



Non-native populations and global invasion potential of the Indian bullfrog *Hoplobatrachus tigerinus*: a synthesis for risk-analysis

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Abstract Invasive amphibians have considerable ecological and socio-economic impact. However, strong taxonomic biases in the existing literature necessitate synthesizing knowledge on emerging invaders. The Indian bullfrog, *Hoplobatrachus tigerinus*, a large dicroglossid frog (snout to vent length: up to 160 mm), is native to the Indian sub-continent. Despite the high likelihood of invasion success for *H. tigerinus*, based on the species' natural history traits and human use, the status of its non-native populations and global invasion potential has not yet been assessed. In this paper, we provide a profile of *H.*

tigerinus as an invasive species to aid in risk analyses and management of existing populations. We review the available knowledge on non-native populations of *H. tigerinus* and model its potential distribution in the non-native range and globally; finally, we evaluate its ecological and socio-economic impact using standard impact classification schemes. We confirm successful invasions on the Andaman archipelago and Madagascar. The ensemble species distribution model, with 'good' predictive ability and transferability, predicts tropical regions of the world to be climatically suitable for the species. Considering potential for propagule pressure, we predict the climatically suitable Mascarene Islands, Malaysia and Indonesia, and East Africa to likely be recipients of bridgehead invasions. We assign the species two impact scores: both socio-economic and environmental scores were 'moderate' with 'medium' confidence levels in our assessment. Finally, this synthesis outlines the invasion process of the genus *Hoplobatrachus*, which is an emerging group of amphibian invaders.

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Alien Taxa · Pet trade

Introduction

Invasive amphibians have a considerably high environmental and socio-economic impact (Measey et al. 2016; Kumschick et al. 2017; Bacher et al. 2018). Globally, 78 non-native species of amphibians are known to have at least one established or invasive population (Capinha et al. 2017), whereas nearly 100 non-native amphibians could be considered to have established populations, with a level of uncertainty (Kraus 2009; Measey et al. 2016). A recent review of non-native occurrence of amphibians recorded 263 species, including those traded and present in captivity (van Wilgen et al. 2018), forecasting future invasions of many more amphibian species. Introductions of amphibians have accelerated in recent decades (Seebens et al. 2017; Capinha et al. 2017). However, studies on amphibian invasions are heavily taxon-biased, with only three species (*Rhinella marina*, *Lithobates catesbeianus*, and *Xenopus laevis*) responsible for ca. 81% of all publications on non-native amphibians (van Wilgen et al. 2018). A focus on emerging and unassessed amphibian invaders is therefore necessary.

The Indian bullfrog, *Hoplobatrachus tigerinus* (Daudin, 1802), a large dicroglossid frog (snout to vent length: up to 160 mm), is native to the Indian sub-continent (Dutta 1997). *H. tigerinus* is consumed regionally and was formerly a part of the international ‘frog leg trade’ (Abdulali 1985; Oza 1990). Its large body size, association with human-modified landscapes (e.g. paddy fields; Daniels, 2005), and use as a food resource make *H. tigerinus* a likely candidate for human-mediated introduction outside its native range (Tingley et al. 2010; van Wilgen et al. 2018). Further, the species has a high establishment probability due to its fecundity (ca. 6000 eggs per clutch; Allen et al. 2017) and ability to breed successfully in ephemeral pools of human-modified habitats. Human consumption also makes the species likely to be moved locally in the non-native range, thereby exacerbating its spread (Liu et al. 2014). The carnivorous tadpoles of *H. tigerinus* prey upon larvae of other anurans (Khan 1996; Grosjean et al. 2004), whereas post-metamorphic individuals consume a broad range of invertebrates and small vertebrates (Padhye et al. 2008), making ecological impacts via predation a matter of concern in the non-native range. Despite the high likelihood of invasion success and impact for *H.*

tigerinus (see Novoa et al. 2020), the status of its non-native populations and its global invasion potential have not yet been assessed.

