Island hopping in a biodiversity hotspot archipelago: reconstructed invasion history and updated status and distribution of alien frogs in the Philippines

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Abstract
Six alien frogs have been introduced in the Philippines: chronologically, Hylarana erythraea, Rhinella marina, Lithobates catesbeianus, Hoplobatrachus rugulosus, Kaloula pulchra, and Eleutherodactylus planirostris. Here, we collected and synthesized historical and geographical data to reconstruct their history of invasion and to update their current invasion status and distribution in the Philippines. Four pathway categories (falling in 8 subcategories) have facilitated their introduction: (1) intentional ‘release’ for biological control and hunting in the wild; (2) ‘escape’ from farms; (3) ‘contamination’ of agricultural commodities, fish stocks, and ornamental plants/nursery materials; and (4) ‘stowaway’ on container/bulk and (hitchhiker on) ship/boat – of which the last two were important in most recent introductions. The spatio-temporal pattern of distribution showed a stratified-diffusion process of spread involving primarily leading-edge and long-distance dispersal. The pathways that facilitated their secondary (post-introduction) long-distance dispersal were either the same as those of their introduction or shifted over time. Estimation of rate of spread showed that H. erythraea, R. marina, H. rugulosus, and K. pulchra have not reached spatial saturation and are conditioning to spread, with the latter spreading fastest. The status of Lithobates catesbeianus, whether it successfully established or not, is undetermined. Meanwhile, the other alien frogs are now considered fully invasive species, of which R. marina is the most widespread, whereas E. planirostris is the least distributed. Our study provides science-based information that can help guide the development and implementation of pathway-specific measures to prevent and control future and current invasions by alien frogs.

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**Introduction**

The Philippines is the second-largest archipelago in the world (after Indonesia). It is composed of more than 7,100 islands, of which about 2,000 are inhabited; 48 islands have a land area greater than 90 km$^2$ (hereafter, *major islands*). The Philippines forms part of the maritime Southeast Asian Region and is located at the western fringes of the Pacific Ocean, extending to the eastern boundary of the South China Sea, and northeastern boundary of the Sunda Shelf (Diesmos et al. 2014). It is globally recognized as a megadiverse nation for its immensely rich biodiversity (Heaney 1985, 1986; Heaney and Mittermeier 1997; Heaney et al. 1999). However, it is also a global biodiversity conservation hotspot due to the ceaseless imperilment of its biodiversity (Heaney et al. 1999, Myers et al. 2000). Major threats to its biodiversity 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).

Invasive alien species are non-native species that cause ecological and evolutionary changes which consequently impair different aspects of human socio-economic activities (Pimentel et al. 2000, 2005, Clout and Williams 2009). They are major threats to global biodiversity conservation (Secretariat of the Convention on Biological Diversity [CBD] 2015) and are the primary cause of global contemporary animal extinctions (Clavero and Garcia-Berthou 2005). To demonstrate the negative impacts of IAS, the invasion of alien frogs (reviewed in Kraus 2015) have been implicated in diminishing native prey and predator species (e.g., the cane toad [*Rhinella marina*] in Australia – Shine 2010; the American bullfrog [*Lithobates catesbeianus*] in United States – Kiesecker et al. 2001; the African clawed frog [*Xenopus laevis*] in France – Lafferty and Page 1997), shrinking geographic ranges of native species (e.g., *X. laevis* in global invasive range – Measey et al. 2012), and transmitting parasites and diseases to native species (e.g., amphibian Chytridomycosis – Fisher et al. 2009; amphibian
iridoviral disease – Jancovich et al. 2005). High densities of alien frogs have resulted in suppressive effects on native biotic communities and disruption of ecosystem dynamics of invaded areas (e.g., effects of *R. marina* to varanid and varanid prey populations in Australia – Doody et al. 2009). Hybridization of alien frogs with native conspecific and congeneric species has led to loss of genetically distinct populations or entire species due to genetic swamping (e.g., *X. laevis* in South Africa – Picker 1985). Alien frogs have affected socio-economic activities in numerous ways, from infrastructure (e.g., localized power outages in Florida, United States, caused by Cuban tree frog [*Osteopilus septentrionalis*] – Johnson 2007 as cited in Kraus 2009), agriculture (e.g., predation of honey bees [*Apis mellifera*] by *R. marina* in Australia – Tyler 1994), aquaculture (e.g., predation of fish fry by Chinese bullfrog [*Hoplobatrachus rugulosus*] in aquaculture facilities in the Philippines – as Y. Ocampo noted in a Manila Bulletin article on January 17, 2018), nursery, tourism, and real estate industry (e.g., noise pollution caused by the coqui frog [*Eleutherodactylus coqui*] in Hawaii – Kraus et al. 1999, Kraus and Campbell 2002), and public health (e.g., *R. marina* as a vector of human pathogens and parasites – Everard 1988; human fatalities after consumption of *R. marina* – Rabor 1952).

Diesmos et al. (2006) provided the first review of the status and distribution of alien frogs in the Philippines that featured five alien frogs namely: the green paddy frog (*Hylarana erythraea* [Schlegel 1837]), the cane toad (*Rhinella marina* [Linnaeus 1758]), the American bullfrog (*Lithobates catesbeianus* [Shaw 1802]), the East Asian bullfrog (*Hoplobatrachus rugulosus* [Wiegmann 1834]), and the Asiatic painted narrowmouth frog (*Kaloula pulchra* Gray 1831). Afterwards, a sixth alien frog, the greenhouse frog (*Eleutherodactylus planirostris* [Cope 1862]), was reported by Olson et al. (2014). The most recent account of the distribution of these frogs was provided by Diesmos et al. (2015), but was presented in passing along with distributions of native Philippine frogs and is still very limited in terms of geographic scope. To
date, there remains a huge knowledge gap in the history of alien frog invasions in the Philippines. Moreover, no recent attempt has been made to synthesize the growing body of knowledge on their current invasion status and distribution. These knowledge gaps limit our capacity to adequately assess their risk and ecological and socio-economic impacts. Moreover, knowledge gaps also limit our capability to develop and implement sound management response strategies and policies to prevent or mitigate invasions (Wittenberg and Cock 2001, Jeschke and Strayer 2006, Hulme 2006, 2009, Hulme et al. 2008).

Here, we reconstructed the invasion history and updated the current invasion status and distribution of the six alien frogs in the Philippines. We focused our study to the historical and geographical features of their invasion (introduction, establishment, and spread). We approached this by: (1) assembling a species-distribution database from geographical and historical data; (2) identifying the origin of propagules, year and locality of first report, and pathways that mediated their dispersal (introduction) into the Philippines; (3) determining the process of spread, modes of dispersion, and pathways that mediated their secondary (post-introduction) dispersal throughout the Philippines; (4) quantifying the rate of spread as revealed by ‘invasion curves’ and ‘proportion curves’; and lastly (5) updating their current invasion status and distribution.

Materials and Methods

Data collection

Geographical data (i.e., species-distribution data) on the six alien frogs in the Philippines were obtained from several Natural History Collections (NHC) – California Academy of Sciences (Scheinberg and Fong 2017), Field Museum of Natural History (Grant and Resetar 2017), Florida Museum of Natural History (Blackburn and Brown 2017), Museum of Comparative Zoology (Harvard University Museum and Morris 2017), National Museum of Natural History/Smithsonian Institute (Orrell and Hollowell 2017), University of Kansas (Brown
through the Global Biodiversity Information Facility (GBIF). This was complemented with historical and geographical data from published and unpublished scientific literature and from our own field surveys, which were also published online via the GBIF (HerpWatch Pilipinas, Inc. [HWP] 2019).

