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Abstract The endemic-rich amphibian fauna of the Philippine Archipelago (ca. 350,000 km^2) includes six alien frogs: the American bullfrog (*Lithobates catesbeianus*), Asiatic painted toad (*Kaloula pulchra*), cane toad (*Rhinella marina*), Chinese bullfrog (*Hoplobatrachus rugulosus*), green paddy frog (*Hylarana erythraea*), and greenhouse frog (*Eleutherodactylus planirostris*). The chronological history of their invasion across the Philippines was reconstructed based on historical and geographic data. Subsequently, we estimated their current and potential distribution through species distribution modelling and Gaussian kernel density smoothing species distribution data. Seven known and potential pathways of introduction into and spread throughout the Philippines were identified, namely, intentional introduction as a (1) biocontrol agent and (2) food source; contamination of (3) agriculture trade, (4) aquaculture trade, and (5) ornamental plant trade; (6) stowaway of cargo; and (7) through the exotic pet trade. Spatio-temporal patterns of distribution showed a stratified diffusion process of spread wherein human-mediated jum dispersal is the primary mode followed by diffusion dispersal. The status of the American bullfrog in the Philippines is unresolved, whether it has successfully established. Meanwhile, the other five alien frogs have established populations in the wild, typically the dominant species in both artificial and disturbed habitats, and are continuously spreading throughout the Philippines. Estimates of current and potential distribution indicate that none of the alien frogs has realised its full potential distribution and that the cane toad is the most widespread, occurring in almost all major islands of the Philippines (ca. 85%), while the greenhouse frog is the least distributed, being found so far in eight provinces and on seven islands. In light of these findings, we provide policy and management recommendations for responding to current and future alien frog invasions.

Keywords: frogs, geographic risk assessment, invasion history, invasive alien species, policy and management

INTRODUCTION

The Philippines (Fig. 1) is the second largest archipelago in the world, with ca. 7,641 islands, and is recognised as a megadiverse nation and a global biodiversity conservation hotspot (Heaney & Mittermeier, 1997; Heaney, et al., 1999; Myers, et al., 2000a). A compelling example of its rich biodiversity is exhibited by the country's amphibian assemblage, which is among the most important faunas in the Indomalayan Region in terms of diversity and endemism (Bain, et al., 2008; Diesmos, et al., 2014). Currently, there are 110 native species of amphibians known from the Philippines, 97 of which (ca. 91%) are endemics (Diesmos, et al., 2015). However, ca. 45% of Philippine amphibians are threatened with extinction: the major threats include habitat loss and deforestation, invasive alien species, emerging infectious diseases, and climate change (Alcala, et al., 2012; Brown, et al., 2012; Diesmos, et al., 2014).

Included in the Philippine amphibian fauna are six introduced frogs, namely, the American bullfrog (*Lithobates catesbeianus* [Shaw, 1802]), the Asiatic painted toad (*Kaloula pulchra* Gray, 1831), the cane toad (*Rhinella marina* [Linnaeus, 1758]), the Chinese bullfrog (*Hoplobatrachus rugulosus* [Wiegmann, 1834]), the green paddy frog (*Hylarana erythraea* [Schlegel, 1837]), and the greenhouse frog (*Eleutherodactylus planirostris* [Cope, 1862]) (Fig. 2; Diesmos, et al., 2006; Diesmos, et al., 2014; Olson, et al., 2014; Diesmos, et al., 2015). Preliminary studies and anecdotal reports indicated that these introduced species, particularly the cane toad and the Chinese bullfrog, are harmful invasives, threatening Philippine wildlife through competitive exclusion and direct predation (Rabor, 1952; Alcala, 1957; Soriano, 1964; Espiritu, 1985; Adraneda, et al., 2005; Diesmos, et al., 2006). Diesmos, et al., (2006) provided the first review on the status and distribution of alien frogs in the Philippines (then only five alien frogs were present). However, there remains a large knowledge gap on their history of invasion and no recent attempts have been made to synthesise the growing body of knowledge on their geographic distribution. By assembling and analysing historical and geographical data of the six alien frogs in the Philippines, we reconstructed the chronological history of invasion and updated their status and distribution. We then estimated their current and potential distribution by projecting suitable areas based on two separate species distribution models ("native range models" and "Philippine models") and, subsequently, Gaussian kernel density smoothing distribution data to delineate occupied suitable areas ("current distribution") and unoccupied suitable areas ("potential distribution").

METHODS

Reconstructing history of invasion

We reconstructed the chronological history of invasion of the six alien frog species in the Philippines based on historical and geographical data ("species distribution data") obtained from the following sources: (1) Natural history collections (NHC): data obtained directly from collections managers of local and international institutions or through the Global Biodiversity Information Facility (GBIF); (2) published and (3) unpublished scientific literature; and (4) personal observations of authors and fellow experts.

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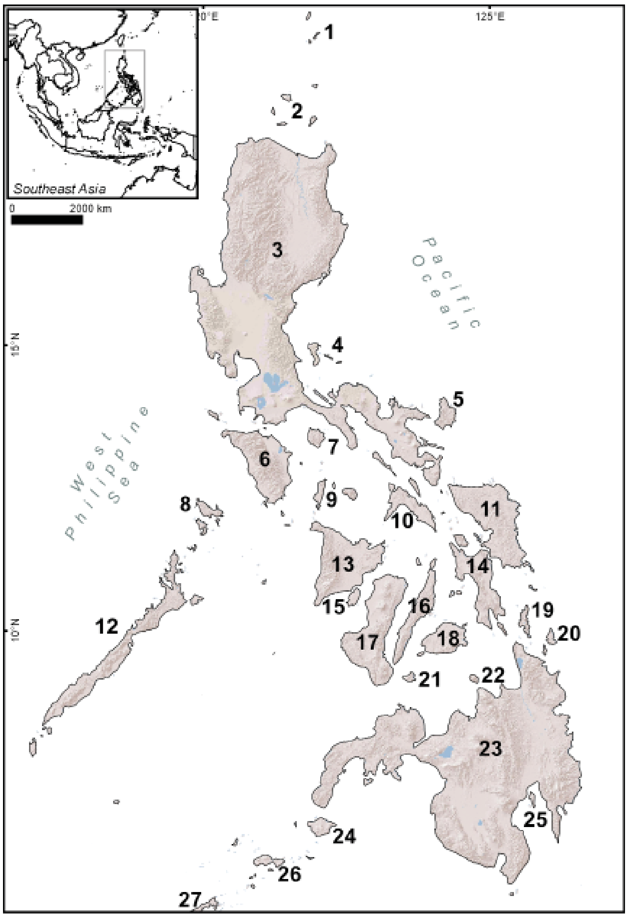

