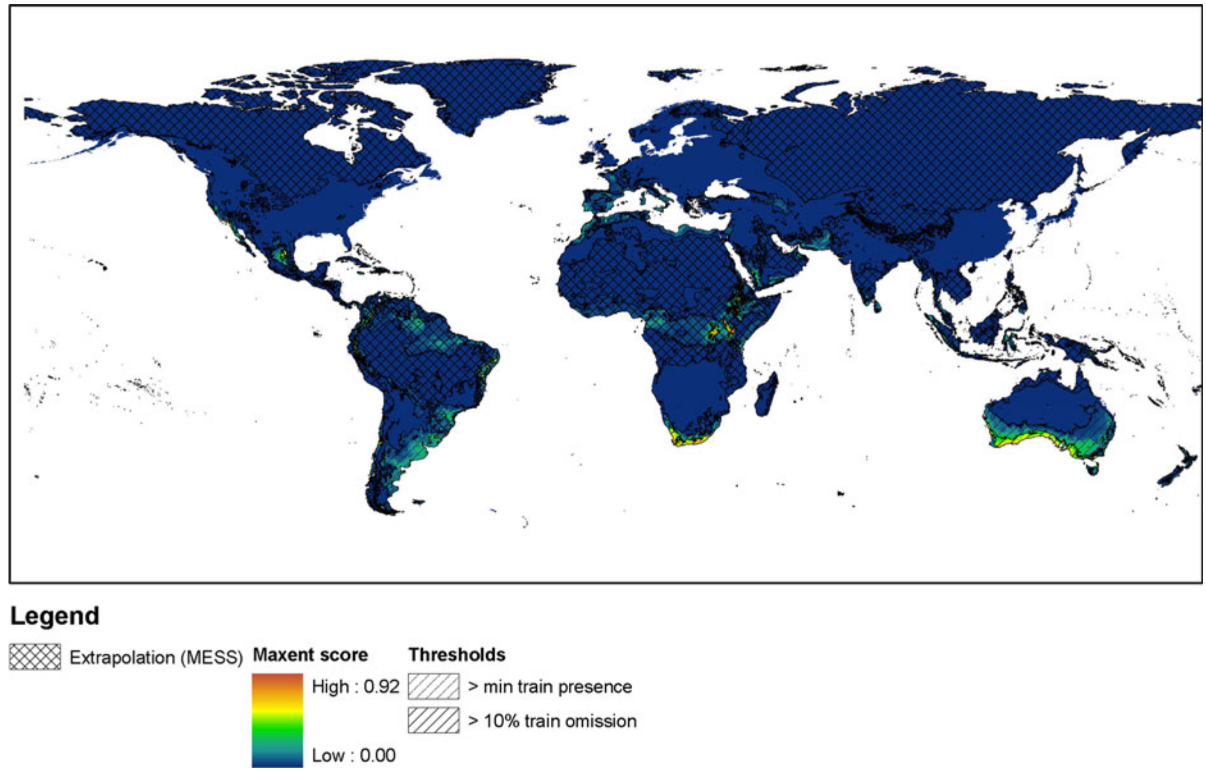

Fig. 2 Global predicted distribution of *Xenopus laevis* with a spatial resolution of 2.5 arcmin from a Maxent model (see text for details). Warmer colours indicate higher climatic suitability. Suitable climatic areas above the minimum training presence logistic threshold are indicated in *light downward diagonal fill*, wherein those optimal areas above the 10 % training omission threshold are indicated in *dark downward diagonal fill*. Areas with bioclimatic conditions exceeding those in the training areas requiring model extrapolation are indicated as crosshatched. For detailed predicted distributions, see Electronic Supplementary Material

optimum, while suitable climate space extends the length of Baja Mexico. Similarly, central Chile also demonstrates a large suitable climatic space for this species, which appears to have the potential to spread much further than the existing invasion (Table 1).

In the rest of the world, the largest climatically optimal areas that are not already known to have established populations of *X. laevis* are in southern Australia and central Mexico. Other climatically suitable areas are in central Africa and eastern South America, but these areas already have native populations of other species of pipid frogs.