**Origin and dispersal pathways**

The origin and the pathways that facilitated the introduction of the alien frogs were determined by reviewing scientific literature. In cases where species data on pathways in the Philippines were lacking, possible pathways were inferred by extrapolating information from areas where comprehensive documentation is available for the species or from inference based on the species’ biology and ecology (Essl et al. 2015, Scalera et al. 2016). Pathways were categorized following the Convention on Biological Diversity’s (CBD) pathways categorization system (Scalera et al. 2016) – a unified and standardized categorization, hierarchy and terminology for alien species pathways, which enables consistent and effective prioritization of pathways and the identification of the best management response (Essl et al. 2015). The CBD’s system recognizes three broad mechanisms by which alien species may arrive and enter a new region: importation of commodity, arrival of a transport vector, or spread from a neighboring region. These mechanisms result to six principal pathways (i.e., pathway categories): intentional ‘release’ in nature, ‘escape’ from confinement, transport-as a ‘contaminant’, transport- as a ‘stowaway’, via a ‘corridor’, and ‘unaided or natural dispersal’. These pathway categories are further categorized into 44 subcategories (i.e., pathway subcategories) (Scalera et al. 2016; see document UNEP/CBD/SCSTTA/18/9/Add.1). The CBD’s system, although a generic scheme,
was chosen over other developed taxon-specific systems (e.g., the system used by Kraus 2007, 2009 for alien amphibians and reptiles) because it is a broad, internationally-agreed nomenclature developed for effective science-communication with environmental authorities to better guide the development and implementation of management strategies and policies against invasive alien species. A comparison of the CBD’s system and that used by Kraus (2007, 2009) for alien amphibians and reptiles is shown in supplemental online material Appendix S1.

*Spatio-temporal spread and current invasion status and distribution.*

To reconstruct the history of the alien frogs’ spread in the Philippines, we partitioned the assembled species-distribution database into distinct periods based on natural breaks in the dataset (i.e., 1885 to 1950, 1885 to 1975, 1885 to 2000, 1885 to 2017). Partitions were plotted separately onto a Philippine map. By examining the spatio-temporal patterns of the alien frogs’ distribution, we identified the potential mechanisms and associated pathways of their secondary dispersal throughout the Philippines following Wilson et al. (2009) and Scalera et al. (2016), respectively. Moreover, by examining the alien frogs’ current distribution (Figure 1) complemented with observations on their invasion (from scientific literature and our own field surveys), their current invasion status was assessed and categorized following Faulkner et al. (2016) as modified from Blackburn et al. (2011).

*Rate of spread*

The rate of spread (i.e., invasion rate) of *H. erythraea, R. marina, H. rugulosus,* and *K. pulchra* was measured using ‘invasion curves’ (*sensu* Pyšek and Prach 1993). Two species, *L. catesbeianus* and *E. planirostris,* were excluded in this analysis because the former appears to have failed in establishing breeding populations in the Philippines and we currently have
insufficient data for the latter. Because the often unclear site descriptions of records which in many cases provided only the municipality, province, and/or island as geographic position, it was not possible to make a GIS-based superimposed grid (e.g., 10 x 10 km square) and use it as a measure of the rate of spread (Hengeveld 1989). Instead, for each alien species, invasion curves were constructed using linear-regression models fitted to the log-transformed cumulative number of first locality records (tested separately under two geographic levels: [1] provincial and [2] island) plotted against time (starting from year when the species was first record to 2017) and the slope $b$ of the regression line was used as a proxy of the rate of spread (Pyšek 1991, Pyšek and Prach 1993). Linear-regressions were modelled using the `ggplot2` R package (Whickham and Chang 2008) conducted under R platform (R core team 2017). To provide a realistic picture of the degree of sampling for frogs in the Philippines, we performed the same procedure for native frogs to construct a “curve of discovery rate,” where the presence of any one of the native frogs in a locality was enough to consider that locality occupied (i.e., certainly surveyed). Species-distribution data of native frogs were obtained from the same sources where species-distribution data of alien frogs were obtained (from NHC complemented with published scientific literature). The curve of discovery rate represents the degree and spatio-temporal distribution of sampling of native frogs in the Philippines (Delisle et al. 2003). However, this does not indicate that the range of native species is expanding over time, but rather their range is simply better known over time (Delisle et al. 2003). To test the equality of collection rate between alien and native frogs, the difference between the slope of the regression line of the invasion curve of alien frogs and that of the curve of discovery rate of native frogs was tested using analysis of covariance (ANCOVA; Chambers and Hastie 1992) using the ‘stats’ R package conducted under R platform (R core team 2017). In principle, the more abrupt the slope of the invasion curve, the more rapidly the alien frog has spread (Pyšek and Prach 1993). It is noteworthy, however, that the
slope may have been affected by the temporal changes in the degree of sampling, where an abrupt slope may indicate high degree of sampling during a limited time period (Delisle et al. 2003). Nonetheless, the slope only estimates the rate of spread and cannot be used to distinguish periods of different levels of expansion (Delisle et al. 2003).

Use of data from different sources suffers from several biases, of which spatio-temporal variation in sampling effort is the most concerning. These biases may drastically affect the quality of reconstructed invasion histories, potentially resulting to misleading interpretations and applications (Graham et al. 2004, Estoup and Guillemaud 2010, Newbold 2010, Lavoie 2013). Here, we accounted for variation in spatio-temporal sampling effort by using a simple and reliable method for objectively delineating periods of expansion of alien species – ‘proportion curves’ (Delisle et al. 2003). For each alien frog, the proportion curve was constructed by, first, dividing the cumulative number of first locality records of the alien frog by the cumulative number of first locality records of the pooled native frogs; then, plotting obtained proportions against time (Delisle et al. 2003). Increasing proportions (of alien frog vs. native frogs) for a particular time period suggests that the invasive range (in the Philippines) of the alien frog is indeed expanding, because it is expanding faster than if it was strictly the result of better spatial coverage of sampling effort. A phase of expansion was defined as a time period of at least 5 years during which the proportion is increasing more than 5%. Stable proportions (i.e., new specimens of alien frog and native frogs were collected at the same time) suggest that the invasive range of the alien species may still be expanding, but this could simply be related to better spatial coverage of sampling effort focused on alien frogs. Declining proportions (negative slopes on the proportion curve) don’t necessarily indicate declining alien frog populations, but instead may be due to the invasive range of the alien frog expanding at a very slow rate (i.e., additional localities occupied by the alien frog are rarely found) (Delisle et al. 2003). Declining
proportions may also mean that the founder populations of the alien frog may be growing within a certain locality (i.e., province, island), but no new first records in other localities were documented (Mosena et al. 2018).

Results

Invasion history of alien frogs in the Philippines

Green paddy frog (Hylarana erythraea [Schlegel 1837])

*Hylarana erythraea* (Family Ranidae) is native to South Asia, mainland Southeast Asia (Myanmar, Thailand, Lao People’s Democratic Republic, Cambodia, Viet Nam, and Peninsular Malaysia), Borneo, and some Islands of Indonesia (Sumatra, Java, Lombok, and Riau Islands). It has been introduced in the Philippines and Sulawesi Island (Indonesia) (Diesmos et al. 2006, Frost 2016). Overlooked in earlier studies, a specimen that was collected on “Isla de Samar” (Samar Island in central Philippines) in 1885 (CSIC 2018) is the earliest confirmed record of the species in the Philippines. Subsequently, it was found on neighboring islands of Negros, Sibuyan, and Tablas (also central Philippines) (Taylor 1920, Taylor 1922, Inger 1954). It was initially thought to be native to the Philippines until Inger (1954) proposed it to be classified as an alien species based on the observed unnaturally disjunct distribution of the then known Philippine populations, exclusively found in central Philippines (Figure 1) with the nearest extra-Philippine populations on Borneo (located southwest of the Philippines). It is speculated to have been introduced as a contaminant of agricultural commodities (i.e., ‘food contaminant’ – Scalera et al., 2016) imported from Borneo Island by Sulu seafarers (Inger 1954).