Systematic literature reviews and species distribution modelling have been used to generate global species profiles for several amphibian invaders (e.g. *Lithobates catesbeianus*, Ficetola et al. 2007a, b; *Xenopus laevis*, Measey et al. 2012). Such assessments can be particularly useful in understanding consistent patterns of invasion dynamics of the species as well as its similarities to other invasions in terms of pathways, species traits, recipient ecosystems—a phenomenon referred to as “invasion syndromes” (Novoa et al. 2020). Risk assessments rely on published information from prior invasions, covering the species’ invasion potential based on species distribution modelling, dispersal pathways, spread rates, potential impact and recommended management action (Kumschick et al. 2019). Potential impacts of species should ideally be recorded using impact classification frameworks, which are particularly useful to assign standardized scores to an invasive species. Based on dietary assessments of adult *H. tigerinus* on the Andaman Islands, an Environmental Impact Classification of Alien Taxa (EICAT; Blackburn et al. 2014) score of ‘minor’ impact was assigned to the species by Mohanty and Measey (2018). Previously, a global evaluation by Kumschick et al. (2017) had resulted in the same environmental impact score, whereas the species was considered ‘data deficient’ under Socio-Economic Impact Classification of Alien Taxa (SEICAT; see supporting information in Bacher et al. 2018). However, a reassessment is deemed necessary in the light of new studies on the ecological and socio-economic impact of the species.

In this paper, we provide a global species profile of the Indian bullfrog, *Hoplobatrachus tigerinus*, as an invader, to aid in risk assessment and management of existing non-native populations. To this end, we aim to (1) synthesize existing knowledge on invasion status, dispersal pathways and spread, impact, and management action, (2) evaluate the global invasion potential using species distribution models, and (3) update standardized metrics of impact (EICAT and SEICAT) for *H. tigerinus* based on current knowledge of the species’ environmental and socio-economic effects.

Methods

Non-native populations

We searched for literature on non-native populations of *Hoplobatrachus tigerinus* on Google Scholar (September 2018) by employing a combination of key words covering taxonomic variation (including the previous taxonomic combinations ‘*Rana tigerina*’ and ‘*Rana tigrina*’) and invasion status (‘alien’, ‘introduced’, ‘non-native’, ‘exotic’, ‘non-indigenous’ and ‘invasive’). We also consulted local researchers and herpetologists, in both native and non-native ranges, for occurrence information where published literature was lacking (Ficetola et al. 2007a). Identified non-native populations were evaluated for their invasion stage (following Blackburn et al. 2011), dispersal pathways (of introduction and secondary transfers), impact (see section ‘Impact Scoring’ below), and management actions undertaken.

Species distribution modelling

Species distribution modelling was carried out to determine global climatic suitability for *H. tigerinus*. We collated occurrence data for *H. tigerinus* from three sources: (1) online databases—the Global Biodiversity Information Facility (www.gbif.org), India biodiversity portal (www.indiabiodiversity.org), iNaturalist (www.inaturalist.org), and HerpNet (www.herpNet.org), (2) field observations (AC and NPM unpublished data), and (3) literature records with accurate geographic co-ordinates (point locations of individuals observed). We ensured the quality of occurrence data by only using geo-referenced locations with at least “municipality” level information. Further, we checked if the occurrence points fell within the known ‘extent of occurrence’ of the species (Padhye et al. 2008). To fill in geographic gaps, we searched for native range records in the literature and citations therein. Sampling bias in occurrence data is an important consideration that may affect model performance and predictions (Merow et al. 2013). As our occurrence records were sourced from a range of data types (museum records, field surveys, and citizen science), we did not expect the data to be inherently biased towards geographical areas with higher human-influence. We also visualized the environmental data in the training extent using bivariate plots, overlaid

with the presence points, and did not find any strong patterns suggesting environmental sampling bias (Supplementary Information 1 Fig. 1). After removing duplicates (at a resolution of 2.5 arc min), a total of 153 presence points was retained from the native range.