Fig. 1 The Philippine archipelago overlaid on a hypsometric raster shaded-relief. (1) Batanes Island Group, (2) Babyan Island Group, (3) Luzon, (4) Polilio, (5) Catanduanes, (6) Mindoro, (7) Marinduque, (8) Busanga, (9) Romblon Island Group, (10) Masbate, (11) Samar, (12) Palawan, (13) Panay, (14) Leyte, (15) Guimaras, (16) Cebu, (17) Negros, (18) Bohol, (19) Dinagat, (20) Siargao, (21) Siquijor, (22) Camiguin, (23) Mindanao, (24) Basilan, (25) Samal, (26) Jolo, and (27) Tawi-Tawi. Copyright ArcGIS.

Species distribution modelling

Species Distribution Modelling (SDM) involves the quantification of species-environment relationships to define a species' ecological niche. The ecological niche models are then projected into geographic space to visualise and yield an estimate of geographic range or suitable areas where a species can or cannot persist (Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005; Elith & Leathwick, 2009). In studies dealing with invasive alien species, predictions of suitable areas are typically made by extrapolating models fitted with data from the species' native range onto areas that could be invaded (Peterson & Vieglais, 2001; Venette, et al., 2010; Araújo & Peterson, 2012). However, empirical studies have shown evident niche shift in invasive populations, suggesting that species can occupy climatically distinct niche spaces following their introduction into a new area (Broennimann, et al., 2007; Beaumont, et al., 2009).

Here, we developed two separate projections of Philippine-suitable areas for the alien frogs based on models fitted with species distribution data and environmental data (1) from the invaded range in the Philippines (hereafter called "*Philippine models*") and (2) from the alien frogs' native ranges (hereafter called "*Native models*"). Because of the limited amount of species distribution data, we did not develop *Philippine models* for the American bullfrog and the greenhouse frog.

Data collection and calibration. The *Philippine models* were fitted using species distribution data from the Philippines (data used in reconstructing history of invasion). Meanwhile, *Native models* were fitted using species distribution data obtained from the GBIF. Sampling bias was corrected through systematic subsampling neighbouring species distribution data to a resolution of one distribution point per five square kilometres or 2.5 arcminutes and by developing bias files (Elith, et al., 2010; Fourcade, et al., 2014).

The original set of environmental variables includes 19 bioclimatic datasets (Worldclim – Hijmans, et al., 2005) and Global Land Cover 2000 (GLC2000) (Fritz, et al., 2003)

Table 1 Calibration of ecological niche models. Shown are the species distribution data used for model training and testing, model validation approach, number of replicates, and the Maxent features (L – linear; Q – quadratic; P – product) used in fitting *Philippine models* (A) and *Native range models* (B) of the alien frogs. Due to the limited amount of species distribution data viable for model fitting, Philippine models of the American bullfrog and the greenhouse frog were not developed.

Species	Training data	Testing data	Validation	Replication	Maxent Features		
					L	Q	P
A. Philippine model							
American bullfrog	10	-	-	-	-	-	-
Asiatic painted toad	23	-	Crossvalidation	10	✓	✓	-
Cane toad	114	38	Subsampling	10	✓	✓	✓
Chinese bullfrog	79	10	Subsampling	10	✓	✓	✓
Green paddy frog	101	33	Subsampling	10	✓	✓	✓
Greenhouse frog	6	-	-	-	-	-	-
B. Native range model							
American bullfrog	3,704	1,234	Subsampling	10	✓	✓	✓
Asiatic painted toad	93	31	Subsampling	10	✓	✓	✓
Cane toad	1,582	527	Subsampling	10	✓	✓	✓
Chinese bullfrog	83	27	Subsampling	10	✓	✓	✓
Green paddy frog	57	18	Subsampling	10	✓	✓	-
Greenhouse frog	32	-	Crossvalidation	10	✓	✓	-

Fig. 2 Photographs in life of (a) the American bullfrog, (b) the Asiatic painted toad, (c) the cane toad, (d) the Chinese bullfrog, (e) the green paddy frog, and (f) the greenhouse frog. Photographs copyright Tony Gerard (a), Arman N. Pili (b), Emerson Y. Sy (c,d,e,f).

with a spatial resolution of 30 arc seconds. Environmental variables used for fitting the *Philippine models* had a spatial coverage from the Philippines only. Meanwhile, *Native model*s had a spatial coverage equivalent to the native range of the species, based on a convex hull polygon of species distribution data. For both *Philippine* and *Native models* of each species, the environmental variables used for model fitting were pre-selected to only include those that are ecologically relevant (Austin, 2002; Wells, 2007) to the species and are not highly inter-correlated (Dormann, et al., 2013). Correlation between variables were assessed using pair-wise Pearson's correlation coefficient (*stats* R version v.3.3.0 by R Core Team, 2016) and, subsequently, we selected only the putatively ecologically most relevant variable from each group of highly inter-correlated variables ($|r| \geq 0.7$) (Dormann, et al., 2013). The final set of environmental variables used for model fitting included (1) diurnal temperature, (2) temperature seasonality, (3) maximum temperature of warmest month, (4) minimum temperature of coldest month, (5) annual precipitation, (6) precipitation seasonality, (7) precipitation of wettest quarter, and (8) Global Land Cover 2000.