In the initial years of its invasion, *H. erythraea* was known only from the central Philippines, and was reported on Luzon Island in the north and Mindanao Island in the south.
(two largest Philippine islands) only in the late 1990s. It spread throughout the Philippines by a combination of leading-edge dispersal and long-distance dispersal (‘cultivation’, a mechanism of dispersal wherein propagules are actively moved and receive resources to establish/persist – Wilson et al. 2009). It may have secondarily dispersed at long-distances through three plausible pathways: (1) as a contaminant of locally-transported agricultural commodities (i.e., food contaminant) as was the case of its introduction and the recent range expansion of co-occurring native frog species (e.g., Asiatic tree frog [Polypedates leucomystax], Philippine oriental frog [Occidozyga laevis], and Philippine grass frog [Fejervarya vittigera] – Inger 1954, Brown and Alcala 1970a, Brown et al. 2010); (2) as a contaminant of locally-transported or traded food fish fingerlings (i.e., contaminant on animals) owing to its propensity to occur in water bodies where fish fingerlings are often collected; and (3) as escapees of gardens since it is sold as an attractive addition to garden ponds (i.e., ornamental purpose other than horticulture) along with terrestrial and aquatic ornamental plants (Sy 2014) (Table 1).

At the provincial level, the slope of the regression line of the invasion curve of *H. erythraea* \( b = 0.12 \) and that of the curve of discovery rate \( b = 0.13 \) does not differ significantly \( (P = 0.27) \) (Figure 2a). Meanwhile, at the island level, the slope of the regression line of the invasion curve of *H. erythraea* \( b = 0.0108 \) is slightly less steep than that of the curve of discovery rate \( b = 0.0134 \) and is significantly different \( (P < 0.001) \) (Figure 2c). Proportion curves showed three major periods of expansion at the provincial level: 1908–1922, 1961–1970, and 1989–2006 (Figure 2b); and three major periods of expansion at the island level: 1908–1923, 1948–1962, and 1993–1997 (Figure 2d).

*Hylarana erythraea* is now a fully invasive species (i.e., “E” invasion status; individuals dispersing, surviving, and reproducing at multiple sites across a greater or lesser spectrum of habitats and extent of occurrence – Blackburn et al. 2011) and was recorded to have been present
so far in 39 provinces (out of 81) on 20 major islands (Table 2, Figure 1). It is highly tolerant of human disturbance, occurring in exceptional numbers in artificial aquatic habitats, such as rice fields and garden ponds, as well as natural aquatic habitats near human habitation, such as swamps, ponds, ditches, creeks, and rivers (Alcala 1955, Alcala 1986, Alcala and Brown 1998, Gaulke 2011). It was also reported to be present in riverine habitats of secondary forest at low- and mid-elevations (Alcala 1955, Brown and Alcala 1961, Brown and Alcala 1970b, Siler et al. 2012) and has penetrated primary-growth forests (Diesmos et al. 2006, Brown 2017, Scheinberg and Fong 2017).

Cane toad (*Rhinella marina* [Linnaeus 1758])

*Rhinella marina* (Family Bufonidae) is native to tropical America. It has been released in the wild as a biological control in many parts of the world, including several countries in Africa, South America (outside its native range), Asia, and Oceania (including Pacific Islands) (Esteal 1981, Kraus 2009, Frost 2016). Similarly, it was released in the Philippines as a biological control for insect and rodent pest in agricultural fields (Merino 1936, Rabor 1952, Soriano 1964). Initially, 28 toads were acquired from the Hawaiian Sugar Planters Association and were brought to the Philippines in 1934 (Merino 1936). Toads were first reared on Luzon Island, initially at the Bureau of Plant Industry compound, Manila, and later in the College of Agriculture of the University of the Philippines – Los Baños, Laguna Province (Rabor 1952).
From 1934–1949, *R. marina* was dispersed by human-mediated long-distance dispersal (cultivation) in six provinces on five major islands as a biological control (Figure 1) (Rabor 1952, Soriano 1964). From sites of initial release, it spread intra-island via ‘leading-edge dispersal’, as was observed by Rabor (1952) on Negros Island. It is noteworthy that most of the records for human-mediated spread were lost during the liberation of Manila during World War II (Rabor 1952). When deemed ineffective in curbing crop pests in the 1950s, it dispersed long-distances (‘mass dispersal’, a mechanism of dispersion where a dispersal route is established – Wilson et al. 2009) throughout the Philippines (Figure 2) as a hitchhiker on ships/boats (rather than being dispersed as a biological control), having been observed by one of us (A.C.D.) on a ship plying the route from Batangas province (Luzon Island) to Busuanga Island of Palawan province. It may have also dispersed long-distances as a stowaway in container/bulk having been transported through such means and subsequently intercepted from entering unininvaded Australian states (Henderson and Bomford 2011) and New Zealand (Chapple et al. 2016).

Moreover, ‘corridors’ (a physical connection of suitable habitat linking a portion of a range to another area – Wilson et al. 2009; e.g., tunnels and bridges) likely facilitated its dispersion between islands separated by biogeographic barriers; for example, the San Juanico Bridge provides a corridor which connects the islands of Samar and Leyte (Table 2).

At the provincial and island level, the slope of the regression line of the invasion curve of *R. marina* ($b = 0.0154$ and $0.0167$, respectively) is steeper than that of the curve of discovery rate ($b = 0.0109$ and $0.0167$, respectively), but does not differ significantly ($P = 0.012$ and $0.06$, respectively) (Figure 2a,c). Several major periods of expansion can be distinguished in its proportion curves: at the provincial level, 1944–1951, 1961–1970, and 1999–2006 (Figure 2b); and at the island level, 1945–1954, 1983–2017 (Figure 2d).
**Rhinella marina** is now a widespread invasive and is the most widespread among the six alien frogs, having been observed so far in 54 provinces on almost all major islands (36 islands) in the Philippines except for the islands of the Provinces of Batanes (northernmost group of islands of the Philippines) and Palawan (westernmost group of islands of the Philippines) (Table 2, Figure 1). Whenever encountered, *R. marina* occurs in abundant numbers, usually in the vicinity of human habitation, in artificial habitats, such as agricultural, cultivation, and agroforestry areas, and in mixed and disturbed aquatic and terrestrial habitats, such as forest edges and secondary-growth forests (Rabor 1952, Alcala 1986, Alcala and Brown 1998, Gaulke 2011). It has also been seldom observed in pristine primary-growth forests (Denzer et al. 1994, Delima et al. 2007), along coastal areas, mangroves, tidal gravel beaches, tidal water bodies, caves (Denzer et al. 1994, Belleza and Nuñeza 2014), and in high-elevation habitats, such as the mountain summits of Mount Makiling (1090 meters above sea level) and Mount Arayat (1026 masl) (Diesmos 1998).

American bullfrog (*Lithobates catesbeianus* [Shaw 1802])

*Lithobates catesbeianus* (Family Ranidae) is native to Eastern North America (Frost 2016). It was introduced in many parts of the world, including several countries in Africa, Central and South America, Asia, and Europe, primarily for hunting in the wild (Kraus 2009). In the Philippines, twenty four mature individuals were imported from Louisiana, United States, in 1966 by a private entrepreneur for captive propagation (Pascual 1987a). In the 1960s, soon after successful acclimatization, the first bullfrog-breeding center was established on Luzon Island in Barangay San Rafael, Montalban and Barrio Kambal, San Mateo, Rizal Province (Ugale 1976, Pascual 1987b, c) (Figure 3). Subsequently, in 1976, the Philippine Bullfrog Industry, Inc. (PBII), a private-owned, for-profit corporation, was established and supplied the high foreign demand
(primarily from the United States) of bullfrog specimens for biomolecular and medical research (Pascual 1987a, Urbanes 1988, Urbanes 1990, Matienzo 1990).