Models can be trained with only native range data when the environmental extent of the non-native range is contained within that of the native range (Gallien et al. 2010) and if native range data are reliable (Hattab et al. 2017). We considered that these two requirements were met in our case. We found the environmental space in the non-native range of *H. tigerinus* to be a subset of its native range (SI 1 Fig. 2). As *H. tigerinus* is a commonly encountered frog with a wide distribution in its native range (Daniels 2005), we considered the collated occurrence data to be of good quality. We also could not assume the non-native populations to have attained equilibrium (Václavik et al. 2012), given their relatively short residence times (Mohanty and Measey 2019a). Finally, we were cognizant of incomplete sampling for *H. tigerinus* on Madagascar. We thus trained the model with native range data only and used data from the non-native range for independent evaluation (see below).

We selected predictors with putative ecological importance for *H. tigerinus* (e.g. Mellert et al. 2011) based on the species’ known ecology and behavior. We also considered known correlates of the distribution of a functionally analogous species, *Lithobates catesbeianus* (Ficetola et al. 2007b), to inform the selection of environmental predictors. To capture the species’ thermal tolerance, we considered two predictors: the maximum temperature of the warmest month and the minimum temperature of the coldest month (following Ficetola et al. 2007b). Adult *H. tigerinus* are dependent on waterlogged ephemeral pools for breeding and development of larvae (Khan 1996); to model this dependence, we chose mean precipitation of the wettest quarter. Mean precipitation of the driest quarter served as an index for lentic water bodies, which are used by adults to avoid desiccation (Daniels 2005). Human effects are important to consider in species distribution modelling, especially for invasive species (Ficetola et al. 2010; Rödder 2009; Gallardo et al. 2015). The frequent use of human-modified environments by *H. tigerinus* (Daniels 2005) was accounted for with the Human Influence Index (HII),

representing a combination of population density, land use, and human accessibility parameters (WCS 2005).

The selected climatic predictors, derived from monthly temperature and rainfall values, were downloaded at a resolution of 2.5 arc minutes from WorldClim version 1 (Hijmans et al. 2005), whereas HII was available at a finer resolution of 30 arc seconds (WCS 2005). To ensure compatibility between these predictor layers, we resampled HII to 2.5 arc minutes by bilinear interpolation, using ArcMap version 10.6.2 (ESRI 2012). For the invaded range, we obtained environmental predictors at 30 arc seconds (Hijmans et al. 2005). After performing pairwise correlation tests for collinearity in predictors (discarded if $r > 0.7$), we retained all hypothesized predictors but mean precipitation of the driest quarter.

Species distribution modelling was carried out in the R environment (version 3.4.4; R Core Team 2019) using the package ‘biomod2’ (Thuiller et al. 2016), designed to perform a range of modelling algorithms and analyze uncertainties. For presence-only species data, pseudo-absence selection should be limited to a meaningful extent that the species could have theoretically sampled over a geological time scale (Barve et al. 2011). In the same geographical area as our study, Tingley et al. (2018) modelled the distribution of the Common Asian toad (*Duttaphrynus melanostictus*) by limiting the training extent to regions south of the Himalayan mountain range which is likely to limit the dispersal of amphibians. We limited the geographical training extent of our models in the Indian sub-continent to the same region (Fig. 1a). Pseudo-absences were drawn randomly within the training extent, multiple times ($n = 1000$, iterations = 5) to reduce sampling bias and weighted to ensure a prevalence of 0.5 (i.e. the weighted sum of presences equals the weighted sum of pseudo-absences). We chose ‘random’ sampling of pseudo-absences as it generally performs well with most model algorithms, especially regression techniques (see below; Barbet-Massin et al. 2012).

We evaluated the models for predictive performance in the native range and for model transferability to new geographical areas. Evaluation metrics included the Boyce index (Hirzel et al. 2006; values range from -1 to 1 ; 0 denotes random agreement and values closer to 1 represent good agreement between prediction and data), the Area Under the receiver operating characteristic Curve (AUC; values range