Model fitting. Species distribution modelling was performed using Maximum Entropy Modelling (Maxent v.3.3.3k) (Phillips, et al., 2004; Phillips, et al., 2006a). Maxent is a general-purpose machine learning method premised on the principle of maximum entropy and with a simple and precise mathematical formulation for presence only (i.e., species distribution data) modelling of species distributions from incomplete information (Phillips, et al., 2004; Phillips, et al., 2006a). Maxent has been found to outperform other statistical approaches based on predictive accuracy (Jeschke & Strayer, 2008; Elith & Graham, 2009). Maxent settings used for fitting species distribution models are shown in Table 2. The Maxent features (i.e. linear, quadratic, product) used for each species' models were selected following Phillips (2005), Phillips, et al. (2006b) and Phillips & Dudik (2008) suggestions and were based on the number of species distribution points after systematic subsampling. Developed *bias files* were incorporated in the bias function of Maxent (Table 1). A logistic output was selected to represent the predicted suitable habitats of the species. Pseudo-absence data or background data were generated at random within the Philippines for *Philippine model*s and within the native geographic range of each species for *Native model*s. All other Maxent settings were set to default.

Model evaluation. Model performance of the *Philippine models* of the cane toad, Chinese bullfrog, and green paddy frog, and *Native Models* of all alien frogs except the greenhouse frog was evaluated using the area under receiver operating characteristic (ROC) curve (AUC) by subsampling (randomly splitting presence/pseudo-absences into two subsets with 70% of the records used for model fitting and the remaining 30% to evaluate the models) and was repeated 10 times (Table 1, Pearce & Ferrier, 2000; Allouche et al., 2006; Araújo & Guisan, 2006). Meanwhile, due to the limited amount of species distribution data, model performance of the *Philippine models* of the Asiatic painted toad and *Native Models* of the greenhouse frog was evaluated using the AUC values by 10-fold cross-validation and was repeated five to 10 times (Pearce & Ferrier, 2000; Allouche, et al., 2006; Araújo & Guisan, 2006) (Table 1). The AUC values were interpreted based on Swets (1988) recommendation where 0.5–0.6 = fail, 0.61–0.7 = poor; 0.71–0.8= fair, 0.81–0.9 = good, and 0.91–1.0 = excellent.

Projection. The models were projected to Philippine geographic space to predict suitable areas for the species. The projections were transformed into binary maps of suitable/unsuitable areas, wherein areas above a minimum training presence threshold (no omission) are referred to as "suitable" areas (Liu, et al., 2005).

Table 2 History of invasion and current status and distribution of alien frogs in the Philippines.

Species	Origin of introduced populations	Year and locality of introduction or first detection	Pathway of introduction and spread	Islands Present	Provinces Present
American bullfrog	Louisiana, USA	1966 in Luzon Island	Food source	5	12
Asiatic painted toad	Unknown	2003 in Luzon Island	Cargo Stowaway, Exotic Pet Trade, Ornamental Plant Trade	6	16
Cane toad	Hawaii, USA	1934 in Luzon Island	Biocontrol agent	36	53
Chinese bullfrog	Unknown	1993 in Luzon Island	Food source, Aquaculture trade	7	26
Green paddy frog	Borneo Island[b]	1800s (unknown locality); 1908 Panay Is	Agricultural trade	20	38
Greenhouse frog	Hawaii, USA[b]	2014 in Mindanao Is	Exotic plant trade	8	7

Estimating current and potential distribution

We define the current and potential distribution of invasive alien species as respectively areas occupied and unoccupied by the alien species conditional on areas of suitable habitat (Gormley, et al., 2011). The geographic ranges of the alien frogs in the Philippines were estimated by two-dimensional Gaussian kernel smoothing assembled species distribution data (*kde2d* function of *MASS* v.7.45 R package; Ripley, et al., 2015). This method applies a two-dimensional Gaussian kernel to compute distribution of an animal within its home range/geographic range (Worton, 1989; Venables & Ripley, 2002; Gaston & Fuller, 2009). The solve-the-equation method (*width.SJ* function *MASS* R package; Sheather & Jones, 1991), was used to select the bandwidth for kernel smoothing, and was defined to include 99.5% of species' distribution data. Estimated geographic ranges were then used to delineate the occupied suitable areas ("current distribution") and unoccupied suitable areas ("potential distribution"). Because of the limited amount of species distribution data, we did not estimate the geographic range of the American bullfrog and the greenhouse frog in the Philippines, and, consequently, we did not delineate their current and potential distribution.

RESULTS

History of invasion

A comprehensive review of the history of invasion, including an assembled species distribution database, of the six alien frogs in the Philippines is prepared in a separate study for future publication. The review provided below will suffice as a general overview of their history of invasion.

The American bullfrog

Individuals of the American bullfrog were imported from Louisiana, United States in 1966 and were first reared on Luzon Island (Ugale, 1976; Pascual, 1987b). Frogs were initially bred for the export production of scientific specimens for biomolecular and medical research and other educational activities (Pascual, 1987a; Urbanes, 1988; Urbanes, 1990; Matienzo, 1990). Subsequently, in 1980, through government efforts to boost food security, the American bullfrog breeding shifted to food production. Another eight American bullfrog breeding centres were established across the Philippines (Table 2; Fig 3a; Ministry of Natural Resources, 1981; Buenviaje, 1983; Inovejas, 1985). Breeding centres ceased operation in 1985. The current status of the American bullfrog in the Philippines, whether they were able to successfully establish populations in the wild, is unknown.

The Asiatic painted toad

The Asiatic painted toad was first reported in the Philippines in 2003 on Luzon Island (Diesmos, et al., 2006). It was earlier suggested that the initial introduction of the Asiatic painted toad was through the exotic pet trade (Diesmos, et al., 2006). Introduction as a contaminant of ornamental plant trade or as cargo stowaway is also plausible. From localities of its initial introduction, the Asiatic painted toad has spread in all directions throughout the Philippines and is now recorded in 16 provinces on six islands (Table 2; Fig. 3b). It is likely that the identified introduction pathways may have mediated its spread throughout the Philippines.