Review of invasions

Europe–France

The site of initial introduction was an artificial village pond in Bouillé-Saint-Paul (Deux Sevres, France). The pond was situated some 150 m from a commercial laboratory supplier for French research institutions, which bred *X. laevis* since the 1950s. The first report of an adult in the pond was from a fisherman in 1981. The owner retired in 1989 and the new owner closed the centre in 1996, and it is believed that all remaining animals were released at this time.

Despite the animals being relatively well known by local residents, the first report was not published until 2001 (Fouquet 2001). The most recent data shows that *X. laevis* have covered an area of 207 km^2 (Table 1) in the Midwest region (northern Deux-Sevres and southern Maine-et-Loire; Grosselet, personal communication). Our model predicts a smaller area of optimal climate (63 km^2), while the continuous suitable climate space includes much of southern Europe (Table 1; Fig. 2; and Electronic Supplementary Material).

This region is primarily stocked with dairy cattle and sheep in small fields that frequently have small

Table 1 Summary of species distribution models for invasive populations of the African clawed frog, *Xenopus laevis*

	MCHP	>10 % training omission	Notes	>Minimum training presence	Notes
Portugal	0.6	0	Smaller than MCHP	1,019,947	Suitable areas extend into Spain, France, mainland Italy, Belgium and the Netherlands
France	207	63	Smaller than MCHP	1,019,947	Suitable areas extend as for Portugal
Italy	300	0	Smaller than MCHP	25,711	The entire island of Sicily is suitable. Note that mainland Italy is included under Portugal and France (above)
UK (Wales)	0.1	0	Smaller than MCHP	914	All of eastern South Wales is considered suitable.
USA (California)	17,592	23,840	Does not include populations to the north of Los Angeles, San Francisco, and Goleta Slough	269,624	Includes San Francisco and Orange County populations but excludes Arizona. Extends into Baja Mexico
Chile	10,432	16,669	Does not include a population in Santa Cruz or those in Administrative Region VI	177,183	Includes all populations and areas to the North and South
Japan	15	0	Smaller than MCHP	0	

All areas are km^2 and include minimum convex hull polygons (MCHP) around existing sites and areas predicted continuous presence from Maxent models. Note that only all but one populations are predicted to have larger suitable climate space to move into (i.e. >minimum training presence)

man-made ponds. The rate of spread has been estimated to be roughly 1 km per year (Fouquet and Measey 2006), but overland or upstream colonisation appears to be slower (0.5 km per year), with greater rates when ponds are close to downstream dispersal corridors (rivers, streams, irrigation channels).

Animals have been seen in large quantities moving along roads during downpours, while individuals have been seen moving alone along grassy paths (J.-M. Thirion personal communication). Eggert and Fouquet (2006) followed an adult female using radio telemetry that moved 80 m from a pond, crossing a meadow, a wooded fence and into a road culvert. Ponds inhabited by *X. laevis* during initial studies in 2001 are still occupied (J.-M. Thirion personal communication).

Europe–Italy

The only known population of *X. laevis* in Italy is on the island of Sicily where the date, site and cause of first release are all unknown. Animals could have originated from laboratories at the University of Palermo where *X. laevis* was used as research model. The oldest documentation of *X. laevis* in Sicily are two specimens in the “Museo Regionale di Storia Naturale e Mostra permanente del Carretto Siciliano” (Terrasini, Palermo district, Sicily) labelled “Diga Iato 5 Settembre 1999” but not identified. The first written report is from June 2004 (Lillo et al. 2005), by which time the area of occupancy was already too large to identify a site of origin.

In 2005, the extent in northeastern Sicily was estimated as 225 km^2 (Faraone et al. 2008), but new data suggests that the ongoing invasion has reached 300 km^2 (Lillo et al. 2011). The region is mainly agricultural land cultivated with vineyards, olive groves and grain fields. It is situated in the catchment basins of the Belice Destro and Jato Rivers where there is a large reservoir (Poma Lake) and hundreds of agricultural ponds with surface areas ranging between 100 and 2,000 m^2.