from 0 to 1 ; $0.8 \leq \text{AUC} < 0.9 = \text{good}$; $0.9 \leq \text{AUC} = \text{excellent}$; Swets 1988), the True Skill Statistic (TSS; Allouche et al. 2006; values range from -1 to 1 ; 0 denotes a random fit and values closer to 1 represent systematically correct predictions), and sensitivity (or percentage of true positives), particularly important for invasive populations (Jiménez-Valverde et al. 2011). To test predictive performance in the native range, the entire dataset of presence and pseudo-absence points was randomly split to set aside 20% of points for evaluation, with five-fold validation. Transferability of the model was tested by geographically splitting the presence and pseudo-absence data into four quadrants, with three quadrants used to train the model and the fourth quadrant used to test the model with the Boyce index (spatially-subset k-fold cross validation; Jiménez-Valverde et al. 2011). This process was repeated for all four combinations of training-evaluation quadrants (SI 1 Fig. 3), across three randomly generated sets of pseudo-absences. Finally, independent evaluation of the model was carried out with the Boyce index using occurrence records from the non-native range (Andaman Islands and Madagascar; $n = 55$; at a resolution of 2.5 arc min).

We used a range of different modelling algorithms because of the known uncertainty arising from algorithm choice (Araújo and New 2007; Garcia et al. 2012). We executed algorithms covering environmental envelope (surface response envelope, SRE), regression (Generalized Linear Model, GLM; Generalized Additive Model, GAM), classification (Classification Tree Analysis, CTA) and machine learning (Generalized Boosting Model, GBM) techniques. Given our aim of predicting potential environmentally suitable regions for *H. tigerinus* occurrence globally, we chose to build simple models to maximize transferability and avoid overfitting (Merow et al. 2014). Therefore, we used a small number of predictors ($n = 4$), employed the biomod2 default features for each modelling technique (as opposed to making them more complex), and assessed the shape of the response curves. An ensemble modelling approach (Araújo and New 2007) was carried out to generate a final model that combined (median value) all modelling techniques, cross-validations and pseudo-absence runs, while disqualifying the only model (SRE) with AUC below 0.7.

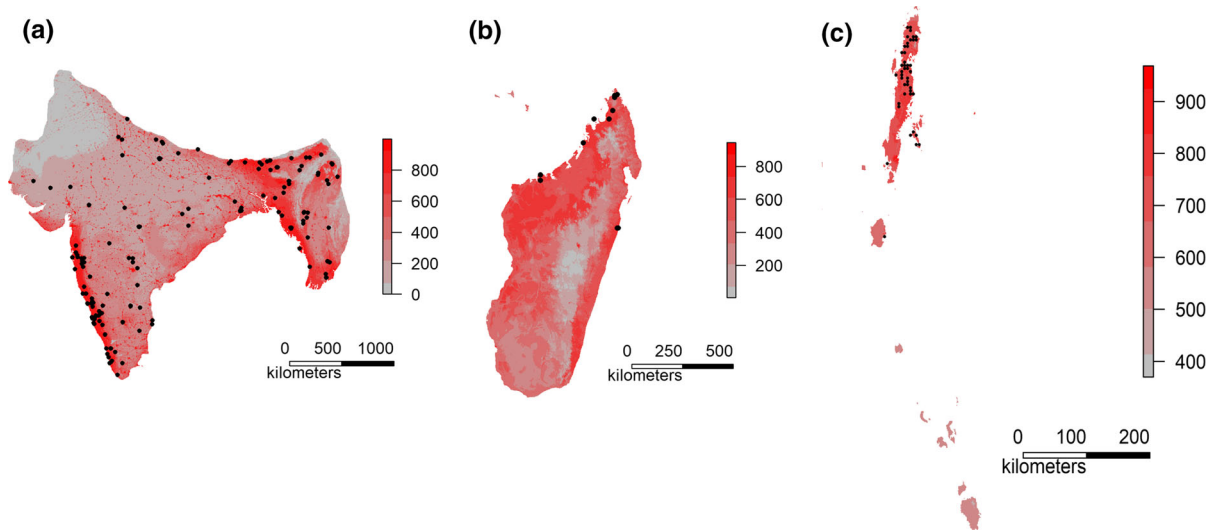


Fig. 1 Predicted environmental suitability of *Hoplobatrachus tigerinus* in **a** the native range (Indian subcontinent) and the confirmed invaded areas of **b** Madagascar and **c** Andaman archipelago, based on ensemble species distribution modelling. Each sub-figure shows the median ensemble projection at 30 arc

second resolution. Predictors included maximum temperature of the warmest month, minimum temperature of the coldest month, mean rainfall of the wettest quarter, and human influence index (HII). See SI 1 Fig. 6 and Fig. 7 for the associated extrapolation and uncertainty maps