The cane toad

The cane toad was intentionally introduced in the Philippines as a part of a national pest control programme (Merino, 1936). Cane toads were secured from the Hawaiian Sugar Planters Association and were brought to the Philippines in 1934 (Merino, 1936). The toads were initially reared on Luzon Island. Since then, they have spread in all directions across islands and onto different islands throughout the Philippines. Their spread is primarily mediated by human movement (deliberate release for biocontrol), as a cargo stowaway, and neighbourhood diffusion dispersal (Rabor, 1952). Today, the cane toad can

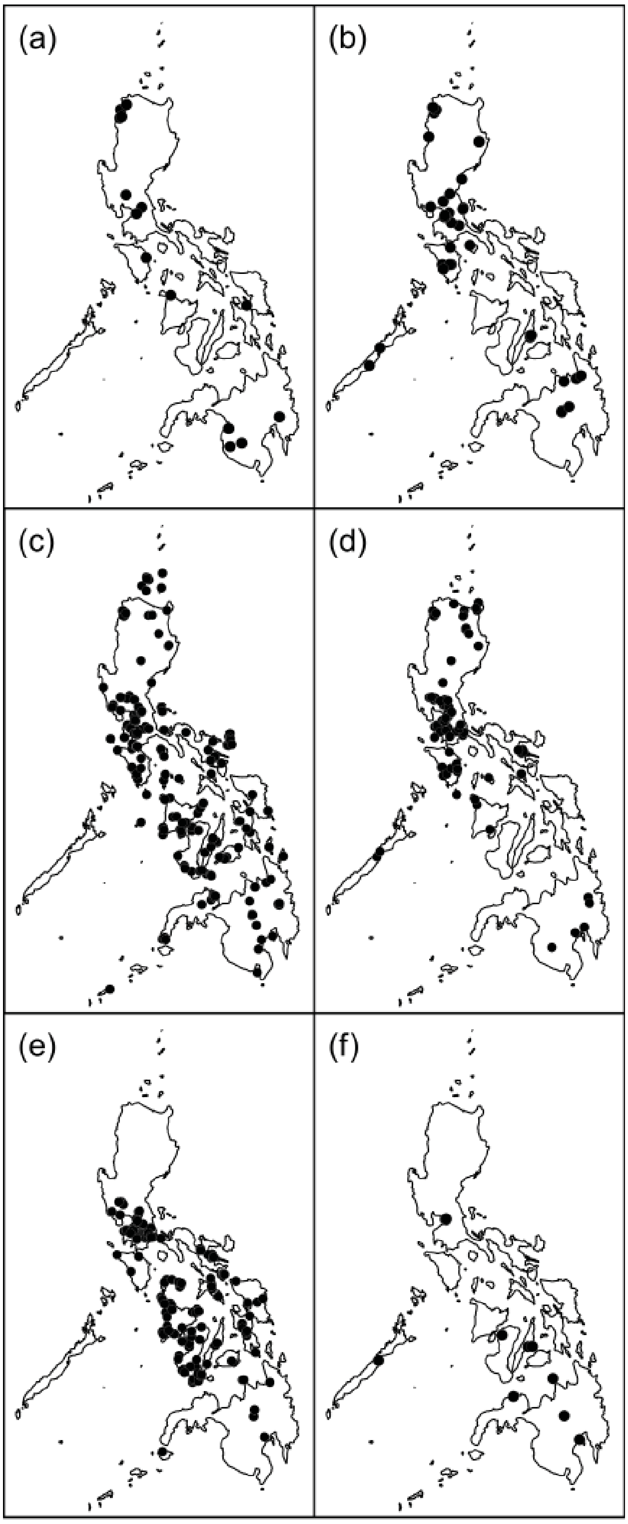

Fig. 3 Geographic distribution of the alien frogs in the Philippines, (a) American bullfrog, (b) Asiatic painted toad, (c) cane toad, (d) Chinese bullfrog, (e) green paddy frog, and (f) greenhouse frog. Points indicate areas where alien frogs were reported present (release sites or areas where bullfrog breeding centres were formerly established for the case of the American bullfrog).

be found on almost all major islands of the Philippines, where it is usually the dominant amphibian species in invaded areas (Table 2; Fig. 3c; Alcala, 1986; Alcala & Brown, 1998; Diesmos, et al., 2006; Diesmos, et al., 2015).

The Chinese bullfrog

The Chinese bullfrog was first reported in the Philippines in 1993 on Luzon Island (Diesmos, 1998; Diesmos et al., 2006). It was speculated that this species was introduced into and spread throughout the Philippines along with American bullfrog breeding in the 1980s (Diesmos, et al., 2006). Other potential pathways of introduction and spread of the Chinese bullfrog throughout the Philippines are contamination of agricultural trade, as for the case of co-occurring alien and native frogs in the Philippines (Inger, 1954; Kuraishi, et al., 2009), and contamination of aquaculture trade, as was the case of its congeneric (Indian bullfrog *Hoplobatrachus tigerinus*) on Andaman Islands, India (Surendran & Vasudevan, 2013). The Chinese bullfrog is now found in 26 provinces on seven islands in the Philippines (Table 2; Fig. 3d).

The green paddy frog

The earliest valid records of the green paddy frog, overlooked in previous discussions regarding its history of invasion (e.g., Inger, 1954), were collections from Panay Island in 1908 (Orrell & Hollowell, 2017). In the early 1900s, the green paddy frog was initially thought to be native to the Philippines with restricted distribution on the islands of Negros, Panay, Sibuyan and Tablas (Taylor, 1920; Taylor, 1922; Inger, 1954). Inger (1954) suggested that the green paddy frog was introduced as a contaminant of agricultural trade owing to its disjunct distribution from the nearest extra-Philippine populations on Borneo Island. The green paddy frog is now found in 38 provinces on 20 islands (Table 2; Fig. 3e). Contamination of agricultural and aquaculture trade may be implicated for its spread throughout the Philippines.

The greenhouse frog

The greenhouse frog was first detected on Mindanao Island in 2013 (Olson, et al., 2014). the propensity of the greenhouse frog to thrive in human-modified environments, especially in gardens (Olson et al., 2014; Sy & Salgo, 2015; Sy, et al., 2015a, b; Sy, 2017a,b), suggests that the trade in exotic ornamental plants is the most plausible pathway of its introduction into and spread throughout the Philippines, as was documented in Hawaii (Kraus, et al., 1999). The greenhouse frog has so far been recorded in eight provinces on seven islands (Table 2; Fig. 3f).