At present the rate of spread is not sufficiently assessed, however observations have been made of newly colonized ponds at a distance of between 400 and 700 m from the nearest pond occupied by *X. laevis*. Irrigation ditches are not present in the area and the ponds are not connected with each other. Although it is possible that the few temporary streams and the Jato River (the only permanent watercourse in the area) could facilitate the dispersal of the species, it is likely that most individuals disperse overland. Both presence/absence thresholds predict suitable bioclimatic conditions over the whole island of Sicily (>25,000 km^2), but we also found that most of mainland Italy is climatically suitable (Table 1).

Europe–Iberian Peninsula

Although unconfirmed, the introduction in Portugal may have occurred in 1979, after a flood that inundated the basement of a Science Research institute at Oeiras, Portugal, which used *X. laevis* for studies of developmental biology. The institute is adjacent to the "Marquês de Pombal" gardens, where animals were first found in 2006, and their presence was first reported in a newspaper article in 2007. The most recent surveys suggest that the population is restricted to two streams, 5 km apart (a total area of only 15 km^2), that empty into the Tejo Estuary, Oeiras County near Lisbon, Portugal (Rebelo et al. 2010). Repeated surveys in 2010 and 2011 have not recorded individuals from upstream dispersal. The stream with the majority of individuals is strongly canalised with a tall concrete wall and high cement gables, which produce 2 m high cascades. The dispersal mechanism to the second stream (around 5 km distant, and still maintaining its natural margins) is unknown. Its colonization may have happened during the 1980s, when parts of the stream basins had not yet been converted into an urban landscape. At that time, two of the tributaries of the first river were about 1 km distant from the second. Starting in 2010, a 5-year program aiming for eradication of this species is being carried out by the Portuguese Governmental Nature Conservation Institute.

Pascual et al. (2007) report the presence and eradication of *X. laevis* larvae from a public ornamental garden in Barcelona, Spain. Following discovery in April 2007, the ponds were drained (yielding 12 *X. laevis* larvae) and no adults or larvae were found again (Pascual et al. 2007).

Europe–United Kingdom

Introductions at three discreet sites are known to have formed viable breeding populations in the United Kingdom, and in addition, a number of adults and tadpoles have been reported from throughout the country (Tinsley and McCoid 1996).

Individuals were deliberately released to some ponds at Brook on the Isle of Wight in 1967 (Lever 2003) and populations continued to persist until the mid-1990s (Tinsley and McCoid 1996). No studies have been carried out on the population on the Isle of Wight since the last review, when this population was thought to be extinct (Tinsley and McCoid 1996). However, a photograph of an individual in a pond in the same area is mentioned in a DEFRA report (unpublished), which suggests that the status of this population requires further investigation.

The first reports of *X. laevis* in South Wales date back to 1979 when populations were already well established in two adjoining watersheds near Bridgend (Tinsley and McCoid 1996). Skeletochronological analysis of phalanges suggests that the oldest known animal metamorphosed in 1974 (Measey and Tinsley 1998). This likely places the introduction into a period when this species was used for pregnancy diagnosis. The area is 5 km from Bridgend and 25 km from Cardiff, and both towns may have had pregnancy diagnosis clinics using *X. laevis* in the 1960s. Although these populations were studied from 1980, the first account was only published in 1996 (Tinsley and McCoid 1996). When first assessed, this population covered 123 km^2, but from 1990 no animals have been found in one of the catchments, reducing the current area to 62 km^2 (Measey and Tinsley 1998), representing an overall reduction in distribution. An extensive capture-mark-recapture program of this population demonstrated movements of 2 km between trapping sites, although this likely included a stretch of river, as well as movement overland (Measey and Tinsley 1998).

Recreational fishermen first reported *X. laevis* from ponds near Scunthorpe, Humberside in the north-east of England in the late 1990s (G. Woodcock, personal communication; Measey 2004b). The source of this population is thought to be due to the closure of a pet shop and deliberate release of adults in the mid 1990s. An eradication campaign was started in 2006 and has achieved significant effect by 2008 when only 11 animals could be found compared to several hundreds in previous years (J. Foster, personal communication). Breeding is known to have taken place and individuals have dispersed to a number of nearby waterbodies within a 5 km^2 area. Ongoing eradication plans are being orchestrated by English conservation authorities (Natural England, UK).