Through the National Bullfrog Development Project (NBDP), a five-year program orchestrated by the Ministry of Natural Resources (now the Department of Environment and Natural Resources) and in cooperation with PBII, another seven bullfrog breeding centers were established across the Philippines from 1980–1985 (Natural Resources Development Corporation of the Ministry of Natural Resources [NRDC-MNR] 1981, Buenviaje 1983, Inovejas 1985). The NBDP was a government effort to develop the bullfrog industry, which promoted the production of breeders for distribution to prospective raisers to develop both local and foreign markets (Buenviaje 1983, Inovejas 1985). Bullfrog breeding centers housed thousands of individuals in different life stages and were established on Luzon Island (Mt. Arayat National Park, Pampanga Province; Paoay, Ilocos Norte Province), Mindanao Island (Cotabato City, Cotabato Province; Nabunturan, Davao del Norte Province [now Compostela Valley Province]; Tacurong, Sultan Kudarat Province), Mindoro Island (Socorro, Oriental Mindoro Province), Leyte Island (Babtangan, Leyte Province), and Panay Island (Tangalan, Aklan Province) (NRDC-MNR 1981, Buenviaje 1983, Inovejas 1985) (Table 2, Figure 3, see supplemental online material Appendix S2). Most, if not all, bullfrog breeding centers ceased operation soon after the termination of the NBDP in 1985 (NRDC-MNR 1987).

During the operation of bullfrog breeding centers and farms in the Philippines from the 1970s to 1980s, numerous individuals of *L. catesbeianus* frequently escaped from confinement by their own means or aided by natural calamities, such as extensive floods (Diesmos et al. 2006, T. Padamada, former Pond Foreman of the Bullfrog Breeding Production Center in Paoay, Ilocos Norte, *pers. comm.*). Moreover, on Luzon Island (Paoay Lake and some areas in Batac, Ilocos Norte, *pers. comm.*).
Norte Province) and Mindanao Island (Lagusan Marsh, Cotabato Province, Maguindanao Province), government programs promoted the release in the wild of thousands of individuals for hunting (Inovejas 1985). Similarly, individuals were released in environs of bullfrog breeding centers after the termination of the NBDP (T. Padamada, pers. comm.).

To date, the status of *L. catesbeianus* in the Philippines – whether it has successfully established in the wild or failed– is undetermined (i.e., introduced/casual; ‘B3’ invasion status; Individuals transported beyond limits of native range, directly released into a novel environment, and fate unknown or may be extinct from novel environment – Blackburn et al. 2011, Faulkner et al. 2016) (Table 2). Recently, a sighting was reported on Luzon Island (Paoay Lake and Biloca, Ilocos Norte Province), but we failed to confirm this in recent surveys in the same area. Previous reports of this species could be misidentified *H. rugulosus*.

East Asian bullfrog (*Hoplobatrachus rugulosus* [Wiegmann 1834])

*Hoplobatrachus rugulosus* (Family Dicroglossidae) is native to East Asia (China and Taiwan) and Mainland Southeast Asia (Myanmar, Thailand, Lao People’s Democratic Republic, Cambodia, Viet Nam, and Peninsular Malaysia). It has been introduced to Borneo and the Philippines (Alcala et al. 1995, Inger and Tan 1996, Frost 2016). It was first reported in the Philippines in 1993 on Luzon Island (University of the Philippines – Los Baños, Laguna Province) (Figure 2) (Alcala et al. 1995, Alcala and Brown 1998, Diesmos 1998, Diesmos et al. 2006). In the same year, it was also reported in other areas on Luzon Island (Metropolitan Manila), Mindanao Island (Davao del Sur Province), Mindoro Island (Occidental Mindoro Province and Oriental Mindoro Province), and Panay Island (Iloilo Province) (Figure 1) (Diesmos et al. 2006).
Diesmos et al. (2006) hypothesized that *H. rugulosus* was farmed alongside *L. catesbeianus* through the NBDP in 1980s. However, its farming was not mentioned in any of the reports of NBDP (NRDC-MNR 1981, 1987). It was likely introduced to the Philippines in the 1990s (post-NBDP) through four pathways: (1) escaped by own means from bullfrog farms (i.e., farmed animals); (2) released for hunting in the wild as was the case of its introduction on Borneo (Inger 1996, Inger and Stuebing 1997); (3) as a contaminant with other transported animals (i.e., imported live fish fingerlings) as was the case of the introduction of its congener, the Indian bullfrog *Hoplobatrachus tigerinus*, in Andaman Island, India (Mohanty and Measey 2018); or (4) stowaway in transported container/bulk in as much as individuals were intercepted from entering New Zealand through such means (Chapple et al. 2016). The exact origin of introduced individuals is unknown. From areas of first report, *H. rugulosus* dispersed throughout the Philippines by leading-edge dispersal and by long-distance dispersal (cultivation and mass dispersal) (Table 1). The same pathways inferred to have facilitated its introduction may have also facilitated its secondary dispersal throughout the Philippines (Table 1).

At the provincial level, the slope of the regression line of the invasion curve of *H. rugulosus* \( b = 0.0308 \) is steeper than that of the curve of discovery rate \( b = 0.0177 \) and differs significantly \( P < 0.001 \) (Figure 2a). Meanwhile, at the island level, the slope of the regression line of its invasion curve \( b = 0.0106 \) is less steep than that of the curve of discovery rate \( b = 0.0259 \) and is significantly different \( P < 0.0001 \) (Figure 2c). Proportion curves showed two major periods of expansion at province level: 1998–2005 and 2012–2014 (Figure 2b) and an apparent major period of invasiveness from 1998–2001 at the island level (Figure 2d).

*Hoplobatrachus rugulosus* is now a fully invasive species and has been reported so far in 27 provinces on seven major islands (Table 2, Figure 1). It is most abundant in disturbed low elevation aquatic habitats, such as rice fields, ponds, lakes, and rivers (Alcala et al. 1995,
Breeding populations were observed in aquatic habitats in pristine, old-growth forests (Diesmos et al. 2006, Brown 2017).

Asiatic painted narrowmouth frog (*Kaloula pulchra* Gray 1831) (*Kaloula pulchra* (Family Microhylidae) is native to Southern East Asia (China), Eastern South Asia (Bangladesh and India), Mainland and Maritime Southeast Asia (Myanmar, Thailand, Lao People’s Democratic Republic, Cambodia, Viet Nam, Peninsular Malaysia, Singapore, and some islands of Indonesia [Sulawesi]). It has been introduced in Borneo, Guam, Taiwan, and the Philippines (Inger and Steubing 1997, Diesmos et al. 2006, Christy et al. 2007a, b, Kuangyang et al. 2016, Frost 2016). It was first reported in the Philippines in 2003 from three localities on Luzon island (Metropolitan Manila, Laguna Province, and Bulacan Province) (Figure 1) (Diesmos et al. 2006).

It was initially thought that *K. pulchra* escaped from the exotic pet trade (i.e., pet/aquarium/terrarium species) (Diesmos et al. 2006). However, the fact that it is of negligible interest in the Philippine exotic pet trade and that sold individuals were locally collected suggests that the pet trade is an unlikely pathway for its introduction into the Philippines (Sy 2014). It may have been introduced into the Philippines through three pathway subcategories: contaminant of nursery materials (Diesmos and Brown 2011, Sy 2014); hitchhikers on ship/boat since individuals were observed onboard a ship from Borneo (Inger 1966); and stowaways in transported container/bulk since individuals have been intercepted from entering Australia (Henderson and Bomford 2011), Guam (Christy et al. 2007b), and New Zealand (Chapple et al. 2012) through such means. The exact origin of introduced individuals is unknown, but they may have come from Borneo. Its spatio-temporal pattern of distribution shows that it spread by leading-edge dispersal and long-distance dispersal via cultivation and mass dispersal (although
corridors via tunnels and land-bridges is also a possible mechanism of dispersal) (Table 1). The same pathways that facilitated its introduction into the Philippines could have also facilitated its secondary dispersal throughout the country (Table 1).