Philippine-suitable areas

Models of the alien frogs indicate fair to excellent training-AUC values (≥70) (Table 3). Based on projections of Philippine-suitable areas of both the *Philippine models* (except American bullfrog and greenhouse frog) and *Native models*, the alien frogs are, to varying extents, suitable to the Philippines. It should be noted that the *Native models* consistently projected a broader range of Philippine-suitable areas (Figs 4 & 5; Table 4). Moreover, both the *Philippine* and *Native models* consistently projected human-modified and disturbed areas to exhibit typical to high probability of suitable conditions for these alien species.

Current and potential distribution

Maps show that the Asiatic painted toad has occupied ca. 30–40% of projected suitable areas (or ca. 20–30% of total Philippine land area), particularly most of central and northern Luzon Island, north-western islands of central Philippines (Cebu, Marinduque, Mindoro, and Palawan Islands), and central Mindanao Island. Potential distribution of the Asiatic painted toad includes islands north of Luzon Island (Babuyanes and Batanes group of islands) areas in north-central (Cordillera Administrative Region), southern (Bicol Region) and most of central Luzon Island, western Mindanao Island, and Sulu Archipelago (Table 5; Fig. 6). The cane toad has occupied almost all projected suitable areas (ca.98–100%) except those on the islands of Batanes Province (northernmost group of islands of the Philippines), islands of Palawan Province (westernmost group of islands), and most of Sulu Archipelago (southernmost islands) (Table 5; Fig. 6). Maps showed that Chinese bullfrog has a disjunct distribution throughout the Philippines, having occupied ca. 40–50% of suitable areas (or ca. 35–40% of total Philippine land area), specifically most of Luzon Island, islands of central

Table 3 Evaluation of the prediction of Species Distribution Models of the six alien frogs. *Philippine models* (**A**) and *Native range models* (**B**) were evaluated by validation of predictions based on the Area Under the Receiver Operating Characteristic (ROC) Curve (AUC).

Species	Training AUC (mean)	Test AUC (mean)	AUC values interpretation	Minimum training presence threshold
A. Philippine model				
American bullfrog	0.78	-	Fair	0.2886
Asiatic painted toad	0.86	-	Good	0.2663
Cane toad	0.72	0.71	Fair	0.0922
Chinese bullfrog	0.84	0.82	Good	0.0858
Green paddy frog	0.82	0.79	Fair	0.1286
Greenhouse frog	0.97	-	Excellent	0.1527
B. Native range model				
American bullfrog	0.70	0.70	Fair	0.0378
Asiatic painted toad	0.86	0.81	Good	0.1243
Cane toad	0.76	0.75	Fair	0.1091
Chinese bullfrog	0.85	0.83	Good	0.0206
Green paddy frog	0.74	0.69	Fair	0.1225
Greenhouse frog	0.78	-	Fair	0.1823

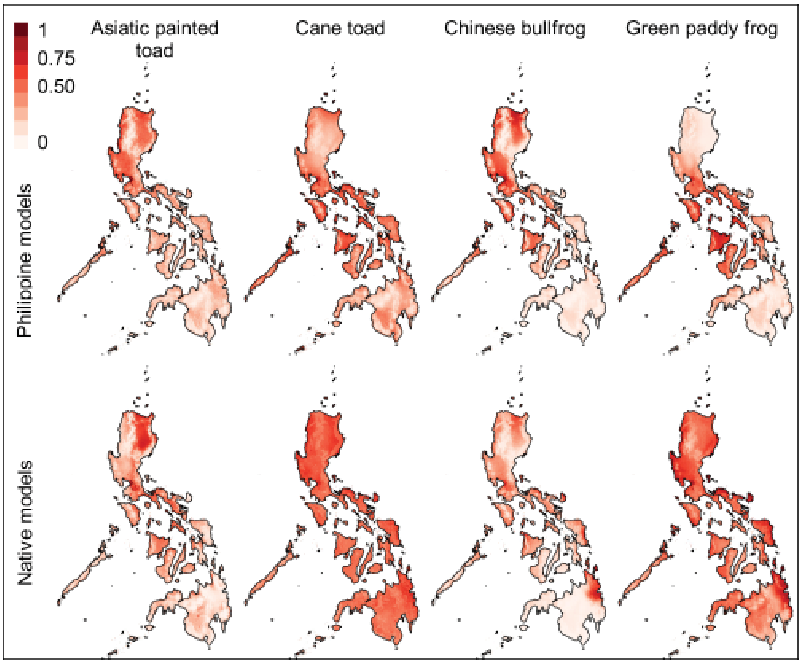

Fig. 4 Projected Philippine-suitable areas for (from left to right) Asiatic painted toad, cane toad, Chinese bullfrog, and green paddy frog, based on (top row) *Philippine model* and (bottom row) *Native model*.

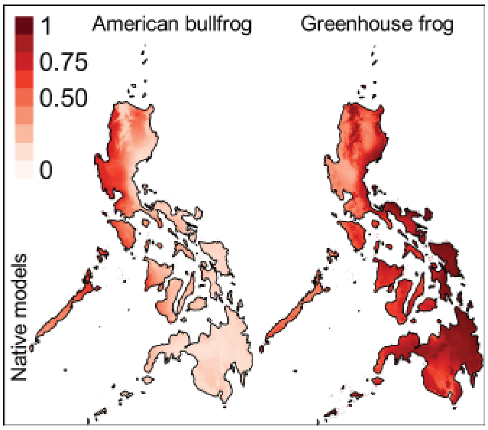

Fig. 5 Projected Philippine-suitable areas for (from left to right) the American bullfrog and the greenhouse frog based on *Native models*.