An adult *X. laevis* and many tadpoles were successfully extirpated in 2001 from a site near a bullfrog (*Lithobates catesbeiana*) colony near Tunbridge Wells on the border of Kent and East Sussex (Cunningham et al. 2005). No further reports of *X. laevis* have occurred in this area.

South America–Chile

The first recorded introduction of *X. laevis* in Chile was to a single lagoon near Santiago's international airport in 1973 (Jaksic 1998; Lobos and Jaksic 2005). However, the first reports of wild populations came in the 1980s confined to an area around Santiago (Veloso and Navarro 1988).

Xenopus laevis has shown a great capacity to colonise aquatic environments in central Chile (Lobos et al. 1999). The area currently established includes Administrative Regions Metropolitan, IV, V and VI from sea level to around 620 m (Lobos and Jaksic 2005; Lobos and Measey 2002). While the distribution around Santiago (Administrative Regions: Metropolitan, V and VI) most probably represent a limited number of introductions and translocations, a study with molecular markers, has shown that isolated populations in Administrative Region IV, represent a relocation from Central Chile (Lobos in press). The exact reason for these introductions is not known, but is presumed to be connected with the use of animals in the pet trade.

Taking the starting point and date as above, *X. laevis* has spread 75 km to the west, with a rate of dispersion of 3.1 km per year (with the farthest point west reached in 1997). To the South about 97 km, with a rate of 3.9 km per year (the farthest point South was reached in 1998). Other authors have calculated a faster rate based on a more recent date of establishment in the 1980s (Glade 1988; Lobos et al. 1999; Veloso and Navarro 1988), and it seems unreasonable to exclude the possibility that some of the spread was human mediated (Lobos and Jaksic 2005).

North America–USA

The first report of invasive populations of *X. laevis* in the USA were from the Santa Ana River in Greater Los Angeles in 1968, but in a detailed account of all US populations, Crayon (2005) lists ten introductions in different Californian counties right up to 1996. Despite legal restriction on sale and transport of this species in California, all available data suggests that introductions are ongoing elsewhere across the state (Crayon 2005). The most recently reported populations were found in Lily Pond, Golden Gate Park, in 2001 (Green et al. 2010; Matz et al. 2005). After persistent removal efforts in 2006 and 2008 (focusing on physical removal of the frogs and a gradual draining of the pond), this population appears to have been eradicated. Multiple trapping visits to this site in 2011 have not yielded any frogs (S. L. Green unpublished data). Nearby sites in the park have also been surveyed and the frogs have not dispersed. Indeed, constant introductions appear to occur throughout the USA with reports in 13 states (Arizona, California, Colorado, Florida, Massachusetts, Nevada, New Mexico, North Carolina, Texas, Utah, Virginia, Wisconsin and Wyoming) spanning a period of the last 40 years (Crayon 2005; Krysko et al. 2011; United States Geological Survey 2011). Introductions appear to result from unwanted pets, pet shops and laboratories (Crayon 2005).

Only populations in Arizona and California are considered to have established breeding populations (see Crayon 2005 for factors why other populations did not become established), although the former is not likely to spread out of its environmentally modified conditions on a golf course in Tucson (Measey 1997). Similarly, Crayon (2005) commented that the population at Edwards Air Force Base, California has not expanded in more than 20 years due to unsuitable surrounding habitat.

Despite some extensive studies on invasive populations in southern California (e.g. McCoid and Fritts 1980, 1995) there is little data on the dispersal and rate of spread for this species. Most populations appear to have been well established prior to these studies, although there is evidence that dispersal has occurred throughout watersheds (see Crayon 2005). Although neighbouring watersheds are invaded, Crayon (2005) considered it more likely that each was the result of a lowland introduction with movement through water courses. Nevertheless, migration overland must be a factor as isolated ponds are known to hold populations, some of which have been estimated as thousands of individuals (Measey 1997).