At the provincial level, the slope of the regression line of the invasion curve of *K. pulchra* \((b = 0.0575)\) is almost equal to that of the curve of discovery rate \((b = 0.0577)\) and does not differ significantly \((P = 0.9581)\) (Figure 2a). Meanwhile, at the island level, the slope of the invasion curve \((b = 0.0692)\) is steeper than that of curve of discovery rate \((b = 0.042)\) and is significantly different \((P < 0.001)\) (Figure 2c). Proportion curves show an apparent major period of invasiveness at the provincial level from 2004–2015 (Figure 2b).

Since the first report, *K. pulchra* has spread in all directions throughout the Philippines, reported so far in 16 provinces on six major islands, and is now a fully invasive species (Table 2, Figure 1). It occurs in abundant numbers in the vicinity of human habitation and artificial and natural terrestrial and aquatic habitats, such as agricultural, cultivation, and agroforestry areas, forest edges, and secondary-growth forests (Siler et al. 2011, McLeod et al. 2011, Bucol et al. 2011, Brown et al. 2012b, Brown et al. 2013, Brown 2017).

**Greenhouse Frog* Eleutherodactylus planirostris* (Cope 1862)**

*Eleutherodactylus planirostris* (Family Eleutherodactylidae) is native to Cuba and the Bahamas. It has been introduced to several countries in North America, Central America, Africa, Guam (USA), Hawaii (USA), the Philippines, Hong Kong (China), and Singapore (Hedges et al. 2004, Olson et al. 2014, Olson 2016, Frost 2016). It was first reported in the Philippines in Davao City, Davao del Sur Province, Mindanao Island, in 2014, but is believed to have been introduced in the late 2000s (Olson et al. 2014). It was introduced into the Philippines as a contaminant of imported or re-exported ornamental plants or nursery materials (i.e., contaminant
nursery materials) that may have originated from Hawaii. This pathway is also reported for its introduction to Hawaii (Kraus et al. 1999). Moreover, it most likely dispersed long-distances (cultivation) throughout the Philippines through the same introduction pathway.

*Eleutherodactylus planirostris* is now a fully invasive species recorded so far in eight provinces on seven major islands (Table 3, Figure 2). Established populations have been observed in disturbed terrestrial habitats, such as gardens and immediate vicinities of human habitation (Olson et al. 2014, Sy et al. 2015).

**Discussion**

By gathering and analyzing geographic and historical data on the invasion of alien frogs in the Philippines, we present a comprehensive documentation of their history of invasion and updated their current invasion status and distribution. We showed that six alien frogs have been introduced in the Philippines since the 1880s, chronologically: *H. erythraea, R. marina, L. catesbeianus, H. rugulosus, K. pulchra*, and *E. planirostris*. Four pathway categories (falling in 8 subcategories) facilitated their introduction: intentional ‘release’ for biological control and hunting in the wild; ‘escape’ from farms; ‘contamination’ of agricultural commodities, fish stocks, and nursery materials; and ‘stowaway’ on container/bulk and (hitchhiker on) ship/boat. Spatio-temporal patterns of distribution (Figure 2) showed that alien frogs dispersed through two main mechanisms: ‘leading-edge dispersal’ and long-distance dispersal primarily via ‘mass dispersal’ and ‘cultivation’ (‘corridors’ also facilitated the spread of some alien frogs between islands connected by man-made land bridges such as the San Juanico Bridge that connects the islands of Samar and Leyte) (Table 1). The pathways that mediated their secondary dispersal were either the same as those of their introduction or included or shifted to other pathways over time (Table 1). For *H. erythraea, R. marina, H. rugulosus*, and *K. pulchra*, the slope of invasion
curves varied between species and between geographic levels, wherein *K. pulchra* is spreading fastest (Figure 1). Similarly, their proportion curves showed several periods of expansion at the geographic levels of province and island (Figure 1). Five alien frogs (*H. erythraea, R. marina, H. rugulosus, K. pulchra*, and *E. planirostris*) are now fully invasive species, whereas *L. catesbeianus* has been released in the wild for hunting, but it is unclear if the species has successfully established viable populations (Table 2, Diesmos et al. 2006). Among the widespread invasive frogs, *R. marina* is the most widespread while *E. planirostris* is the least distributed (Figure 1, Table 2). We further discuss here implications of our findings and provide recommendations for invasive alien-frogs management in the Philippines.

**Introduction pathways**

Our findings show temporal variation in the importance of different pathways that facilitated the introduction of the alien frogs in the Philippines (Table 1). Contamination of transported commodities (i.e., transport-contaminant) and stowaways on transporting vessels and associated equipment and media (i.e., transport-stowaway) are the most important and current pathways for alien frog introductions, having facilitated the introduction of the two most recent introduced alien frogs (*K. pulchra* and *E. planirostris* in the 2000s). The importance of this pathway in alien frog introductions has also been observed in several island and island archipelagoes such as Guam (Christy et al. 2007a,b), Hawaii (Kraus et al. 1999), and Singapore (Ng and Yeo 2012), as well as in other parts of the world (Kraus 2009, Capinha et al. 2017). Meanwhile, the last documented intentional release of an alien frog was in 1990s. This pattern has been similarly observed in global alien amphibian and reptile species introductions (Kraus 2009), and in other alien-vertebrate species introductions in island archipelagoes such as Galapagos Islands (Phillips et al. 2012) and continental areas such as Europe (Hulme et al. 2008).
and South Africa (Faulkner et al. 2016). Interestingly, recent studies on interceptions of alien species in Australia (Henderson and Bomford 2011) and New Zealand (Chapple et al. 2016) suggested that substantially more amphibian and reptile species are being moved via transport-stowaway than previously thought, owing to the lack of comprehensive biosecurity measures in other jurisdictions (Chapple et al. 2016).

Changes in pathway of introduction and long-distance dispersal

Our findings show that the pathways that facilitated the introduction and secondary dispersal of alien frogs in the Philippines may vary, and that pathways that facilitated secondary dispersal may have changed over time. For instance, so far, the introduction and secondary dispersal of *L. catesbeianus*, *K. pulchra*, *H. rugulosus*, and *E. planirostris* are most likely through the same pathways. In contrast, in the initial years of its invasion, *R. marina* was introduced in the Philippines as biological control and was similarly dispersed by humans to several islands throughout the archipelago through the same pathway. The importance of this pathway decreased and was soon deemed insignificant by the 1950s when *R. marina*’s ability to curb the population of crop pests was found to have been ineffective and when studies abroad that demonstrated the ecological impacts of *R. marina*’s invasion deterred its use as a biological control agent (Rabor 1952, Eastael 1981, Diesmos et al. 2006). It has since dispersed at long-distances by hitchhiking on boats/ships, as was observed by A. C. Diesmos on a ship plying Batangas Province, Luzon Island, to Busuanga Island, Palawan Province. Further, it has often been intercepted as a stowaway in container/bulk in New Zealand (Chapple et al. 2016), suggesting the possibility of that it may utilize this pathway to disperse throughout the Philippines. Another example is the case of *H. erythraea*, which was introduced as a contaminant of agricultural commodities and was similarly secondarily dispersed at long-distances through
the same pathway. Moreover, given that it is sold for ornamental purpose other than horticulture (Sy 2014), it may have been transported to different islands for commercial purposes and, subsequently, escaped from garden ponds. Further, its propensity to live in aquatic habitats where fish fingerlings are usually extracted for translocation suggests that its contamination of translocated fish fingerlings (i.e., contaminant on animals) may have as well facilitated its long-distance dispersal, as was the case of *F. moodiei* (previously identified as *F. cancrivora*), a co-occurring Philippine native species, that has been introduced to Guam (Christy 2007a).