Philippines (Mindoro and Panay Island), and central and eastern Mindanao Island. Most of its potential distribution are the islands north of Luzon Island (Babuyanes and Batanes group of islands), some areas in central Philippines (Central Visayas Region and Eastern Visayas Region), and most of Mindanao Island including Sulu Archipelago (Table 5; Fig. 6). Despite being present in the Philippines for more than a century, the green paddy frog has only invaded ca. 40–60% of projected suitable areas or 30–40% of the Philippines. The current distribution of the green paddy frog is mainly in Central Philippines, southern and central parts of Luzon Island, disjunct areas in Mindanao Island, and Basilan Island. Potential distribution of the green paddy frog includes most of the islands of Palawan Province, Mindanao Island, and central to northern Luzon Island (Table 5; Fig. 6). Lastly, due to the limited amount of species distribution data, the current and potential distribution of the American bullfrog and the greenhouse frog were not estimated. Interestingly, projections show that almost all of the Philippines is suitable for both species (Fig. 7).

Collectively, maps showed that none of the alien frogs has fully occupied all projected Philippine-suitable areas, and that all alien frogs are on Luzon Island and Mindanao Island, the two largest islands of the Philippines. The islands of Batanes Province (Northernmost group of islands of the Philippines) are the only remaining places in the Philippines with no record of alien frogs.

DISCUSSION

We first discuss here how our study filled knowledge gaps on the invasion history and the status of the alien frogs in the Philippines. At the end of this section, we provide policy and management recommendations.

Invasion history: conceptual background

Our study is the first to reconstruct the invasion history of the six alien frogs in the Philippines. History of invasion refers to the historical, demographical and geographical features of a species' invasion processes. This may include information on the source of propagules and propagule pressure, the dispersal pathways and associated vectors, and the geographical and demographical dynamics of the spread of the adventive populations (Dlugosch & Parker, 2008; Estoup & Guillemaud, 2010). Knowledge of the invasion history forms the foundation of invasion biology by addressing practical and theoretical questions as well as testing different hypotheses concerning the ecology and evolution underlying biological invasions (Estoup & Guillemaud, 2010). More importantly, elucidating invasion history can provide invaluable insights for the

Table 4 Estimates of suitable area in the Philippines (PH) for the six alien frogs. Total area (km²) and percentage (%) of total Philippine land area that is suitable (above minimum training presence threshold) to the alien frogs.

Species	Philippine model		Native range model	
	km²	(%) of total PH	km²	(%) of total PH
American bullfrog	-	-	349,107	99.64
Asiatic painted toad	193,964	55.36	280,825	80.15
Cane toad	344,317	98.27	349,106	99.64
Chinese bullfrog	272,797	77.86	325,179	92.81
Green paddy frog	237,825	67.88	349,104	99.64
Greenhouse frog	-	-	349,107	99.64

Table 5 Estimate of suitable area (current distribution) in the Philippines (PH) occupied by the Asiatic painted toad, the cane toad, the Chinese bullfrog, and the green paddy frog. Shown are total area (km2), percentage (%) of total suitable (Minimum Training Threshold) area, and percentage (%) of PH total land area that is occupied by the alien frogs.

Species	Philippine model			Native range model		
	Occupied suitable area (km^2)	(%) of total suitable	(%) total PH	Occupied suitable area (km^2)	(%) of total suitable	(%) total PH
Asiatic painted toad	81,262	41.90	23.19	106,894	38.064	30.51
Cane toad	293,061	85.11	83.64	296,938	85.057	84.75
Chinese bullfrog	127,185	46.62	36.30	141,797	43.606	40.47
Green paddy frog	141,927	59.68	40.51	160,700	46.032	45.86

development and implementation of sound strategies and science-based policies for the management of invasive alien species, particularly in preventing future introductions and controlling incursions (Hulme, et al., 2008; Estoup & Guillemaud, 2010; Kulhanek, et al., 2011). Here, we reconstructed the chronological history of invasion, identified known and potential pathways involved in introduction, and updated the current status and distribution of invasive frog species in the Philippines. Below we discuss further the dynamics and mechanisms underlying their spread based on spatio-temporal patterns of species distribution.

Invasion history: pathways of introduction of the alien frogs

Identifying the geographical origin, causative pathways, and associated vectors of past introductions can help guide the development of preventive measures, such as monitoring and quarantine schemes, which are most effective when specifically targeted to ports of entry and trade of commodities associated with identified pathways of introduction (Hulme, 2006; Hulme, 2009; Hulme, et al., 2008). Six principal pathways are involved in the global movement of species into new areas: alien species may be commodities (intentionally released and escapees), contaminants of commodities, stowaways on vectors, opportunists exploiting corridors resulting from transport infrastructures, or they may spread naturally (Hulme, et al., 2008). It is noteworthy that the number of total introductions through each pathway may vary among taxonomic groups. For instance, global alien amphibian introductions are most frequently through intentional release as biocontrol agent and food source, contaminant of ornamental plant trade, stowaway of cargo, and escapees from exotic pet trade (Kraus, 2009). In addition to these, herein we identified two other pathways by which alien frogs were introduced into the Philippines: as a contaminant of agricultural trade and aquaculture trade.

Invasion history: dynamics and mechanisms of spread of the alien frogs

Understanding the pattern and rate of spread of invasions are essential components of risk assessment of invasive alien species (Stohlgren & Schnase, 2006;

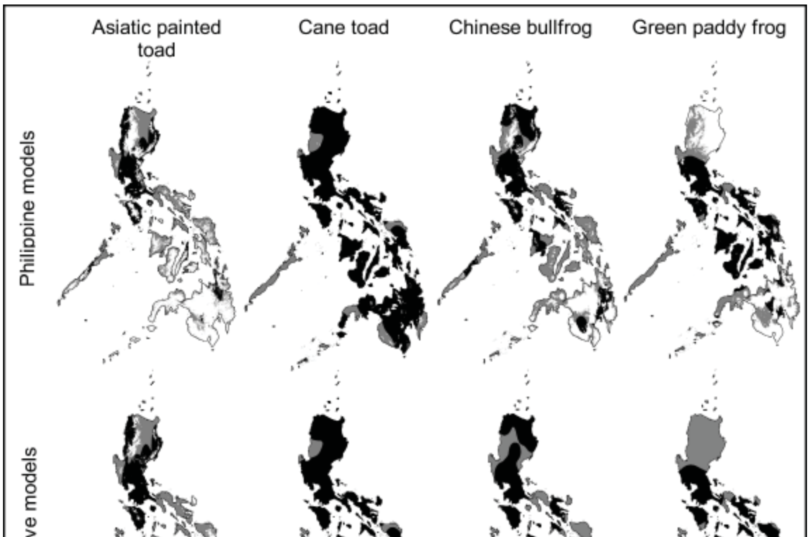

Fig. 6 Current and potential distribution in the Philippines of (from left to right) the Asiatic painted toad, cane toad, Chinese bullfrog, and the green paddy frog based on estimates of geographic range and Philippine-suitable areas projected by (top row) *Philippine models* and (bottom row) *Native models*.