North America–Mexico

Tinsley and McCoid (1996) commented that invasive populations are also likely to occur in neighbouring

Baja Mexico, although no studies or reports of this invasive species are known from this area. A recent survey of the southern peninsula's oases for invasive American bullfrogs (*Lithobates catesbeianus*) (Luja and Rodrıguez-Estrella 2010) did not find any *X. laevis* using dip nets, tracking and visual inspections (V. Luja, personal communication).

Asia–Japan

Introductions in Japan appear to have multiple unknown origins in at least six areas in four Prefectures. *Xenopus laevis* is available in Japan both in the pet trade, and it is widely used in laboratory studies (Kobayashi and Hasegawa 2005). The first records and largest established populations are in Chiba Prefecture in the lower reaches of the Tone River, dating back to the late 1990s (Kobayashi and Hasegawa 2005). Mitsuoka et al. (2011) reported that *X. laevis* were found in an area extending 5 by 3 km where rice and lotus are cultivated. In addition, an adult and more than 10 tadpoles were found from a channel in Shisui Town in 2001, and a ditch in Nagara Town in 2002 (Kobayashi and Hasegawa 2005). However, *X. laevis* have been not reported from these areas since, despite annual surveys. We note that, the substantial areas of lowland freshwater related agriculture are likely to make dispersal of this species through irrigation channels particularly easy.

In 1998, 109 tadpoles and two frogs were collected from an ephemeral pond in Fujisawa City, Kanagawa Prefecture. Although annual surveys were performed, *X. laevis* have not been reported since then (Kobayashi and Hasegawa 2005).

Xenopus laevis have been farmed in Nishi-ku, Hamamatsu City, Shizuoka Prefecture, since the 1980s. Adults and tadpoles have been reported since 1997 from many water areas such as a lake, channels, farm ponds, culture ponds, paddy fields and culture ponds in Nishi-ku, Hamamatsu City (Arao and Kitano 2006). In Tanabe City, Wakayama Prefecture, frogs and tadpoles have been found from farm ponds since 2007 (Tamai, personal communication).

Asia–Java

Various websites claim that *X. laevis* is present on Java (Indonesia) (e.g. Tinsley et al. 2008). This assertion may stem from Iskandar's (1998) use of the term "introduced" instead of "imported" (F. Kraus, personal communication). At the time of his writing, there was no established population of *X. laevis* on Java, and no current presence of this species on Java could be substantiated.

Rest of world

Ascension Island: Tinsley and McCoid (1996) mentioned a population of *X. laevis* on Ascension Island based on a report from Loveridge (1959) and Duffey (1964) who mentioned both adults and tadpoles. Rowlands (2001) states that *X. laevis* had not been seen for some years, and similarly a letter to The Islander in 2001 yielded only comments that no-one had seen the frogs at the localities described by Loveridge and Duffey for many years.

Israel: A single female *X. laevis* was recorded in the area of Emek Hefer in 1996 (32°20′43.05″N 34°55′6.93″E) and was believed to have escaped from a nearby breeding facility (O. Hatzofe, personal communication). Several other sightings in this area have not been confirmed.

Sweden: A single animal exists in the collection of the Gothenberg Natural History Museum collected in 2007 with the locality: Död hos Wennerberg erh. fr. Björkegren.

Discussion

Our results show that the origins of invasive populations of *X. laevis* do not all date from a single period, but have been continuous over the last 50 years, from the first period that large numbers of this species were exported from South Africa (Gurdon and Hopwood 2000). The continued use of this species in research and the pet trade has led to the release of individuals resulting in invasive populations in Asia, Europe, North and South America. A number of invasive populations were deliberate releases of large numbers of frogs into local environments, sometimes out of curiosity (e.g. Arizona, USA), and at other times out of misguided ethical principles (e.g. Humberside, UK and France; see Table 2).