**Spatio-temporal pattern of spread and associated pathways**

Spatio-temporal patterns of distribution showed that the spread of alien frogs throughout the Philippines followed a stratified diffusion process, which involves an initial range expansion through leading-edge dispersal (i.e., neighborhood diffusion) and new colonies (i.e., foci) that are successively created through human-mediated long-distance dispersal events (Van der Plank 1967, Hengeveld 1989, Shigesada et al. 1995, Higgins and Richardson 1999). For invading organisms, especially species that associate closely with humans, a stratified diffusion process of spread “seems to be the rule rather than the exception” (Higgins and Richardson 1999) (e.g., Argentine ants *Linepithema humile* in the United States [Suarez et al. 2001], red fire ants *Solenopsis invicta* in United States [Porter et al. 1988], and the common ragweed *Ambrosia artemisiifolia* in France [Chauvel et al. 2006]). Given the innate limitations in amphibians’ natural dispersal capabilities, it can be said that the inter-island spread of the alien frogs throughout the Philippines is primarily by long-distance dispersal via cultivation and mass dispersal, and facilitated by several pathways (Table 1). Meanwhile, the intra-island spread of alien frogs is predominantly through unaided leading-edge dispersal and, especially for larger
islands such as Luzon and Mindanao, long-distance dispersal which was likely facilitated by the same pathways that facilitated inter-island long-distance dispersal (Table 1).

**Current invasion status and distribution**

We presented here an updated, comprehensive, and detailed account on the invasion status and current distribution of all known alien amphibian species in the Philippines (Table 2, Figure 1). A significant body of data from previously overlooked published and unpublished literature, natural history collections from several museums, as well as our personal observations were included for the first time. We reported evidence that *H. erythraea*, *R. marina*, *H. rugulosus*, *K. pulchra*, and *E. planirostris* are now fully invasive species, having established populations in the wild, with individuals dispersing, surviving, and reproducing at multiple sites, typically the dominant species in both artificial and disturbed habitats, and are continuously spreading throughout the Philippines (Blackburn et al. 2011, Faulkner et al. 2016). Meanwhile, the status of *L. catesbeianus* in the Philippines is undetermined. We identified the localities where breeding centers of *L. catesbeianus* were established in the 1960s to 1980s, as well as release sites (Figure 3, see supplemental online material Appendix S2). Until further surveys are conducted in these areas, we remain cautious in determining the status of *L. catesbeianus* in the Philippines. It is noteworthy that recent field surveys conducted by the authors in Northern Luzon Island (Paoay, Ilocos Norte Province – one of the sites where bullfrog breeding centers were formerly established) failed to report the occurrence of *L. catesbeianus*.

We showed that *R. marina* is currently the most widely-distributed alien frog, having dispersed to almost all Philippine islands, except on the islands in the provinces of Palawan (westernmost Philippines) and Batanes (Northernmost Philippines) (Figure 1). However, the fact that individuals of *R. marina* were observed by A.C. Diesmos hitchhiking on a ship from
Batangas Province, Luzon Island, to Busuanga Island, the northernmost island of Palawan Province, in 1995, emphasizes the need for surveys on Busuanga Island. Meanwhile, it is also possible that *R. marina* has already been introduced to islands of Batanes Province, due to the availability of potential pathways – hitchhikers on ships/boats. The availability of such pathway is supported by the recent dispersal of a Philippine native species, *Polypedates leucomystax*, possibly as a contaminant of agricultural commodities, onto Batanes Island of Batanes Province (Brown et al. 2010). It is noteworthy that *R. marina* has already reached Tawi-Tawi Island, Tawi-Tawi Province, which is its current southernmost range in the Philippines and is about 50 km from Borneo.

There have not been significant changes in the distribution of *H. erythraea* and *H. rugulosus* since the review of Diesmos et al. (2006), with only a few new provincial and island records (Figure 1). Meanwhile, the distribution of *K. pulchra* in 2006 was restricted to three provinces on Luzon Island. Since then, it has rapidly dispersed across 16 provinces on six islands (Figure 1). Lastly, this is the first review on the status and distribution of *E. planirostris* in the Philippines (Figure 1). Established populations of *E. planirostris* have only been observed in artificial habitats, and it is anticipated to disperse into natural habitats in the future, as in the case in Hawaii (Olson et al. 2012).

*Rate of spread and projected distribution in the future*

Our findings show that *H. erythraea*, *R. marina*, *H. rugulosus*, and *K. pulchra* are continuously spreading, wherein *K. pulchra* is spreading fastest. Invasion curves show that the alien frogs, especially for the cases of the most widespread – *H. erythraea* and *R. marina* – have not reached spatial saturation, suggesting that the species will continue to spread (Figure 2). Meanwhile, proportion curves (Figure 2) showed that the alien frogs seem to have undergone
several periods of expansion during the course of their invasion in the Philippines. Such periods of expansion may reflect coincidental increase in human transportation and commerce or temporal and species sampling bias owing to the increased interest in Philippine frogs and invasive alien species during the past 30 years (Diesmos et al. 2006, Diesmos et al. 2014).

Management recommendations for alien frog invasions in the Philippines

Our findings provide much needed-science based information that can help guide the development and implementation of sound management strategies for current and future alien frog invasions in the Philippines. Local trends (as presented in this study) as well as global trends (Kraus 2009) on alien frog introductions show that transport-contaminant and transport-stowaway pathways are highly likely to mediate future alien frog introductions in the country and, thus, should be a priority for management and legislation. Further, the future importance of these introduction pathways is manifested in the trend in the Philippines’ international trade, travel, and transport; the magnitude of arriving imported commodities (an annual average of about 404.6 million kilos of agricultural commodities, 370 thousand kilos of live fish, and 1.5 million kilos of nursery materials from 2011–2015) and sea traffic (an annual average of about 10 thousand foreign ship calls, 1.6 million 20-foot unit containers, and 62.4 million metric tons of cargo from 2011–2015) (Philippine Ports Authority 2015, Philippine Statistical Authority 2016) can be said to present high propagule pressure and, hence, risk of future alien species introduction through these pathways. Although none of the alien frogs in the Philippines was introduced through ‘escape from confinement’ pathway as pet/aquarium/terrarium species, the fact that this pathway is currently a major introduction pathway for global vertebrate species (Hulme et al. 2008), including frogs (Kraus 2009), and that the local undocumented pet trade of alien frogs is notoriously rampant in the Philippines (Sy 2015), emphasizes the need to improve
or develop stricter regulations for the local pet trade. Finally, despite the recent decreasing importance of the ‘release in nature’ pathway in global and Philippine alien frog introductions, management strategies and legislation are needed to prevent future introductions through this pathway.

We elucidated here the current distributions of the alien frogs, through point-locality maps complemented with species-distribution database (HWP 2019), which can help guide decision-making and the strategic spatial implementation of management schemes (Stohlgren and Schnase 2006, Stohlgren and Jarnevich 2009). For instance, the maps show that *K. pulchra* and *H. rugulosus* are only known from a few islands; their spread to other islands should be controlled or prevented. Having also demonstrated in this study the paramount importance of human-mediated long-distance dispersal in the spread of alien frogs in the Philippines, we recommend focusing on preventing their secondary long-distance dispersion onto novel areas (i.e., uninvaded islands) through pathway-specific approaches, rather than focusing efforts on leading-edges of invasions (Moody and Mack 1988). This should also integrate schemes to eliminate new incursions through frequent surveys of susceptible sites (e.g., ports-of-entry, nurseries and garden centers, etc.) and rapid eradication of incursions (Moody and Mack 1988).

Acknowledgements

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Tables

Table 1. Introduction pathways, mechanism(s) of secondary (post-introduction) dispersal, and associated secondary dispersal pathways of the alien frogs in the Philippines.