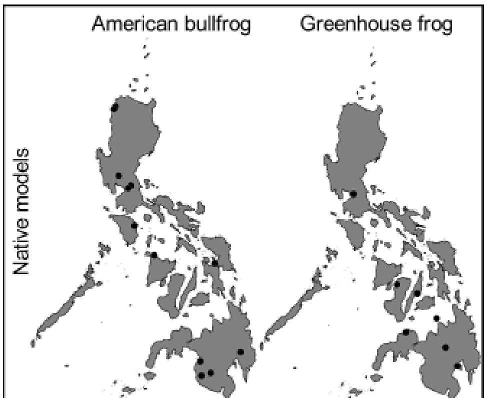

Fig. 7 Current and potential distribution in the Philippines of (from left to right) the American bullfrog and the greenhouse frog based on overlaid species distribution data over Philippine-suitable areas projected by *Native models*. Points indicate areas where alien frogs were reported present (release sites or areas where bullfrog breeding centres were formerly established for the case of the American bullfrog).

Stohlgren & Jarnevich, 2009). For invading organisms, a stratified diffusion process of spread "seems to be the rule rather than the exception" (Higgins & Richardson, 1999). In a stratified diffusion process, initial range expansion occurs though neighbourhood diffusion and new colonies are successively created through jump dispersal events by long-distance migrants, accelerating the rate of overall invasion (Van der Plank, 1967 as cited in Hengeveld, 1989; Shigesada, et al., 1995; Higgins & Richardson, 1999). Jump dispersal events are particularly common for species that are closely associated with humans (Suarez, et al., 2001). For instance, human-mediated jum dispersal has been documented in *Eleutherodactylus* spp. in Hawaii (Kraus & Campbell, 2002), Argentine ants (*Linepithema humile*) in the United States (Suarez, et al., 2001), common ragweed (*Ambrosia artemisiifolia*) in France (Chauvel, et al., 2006).

The reconstructed history of invasion showed that the spread of alien frogs in the Philippines followed a stratified diffusion process wherein human-mediated jump dispersal and neighbourhood diffusion dispersal were the main modes of spread. Given the innate physiological limitations of frogs to cross marine barriers and the close affinity of alien frogs with humans (Wells, 2007), human-mediated jump dispersal is the most plausible primary mode of dispersal of alien frogs inter- and intra-island. Numerous jump dispersal events throughout the course of the invasion of alien frogs in the Philippines can be observed in the spatio-temporal distribution patterns shown in the generated species' distribution maps (Fig. 3). This is particularly evident in the invasion of the cane toad, wherein from founder populations on five islands, it has invaded almost all major islands in the Philippines in a matter of decades (Rabor, 1952). The dispersal of the green paddy frog to Basilan Island, some 300 km from the nearest introduced population in Negros Island in the 1960s and 350 km from nearest native population on Borneo Island, demonstrates a good example of either long-distance jump dispersal or perhaps a secondary introduction event. For the cases of the Asiatic painted toad, the Chinese bullfrog, and the greenhouse frog, it is unclear whether their presence on different islands is caused by jump dispersal events from a single founder population or the result of multiple, independent introduction events.

The same pathways implicated for alien frog introductions may have served as the same pathways that mediated their jump-dispersal throughout the Philippines. Spread of the cane toad was primarily human-mediated, being released deliberately by both government and private individuals with the belief that the frogs would control insect and rodent pests in agricultural fields (Merino, 1936; Rabor, 1952; Soriano, 1964). Observations in the Philippines and on Borneo reported cane toads and the Asiatic painted toads in cargo and vehicles of transport and trade as stowaways (Inger, 1966; A.C. Diesmos personal observation). The greenhouse frog may have spread throughout the Philippines as a contaminant of ornamental plant trade and nursery plants, as happened in Hawaii (Kraus, et al., 1999; Olson, et al., 2012). Similarly, the propensity of the Asiatic painted toad to seek refuge in greenhouse materials (e.g. potted plants, soil, etc.) implicate ornamental plant trade and movement of nursery plants as a potential pathway for its spread (E.Y. Sy personal observation). The American bullfrog, despite having an unresolved status in the Philippines, was dispersed throughout the Philippines as a food source. It was earlier speculated that the Chinese bullfrog may have been introduced and spread throughout the Philippines alongside the proliferation of American bullfrog breeding centres in the 1980s (Diesmos, et al., 2006). Moreover, agricultural trade and aquaculture trade may have served as dispersal pathways for the Chinese bullfrog and as well as the green paddy frog. Agricultural trade has been attributed to recent range expansion of some Philippine native species such as the Philippine common tree frog (*Polpedates leucomystax*), the common mud frog (*Occidozyga laevis*), and the Philippine paddy frog (*Fejervarya vittigera*) (Inger, 1954; Brown, et al., 2010). Meanwhile, the aquaculture trade served as a minor pathway of global introduction for alien frogs and has been well documented in some alien frogs on Guam (Christy, et al., 2007; Kraus, 2007; Kraus, 2009).

Neighbourhood diffusion dispersal also played an invaluable role in the spread of alien frogs within islands. For instance, it was observed that the cane toad has diffused up to 20 km around Dumaguete City, Negros Island in a matter of 15 years (Rabor, 1952). Though this observation was not supported by empirical data, in Australia, the cane toad was observed to travel up to 1.8 km per night, especially during the rainy months (Phillips, et al., 2006b). Moreover, short-distance dispersal may be aided by other "natural" processes such as extensive floods, which are common in most parts of the Philippines.