Although scientists that use *X. laevis* as a model organism may now be aware of the risks posed by invasive species (Vogel 2008), the maintenance staff in laboratories and in the pet trade may not have

Table 2 Summary of currently established invasive populations of the African clawed frog, *Xenopus laevis*

Population name	Date of likely introduction	First seen	Source	Spread (km^2)	Deliberate/accidental
Europe					
Portugal	1979	2006	Possibly the Instituto Gulbenkian de Ciência research laboratory	0.6	acc
France	1970s*	1981	Bouillé-Saint-Paul—research breeding facility	207	acc/del
Italy	Unknown	1999	Unknown—possibly laboratories at the University of Palermo	300	Unknown
UK (Humberside)	1990s	2000	Pet shop	5	del
UK (Wales)	Unknown	1979	Unknown—possibly pregnancy test clinic – Bridgend	0.1	del
North America					
USA (Arizona)	1960s		A curious individual	0.1	del
USA (California Orange County)	1960s	1968	Pet traders	17,592	acc
USA (California San Francisco)	2000s	2004	Probably unwanted pets	0.1	del
South America					
Chile	Unknown	1983	Possibly unwanted pets or escaped laboratory stock	10,432	Unknown
Asia					
Japan	1990s	2004	Possibly unwanted pets or escaped laboratory stock	15	Unknown

* 1996 centre closed and all remaining frogs released

appropriate information or relevant training. One (anonymous) technician admitted (to GJM) that they had been releasing tadpoles of *X. laevis* into a pond on university property routinely for many years, despite being instructed to euthanise the same according to government regulations. Other technicians admitted having given tadpoles to local schools and friends for early learning purposes. Biosecurity at breeding facilities is clearly of paramount importance (Meyerson and Reaser 2002), and instances where this has failed are suspected to have been the source of at least two invasive populations (Portugal and France), and possibly more.

Pets and pet shops represent an additional invasion pathway that is the suspected source of at least two populations (Humberside, UK and California, USA), and dumping of stock has been reported elsewhere (King and Krakauer 1996). The pet trade invasion pathway has recently been assessed as being responsible for the introduction of 84 % of Florida's 137 introduced amphibian and reptile taxa (Krysko et al. 2011). However, globally the pet trade pathway was found to be comparatively small (~2 %) compared to other invasion pathways for anuran taxa (Kraus 2009). Certainly, *X. laevis* is widely available in the pet trade, despite no export for this purpose from South Africa (Weldon et al. 2007), and the ban of trade of this species in a growing number of countries (Tinsley and McCoid 1996). Black market sales of this species in the US aquarium hobbyist trade persisted at least into the 1980s (Stebbins 1985), and doubtless continue there and elsewhere. The growing trade in herpetofauna in general is of concern with respect to the increasing numbers of invasive populations that this produces (van Wilgen et al. 2010).

The aquatic nature of *X. laevis* (Elepfandt et al. 2000), quiet submerged calling (Tobias et al. 1998), and infrequent overland movements often during torrential downpours (Lobos and Jaksic 2005) has made it hard to detect in the majority of invasive populations. One unexpected finding from our review of the literature is the years or even decades during which many established populations remained unreported. Recreational fishing has detected at least two populations (Humberside, UK and France), while others have been recognised due to a renewed interest in amphibian surveys following the well publicised amphibian decline phenomenon (e.g. Beebee and Griffiths 2005). In cases where the release date is known or can be approximated, there is a lag of 2–25 years before the first reports of the invasion and even longer periods before the first studies. Despite documentation and publicity about the negative impacts of this invasive species (see above), very few attempts are being made to eliminate populations. Organised extirpation has been recorded from only a handful of populations (Tinsley and McCoid 1996), although ongoing programs are active in Humberside, UK (Natural England), and Portugal (Instituto Nacional para a Conservação da Natureza e da Biodiversidade, and Oeiras township).

Three mechanisms of dispersal of *X. laevis* have been identified: (a) Irrigation channels and streams or rivers appear to be the major routes for dispersal for many invasions (Fouquet and Measey 2006; Lobos and Jaksic 2005; Crayon 2005; Lobos and Measey 2002; Measey and Tinsley 1998). When these run close to artificial dams or ponds, large populations quickly become established. (b) Overland migration appears to be slower than movement through channels (Fouquet and Measey 2006) but is potentially the only means of dispersal in some areas (e.g. Lillo et al. 2011), and while migrations are best documented to move with heavy rains, individuals have been documented moving in completely dry conditions (Lobos and Garín 2002), as well as with thousands of animals moving en mass from a drying dam (Lobos and Jaksic 2005). (c) Anthropogenically assisted movement occurs not only to original sites of invasion, but from one invasion site to another. One clear example is movement from the centrally invaded area to the IV Administrative Region of Chile, around 400 km north of Santiago (G. Lobos unpublished data).