<table>
<thead>
<tr>
<th>Hylarana erythraea</th>
<th>Introduction pathway sub-category</th>
<th>Mechanism(s) of dispersal</th>
<th>Secondary dispersal pathway category</th>
<th>Secondary dispersal pathway sub-category</th>
</tr>
</thead>
<tbody>
<tr>
<td>Transport-contaminant</td>
<td>Food contaminant</td>
<td>Cultivation</td>
<td>Transport-contaminant</td>
<td>Food contaminant</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Escape from confinement</td>
<td>Contaminant on animals</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Leading-edge</td>
<td>Natural dispersal</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Rhinella marina</th>
<th>Introduction pathway sub-category</th>
<th>Mechanism(s) of dispersal</th>
<th>Secondary dispersal pathway category</th>
<th>Secondary dispersal pathway sub-category</th>
</tr>
</thead>
<tbody>
<tr>
<td>Release in nature</td>
<td>Biological control</td>
<td>Cultivation</td>
<td>Release in nature</td>
<td>Biological control</td>
</tr>
<tr>
<td>Mass dispersal</td>
<td>Transport-stowaway</td>
<td>Hitchhikers on ship/boat</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leading-edge</td>
<td>Unaided</td>
<td>Natural dispersal</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Corridor</td>
<td>Corridors</td>
<td>Tunnels and land bridges</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Lithobates catesbeianus</th>
<th>Introduction pathway sub-category</th>
<th>Mechanism(s) of dispersal</th>
<th>Secondary dispersal pathway category</th>
<th>Secondary dispersal pathway sub-category</th>
</tr>
</thead>
<tbody>
<tr>
<td>Release in nature</td>
<td>Hunting in the wild</td>
<td>Cultivation</td>
<td>Release in nature</td>
<td>Hunting in the wild</td>
</tr>
<tr>
<td>Escape from confinement</td>
<td>Farmed animals</td>
<td>Escape from confinement</td>
<td>Farmed animals</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Hoplobatrachus rugulosus</th>
<th>Introduction pathway sub-category</th>
<th>Mechanism(s) of dispersal</th>
<th>Secondary dispersal pathway category</th>
<th>Secondary dispersal pathway sub-category</th>
</tr>
</thead>
<tbody>
<tr>
<td>Release in nature</td>
<td>Hunting in the wild</td>
<td>Cultivation</td>
<td>Release in nature</td>
<td>Hunting</td>
</tr>
<tr>
<td>Escape from confinement</td>
<td>Farmed animals</td>
<td>Escape from confinement</td>
<td>Farmed animals</td>
<td></td>
</tr>
<tr>
<td>Transport-contaminant</td>
<td>Contaminant on animals</td>
<td>Transport-contaminant</td>
<td>Contaminant on animals</td>
<td></td>
</tr>
<tr>
<td>Transport-stowaway</td>
<td>Container/bulk</td>
<td>Mass dispersal</td>
<td>Container/bulk</td>
<td></td>
</tr>
</tbody>
</table>
Pathway and pathway sub-categories were classified following Scalera et al. (2016). Mode of dispersal was classified following Wilson et al. (2009).
Table 2. Origin, first geographic records, and current invasion status and distribution of the six alien anuran species in the Philippines.

<table>
<thead>
<tr>
<th>Species</th>
<th>Origin</th>
<th>Locality/Localities first recorded</th>
<th>Period introduced</th>
<th>Distribution in the Philippines</th>
<th>Invasion status in the Philippines</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Hylarana erythraea</em></td>
<td>Unknown</td>
<td>Samar Island</td>
<td>1800s(^1)</td>
<td>20</td>
<td>39 E</td>
</tr>
<tr>
<td><em>Rhinella marina</em></td>
<td>Hawaii, United States</td>
<td>Metropolitan Manila and</td>
<td>1934(^2)</td>
<td>36</td>
<td>54 E</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Laguna Province, Luzon Island</td>
<td></td>
<td></td>
<td>Widespread invasive</td>
</tr>
<tr>
<td><em>Lithobates catesbeianus</em></td>
<td>Louisiana, United States</td>
<td>Rizal Province, Luzon Island</td>
<td>1966(^3)</td>
<td>5</td>
<td>12 B3 Casual/Introduced</td>
</tr>
<tr>
<td><em>Hoplobatrachus rugulosus</em></td>
<td>Unknown</td>
<td>Laguna Province and Metropolitan</td>
<td>1990s(^4)</td>
<td>7</td>
<td>27 E</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Manila, Luzon Island; Iloilo</td>
<td></td>
<td></td>
<td>Widespread invasive</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Province, Panay Island; Occidental</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mindoro and Oriental Mindore</td>
<td></td>
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</tr>
<tr>
<td></td>
<td></td>
<td>Province, Mindoro Island</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Kaloula pulchra</em></td>
<td>Unknown</td>
<td>Metropolitan Manila,</td>
<td>2000s(^4)</td>
<td>6</td>
<td>17 E</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Laguna Province, and Bulacan</td>
<td></td>
<td></td>
<td>Widespread invasive</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Province, Luzon Island</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Eleutherodactylus planirostris</em></td>
<td>Hawaii, United States</td>
<td>Davao del Sur Province, Mindanao</td>
<td>2010s(^5)</td>
<td>7</td>
<td>8 E</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Island</td>
<td></td>
<td></td>
<td>Widespread invasive</td>
</tr>
</tbody>
</table>

\(^1\)CSIC (2018); \(^2\)Merino (1936); \(^3\)Pascual (1987a); \(^4\)Diesmos et al. (2006); \(^5\)Olson et al. (2014); Invading category and invasion status of the alien amphibians in the Philippines were classified following Faulkner et al. (2016) as modified from Blackburn et al. (2011). Invasion category E defined are fully invasive species, with individuals dispersing, surviving and reproducing at multiple sites across a greater or lesser spectrum of habitats and extent of occurrence; Invasion category B3 defined as individuals transported beyond limits of native range, and directly released into a novel environment (fate unknown).
Figure 1. Point-locality maps of the Philippine invaded-range distribution of (from left to right) Hylarana erythraea, Rhinella marina, Hoplobatrachus rugulosus, Kaloula pulchra, and Eleutherodactylus planirostris through time. Species distribution records (black dots) were partitioned into periods: before 1950, before 1975, before 2000, and after 2000-Present and plotted onto Philippine map. The year and location of first species record(s) is/are indicated.
Figure 2. Rate of spread of (from left to right) Hylarana erythraea, Rhinella marina, Hoplobatrachus rugulosus, and Kaloula pulchra. The invasion curve of each alien frog (solid lines and closed circles) was compared with the curve of discovery rate of native frogs taken as a whole (dotted lines and open circles) at province (A) and island (C) level. Results are expressed as the logarithm of the cumulative number of new provincial or island records over time. Invasion rate (slope b of the regression equation) is given for each alien frog and for the native frogs as a whole. The difference (P value) between the slope of linear regression models of alien frogs and that of native frogs as a whole is given for each alien frog. Proportion curves (logarithm of the cumulative number of new provincial or island records for alien species divided by that for native species taken as a whole) at province (B) and island (D) level was calculated for each year on record for the four alien frogs. Periods of expansion, as determined by a positive slope extending for at least five years, are indicated by grey zones.
Figure 3. Point locality map of the established bullfrog breeding centers and farms in the Philippines from 1960s to 1980s.
## Supplemental Materials