Policy and management recommendations

Given the potential negative ecological and economic implications of alien frogs (Kraus, 2015), policies and management strategies for alien frog invasions in the Philippines are urgently needed. Our study filled knowledge gaps on the invasion of the alien frogs in the Philippines, which can guide the development and implementation of sound policies and management strategies, particularly the Philippines' National Invasive Species Strategy and Action Plan (NISSAP; DENR-PAWB, 2013).

Prevention of future alien introductions.

Of the six alien frogs currently occurring in the Philippines, three were introduced only in the past three decades, with the greenhouse frog being the most recently reported. Given the lack of measures to prevent invasions in the Philippines, future alien frog introductions seem inevitable. In fact, a recent survey conducted by the authors reported a seventh alien frog is now present (A.C. Diesmos, *for future publication*). A useful preventive measure are early-warning systems (i.e., black-white lists, watch lists, etc.). These systems direct border preventive measures, such as inspection, quarantine, and policies banning entry, by identifying alien species with the potential to threaten native biodiversity (Heger & Trepl, 2003; Hulme, 2006; Maynard & Nowell, 2009). A separate study conducted by the authors for future publication identified alien amphibians that can potentially threaten Philippine biodiversity based on three factors of invasion success, namely history of invasion elsewhere, climate match, and propagule pressure.

To prevent future alien frog introductions, preventive measures are best focused on potential pathways and associated vectors (Perrings, et al., 2005; Hulme, 2006; Hulme, 2009; Hulme, et al., 2008). Some examples of preventive measures include (1) prohibition or developing stricter regulations and standards for the breeding, trading, and keeping of exotic pets (e.g., Taiwan, Australia, and New Zealand) and animals for food production (e.g., European Union States), (2) post-border inspection, quarantine, and treatment of imported commodities such as ornamental plants (e.g., Hawaii and Guam), fish fingerlings, and agricultural products, standardising risk assessment of candidate biocontrol species, and (3) early detection and rapid eradication schemes at ports of entry such as seaports and airports (reviewed in Hulme, 2009; preventive measures focusing on alien amphibians and reptiles are reviewed in Kraus, 2009).

Management of spread between islands

Developing measures to control the inter-island spread of alien frogs is critical in archipelagic systems, such as the Philippines. Like prevention, measures to control the inter-island spread of alien species are best focused on the identified potential pathways of spread and their associated vectors (Hulme, 2006; Hulme, 2009; Hulme, et al., 2008). Some examples of control measures include: for the American bullfrog, Asiatic painted toad, and the Chinese bullfrog, prohibition of release and implementation of standards and regulations for possession or breeding either as pets or for farming (although no bullfrog breeding centres are operational to date); for the Asiatic painted toad and greenhouse frog, quarantine, inspection, and treatment of traded and transported ornamental plants, nursery plants, and greenhouse material; for the Asiatic painted toad and cane toad, early detection and rapid eradication schemes on ports of entry such as seaports and airports and inspection of cargo; for the Chinese bullfrog and green paddy frog, inspection of products of agricultural trade and prohibition of fish fingerling collection for release in novel areas. These control measures should be focused on unoccupied but suitable islands (Leung, et al., 2005), especially in the Batanes Island Group.

It is noteworthy that the Philippines has perhaps the moral responsibility to contain these exotics from spreading into neighboring foreign areas. For example, the southernmost extent of invasion of the cane toad in the Philippines is on Basilan Island, which is about 100 kilometers from Borneo Island (Malaysia) and where the species is alien. The spread of the alien frogs to foreign countries can be prevented by inspection of commodities for export, especially those associated with pathways of introduction and spread. In fact, the Philippine common treefrog was introduced into Ryukyu Archipelago, Japan by contaminated traded agricultural commodities (Kuraishi, et al., 2009).

Maps of current and potential distribution as a guide for management schemes.

Estimating and delineating the potential and current geographical range of alien species is a critical component of risk assessment by providing science-based information that can help guide the strategic allocation of limited resources for the management of invasive alien species (Stohlgren & Schnase, 2006; Stohlgren & Jarnevich, 2009; Venette, et al., 2010). For instance, surveys and monitoring schemes should be focused in areas with no information on the status of the alien frogs or areas of high conservation concern (Wittenberg & Cock, 2001; McGeoch & Squires, 2015), such as in most Protected Areas in the Philippines, on central Luzon Island (Cordillera Administrative Region), western Mindanao Island, and islands in the Batanes Province. More importantly, field surveys are warranted in areas where bullfrog breeding centers were formerly established as well as in release sites, so to confirm the status of the American bullfrog in the Philippines (Fig. 3a). Control and containment of incursions and mitigation of impacts should be focused on invaded areas, especially in areas of high conservation value such as protected areas and nature reserves (Myers, et al., 2000b; Wittenberg & Cock, 2001; Parrish, et al., 2003). Early detection and rapid eradication schemes are best focused on the interface between the potential and current distribution (Hulme, 2006), such as the invasion front of the green paddy frog on central Luzon Island (Fig. 3e).

Recognizing the variability in projected suitable areas between the *Philippine* and *Native models*, and that different modelling techniques yield different results even if calibrated with same set of data, we developed in a separate study for future publication projections of suitable areas based on ensembles of models fitted with data from the entire range (native range and all invaded range/s) and using different statistical techniques. Moreover, evaluation of the accuracy of projections and estimates through ground truthing are underway.

Recommendations for future research

The following recommendations for future research on alien amphibian invasions in the Philippines are suggested: data mining grey literature, conducting interviews, and targeted field work to populate the assembled species distribution database and improve reconstructed invasion history; vector analysis of the pathways so as to understand their importance to current and future alien amphibian invasions; identify 'native exotics' and understand their invasion histories (e.g. dynamics and mechanisms involved in their spatial spread) and impact to ecosystems; comprehensive risk analysis of the alien frogs, specifically research on their ecological and socio-economic impacts; test different hypothesis on the evolution and ecology of alien species invasions.

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