Propagule pressure is recognised as playing a pivotal role in the establishment of invasive species (Reaser et al. 2008), and there is some evidence that this is the case with invasive populations of *X. laevis*. Some of the populations became established after the release of large numbers of animals from breeding facilities (laboratory and pet supplies). In other cases the number of propagules is not known, but no established populations are known to be the result of the release of very few animals. However, studies on the invasive population in South Wales do demonstrate the ability of the recovery of *X. laevis* from very low numbers to hundreds of individuals at a very small site (0.3 ha) in one successful season (Measey 2001; Measey and Tinsley 1998). Single adults have been caught in many locations in the southwestern United Kingdom, apparently without establishing invasions (Tinsley and McCoid 1996), and the same is true in many parts of the USA (United States Geological Survey 2011). However, it should be noted that these areas fall outside the predicted areas of suitable climate space for this species, and it may be that low propagule density would be more likely to produce invasive populations in areas of optimal climate.

Our models provide the first information on areas currently without known invasions that may be at great risk if *X. laevis* is released. Both central Mexico and southern Australia have laboratories conducting research on this species. Australians are familiar with invasion by anuran amphibians, but central Mexico (San Louis and environs) may be particularly vulnerable. The models also demonstrate that this species may not have reached its full invasive potential in the optimal climates of central Chile and California (and presumably adjoining Baja Mexico). In addition, suitable climatic space in southwestern Europe includes regions where invasive populations are already established. We suggest that authorities in these areas adopt an Early Detection Rapid Response (EDRR) reaction to any reports of *X. laevis*.

Within South Africa, *X. laevis* has one of the most extensive distributions of any amphibians (Measey 2004a), and has recently been termed a ‘domestic exotic’ (Measey and Davies 2011) as defined by Guo and Ricklefs (2011). Indeed, in South Africa *X. laevis* is renowned for quickly moving into disturbed habitats and making use of irrigation channels to disperse. In the southwestern Cape, the endemic *Xenopus gilli* has been displaced from much of its former range by *X. laevis*, which had previously been inhibited by low pH levels (Measey and Davies 2011; Picker 1985; Picker and De Villiers 1989). Grave conservation concerns exist where this species continually invades the few remaining sites where *X. gilli* occurs (Evans et al. 1998). Movement through irrigation channels is thought to have spread previously localised haplotypes over a much wider area (Measey and Channing 2003), in addition to deliberate movements of this species for fishing bait (Weldon et al. 2007), and either explanation could explain the mixed assemblages of haplotypes found at some localities (Du Preez et al. 2009; Measey and Channing 2003). We note that comparatively few reports exist of *X. laevis* in its natural habitat, and we continue to be ignorant of the native ecology and natural dispersal of this globally invasive species.

Conclusion

Xenopus laevis is one of the world's most widely distributed amphibian species, and invasive populations have become established on four continents due to deliberate and accidental introductions from laboratory and pet suppliers over the past five decades. Two of four large optimal climatic spaces identified already harbour large invasive populations, although only part of this area is currently invaded. Another large population occurs in climatic space that is modelled as suitable but not optimal. We therefore conclude that the invasion potential of *X. laevis* has been severely underestimated. It follows that biosecurity against release of this species should be generally enforced, but with special attention to the optimal climate space in central Mexico and southern Australia, as well as suitable climatic areas in southern South America and southwestern Europe, where EDRR protocols should be in place for this species. We suggest that authorities be particularly strict on the euthanasia of frogs in laboratories that are ending research on this species, none should be given as pets, and preserved bodies should preferentially be deposited in local museums. While a complete ban of trade for this species is clearly not acceptable or desirable, there needs to be a paradigm shift in the minds of many, and particularly those who are responsible for maintenance of pet and laboratory stocks.

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