<table>
<thead>
<tr>
<th>CBD category pathway</th>
<th>CBD sub-category pathway</th>
<th>Kraus 2007, 2009 category pathway</th>
</tr>
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<tr>
<td><strong>Release in nature</strong></td>
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<td>Biological control</td>
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<td>Biocontrol</td>
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<td>Introduction for conservation purposes</td>
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<td>Conservation</td>
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<tr>
<td>Release in nature for use (other than above, e.g., fur, transport, medical use)</td>
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<td>Medicine</td>
</tr>
<tr>
<td>Landscape/flora/fauna “improvement” in the wild</td>
<td></td>
<td>“intentional”</td>
</tr>
<tr>
<td>Other intentional release</td>
<td></td>
<td>“intentional”, religious, lab release</td>
</tr>
<tr>
<td>Erosion control/ dune stabilization</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Fishery in the wild (including game fishing)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pet/aquarium/terrarium species (including live food for such species)</td>
<td></td>
<td>Pet trade</td>
</tr>
<tr>
<td>Ornamental purpose other than horticulture</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Botanical garden/zoo/aquaria (excluding domestic aquaria)</td>
<td></td>
<td>Zoo trade*, exhibit</td>
</tr>
<tr>
<td>Farmed animals (including animals left under limited control)</td>
<td></td>
<td>Food</td>
</tr>
<tr>
<td>Research and ex-situ breeding (in facilities)</td>
<td></td>
<td>Research</td>
</tr>
<tr>
<td>Live food and live bait</td>
<td></td>
<td>Duck food, bait use</td>
</tr>
<tr>
<td>Agriculture (including Biofuel feedstock)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aquaculture / mariculture</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Forestry (including reforestation)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fur farms</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Horticulture</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Food contaminant (including of live food)</td>
<td></td>
<td>Cargo stowaway</td>
</tr>
<tr>
<td>Timber trade</td>
<td></td>
<td>Cargo stowaway</td>
</tr>
<tr>
<td>Contaminant nursery material</td>
<td></td>
<td>Nursery trade</td>
</tr>
<tr>
<td>Contaminant on animals (except parasites, species transported by host/vector)</td>
<td></td>
<td>Aquaculture contaminant</td>
</tr>
<tr>
<td>Parasites on animals (including species transported by host and vector)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Contaminant on plants (except parasites, species transported by host/vector)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Parasites on plants (including species transported by host and vector)
Seed contaminant

Contaminated bait

Transportation of habitat material (soil, vegetation, …)

<table>
<thead>
<tr>
<th>Transport-stowaway</th>
<th>Cargo stowaway</th>
</tr>
</thead>
<tbody>
<tr>
<td>Container/bulk</td>
<td>Cargo stowaway</td>
</tr>
<tr>
<td>Machinery/equipment</td>
<td>Cargo stowaway</td>
</tr>
<tr>
<td>People and their luggage/equipment</td>
<td>Cargo stowaway</td>
</tr>
<tr>
<td>(in particular tourism)</td>
<td></td>
</tr>
<tr>
<td>Hitchhikers in or on airplane</td>
<td>Aircraft stowaway</td>
</tr>
<tr>
<td>Hitchhikers on ship/boat (excluding</td>
<td>Boat</td>
</tr>
<tr>
<td>ballast water and hull fouling)</td>
<td></td>
</tr>
<tr>
<td>Ship/boat ballast water</td>
<td>Ballast</td>
</tr>
<tr>
<td>Vehicles (car, train, …)</td>
<td>Vehicle</td>
</tr>
</tbody>
</table>

Other means of transport

Angling/fishing equipment

Organic packaging material, in particular wood packaging

Ship/boat hull fouling

Interconnected waterways/basins/seas
Tunnels and land bridges

Unaided Natural dispersal across borders of invasive alien species that have been introduced through pathways 1 to 5. Spread from adjacent introduction

*CBD pathway subcategories in grey and italicized is unlikely to or have not to date been reported to facilitate the dispersal of an alien frog.
Appendix S2. Location of bullfrog breeding centers and bullfrog farms in the Philippines where the American bullfrog (*Lithobates catesbeianus*) was bred from 1960s to 1980s.

<table>
<thead>
<tr>
<th>Species</th>
<th>Longitude</th>
<th>Latitude</th>
<th>Island</th>
<th>Province</th>
<th>Municipality</th>
<th>Year</th>
<th>Source</th>
<th>Remarks</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Lithobates catesbeianus</em></td>
<td>121.2508</td>
<td>14.7744</td>
<td>Luzon Island</td>
<td>Rizal</td>
<td>Montalban</td>
<td>1966</td>
<td>Ugale 1976</td>
<td>Bullfrog farm</td>
</tr>
<tr>
<td><em>Lithobates catesbeianus</em></td>
<td>no data</td>
<td>no data</td>
<td>Luzon Island</td>
<td>Rizal</td>
<td>no data</td>
<td>1970s</td>
<td>Matienzo 1990</td>
<td>Bullfrog farm</td>
</tr>
<tr>
<td><em>Lithobates catesbeianus</em></td>
<td>no data</td>
<td>no data</td>
<td>Luzon Island</td>
<td>Bulacan</td>
<td>no data</td>
<td>1970s</td>
<td>Matienzo 1990</td>
<td>Bullfrog farm</td>
</tr>
<tr>
<td><em>Lithobates catesbeianus</em></td>
<td>no data</td>
<td>no data</td>
<td>Luzon Island</td>
<td>Bataan</td>
<td>no data</td>
<td>1970s</td>
<td>Matienzo 1990</td>
<td>Bullfrog farm</td>
</tr>
<tr>
<td><em>Lithobates catesbeianus</em></td>
<td>120.5371</td>
<td>18.1205</td>
<td>Luzon Island</td>
<td>Ilocos Norte</td>
<td>Paoay</td>
<td>1980s</td>
<td>Buenviaje 1983, Inovejas 1985</td>
<td>Bullfrog breeding center</td>
</tr>
<tr>
<td><em>Lithobates catesbeianus</em></td>
<td>120.7167</td>
<td>15.2</td>
<td>Luzon Island</td>
<td>Pampanga</td>
<td>Magalang</td>
<td>1980s</td>
<td>Buenviaje 1983, Inovejas 1985</td>
<td>Bullfrog breeding center</td>
</tr>
<tr>
<td><em>Lithobates catesbeianus</em></td>
<td>121.4</td>
<td>13.05</td>
<td>Mindoro Island</td>
<td>Oriental Mindoro</td>
<td>Soccoro</td>
<td>1980s</td>
<td>Buenviaje 1983, Inovejas 1985</td>
<td>Bullfrog breeding center</td>
</tr>
<tr>
<td><em>Lithobates catesbeianus</em></td>
<td>125.9667</td>
<td>7.6</td>
<td>Mindanao Island</td>
<td>Compostela Valley</td>
<td>Nabuntaran</td>
<td>1980s</td>
<td>Buenviaje 1983, Inovejas 1985</td>
<td>Bullfrog breeding center</td>
</tr>
<tr>
<td><em>Lithobates catesbeianus</em></td>
<td>124.2833</td>
<td>6.5833</td>
<td>Mindanao Island</td>
<td>Maguindanao</td>
<td>Liguasan Marsh</td>
<td>1980s</td>
<td>Diesmos et al. 2006</td>
<td>Release sites</td>
</tr>
<tr>
<td><em>Lithobates catesbeianus</em></td>
<td>no data</td>
<td>no data</td>
<td>Mindanao Island</td>
<td>Maguindanao</td>
<td>no data</td>
<td>1980s</td>
<td>Buenviaje 1983</td>
<td>Release sites</td>
</tr>
<tr>
<td><em>Lithobates catesbeianus</em></td>
<td>120.5</td>
<td>18.0667</td>
<td>Luzon Island</td>
<td>Ilocos Norte</td>
<td>Batac City</td>
<td>2002</td>
<td>Diesmos et al. 2006</td>
<td>Reported sightings (unverified)</td>
</tr>
<tr>
<td><em>Lithobates catesbeianus</em></td>
<td>120.579</td>
<td>18.2</td>
<td>Luzon Island</td>
<td>Ilocos Norte</td>
<td>Batac City</td>
<td>2002</td>
<td>Diesmos et al. 2006</td>
<td>Reported sightings (unverified)</td>
</tr>
<tr>
<td><em>Lithobates catesbeianus</em></td>
<td>120.5333</td>
<td>18.1</td>
<td>Luzon Island</td>
<td>Ilocos Norte</td>
<td>Laoag</td>
<td>2002</td>
<td>Diesmos et al. 2006</td>
<td>Reported sightings (unverified)</td>
</tr>
</tbody>
</table>