To assess uncertainty in projections, we generated coefficient of variation maps (calculated across all included models) for the regions of interest, based on the ensemble model. Correlative species distribution models assume that the training data are representative of conditions to which the models are projected, which may not be valid in the case of biological invasions (Elith et al. 2010). Therefore, extrapolation areas were mapped to explicitly identify grid cells with predictor values falling outside the extent of values used for training the models, where confidence in model outputs would be lower. Finally, we projected the ensemble model globally at the original resolution (2.5 arc min) and in the invaded range at a finer resolution of 30 arc second.

Impact scoring

We scored the invasive *Hoplobatrachus tigerinus* for impact using literature on non-native populations (see above), based on two impact scoring systems. Our assessments were independent of previous classification scores and their underlying literature. First, we followed the EICAT scheme proposed by Blackburn et al. (2014), supplemented with guidelines by Hawkins et al. (2015). Second, we used the SEICAT scheme as described by Bacher et al. (2018). In both

scoring systems, one or more impact mechanisms are identified based on literature (e.g. predation; Table 1); the intensity of each impact mechanism, ranging over five categories, is then assessed. The lowest category in both schemes ('minimal concern') corresponds to no change in fitness of individuals of other native species (EICAT) or human well-being (SEICAT). The highest category ('massive') corresponds to irreversible changes such as local disappearance of a human activity caused by the alien species or changes to ecosystem properties (see Hawkins et al. 2015 and Bacher et al. 2018 for details). A confidence score is assigned to each assessment ('low', 'medium' or 'high') based on the nature and scale of evidence. Finally, the 'maximum recorded impact' based on currently available literature is ascribed to the species (Hawkins et al. 2015).

Results and discussion

Non-native populations

Andaman Islands

Hoplobatrachus tigerinus was first reported from two localities on the Andaman archipelago (Mayabunder,

Table 1 Impact scores (and associated confidence level) of the Indian bullfrog *Hoplobatrachus tigerinus* in all categories of the ‘Environmental Impact Classification of Alien Taxa’ (EICAT) and the relevant category of ‘Socio-Economic Impact Classification of Alien Taxa’ (SEICAT)

Impact mechanism	Score	Confidence	Remarks
Competition	MN	High	Mohanty and Measey (2018); competition for acoustic niche is probable
Predation	MO	Medium	Mohanty and Measey (2018, 2019b); indirect predation of native species by predator supplementation
Hybridisation	DD		Probable if introduced to regions with congeneric species (e.g. <i>H. occipitalis</i>)
Transmission of diseases to native species	DD		Probable chytridiomycosis vector
Parasitism	DD		Unlikely
Poisoning/toxicity	DD		Unlikely
Bio-fouling	DD		Unlikely
Grazing/herbivory/browsing	MN	Medium	Mohanty and Measey (2019b); tadpoles also graze on algae
Chemical, physical, or structural impact on ecosystems	DD		Unlikely
Interaction with other alien species	DD		May facilitate survival of larval <i>Duttaphrynus melanostictus</i> on Madagascar
Material and immaterial assets (SEICAT)	MO	Medium	Mohanty and Measey (2019a)

ML minimal, *MN* minor, *MO* moderate, *MR* major, *MV* massive, *DD* data deficient

Middle Andaman and Wandoor, South Andaman) in 2013, with the view that it was intentionally introduced in 2009–2010 from the Indian mainland (Harikrishnan and Vasudevan 2013). Subsequently, Rangasamy et al. (2014) reported occurrence on two other islands of the archipelago—Neil and Havelock Islands. Using public surveys to retrospectively assess invasion history, Mohanty and Measey (2019a) reported first establishment in 2001, followed by a lag phase of eight to ten years. However, a record of *H. tigerinus* from 1978 from the archipelago still needs verification (Harikrishnan and Vasudevan 2018). After 2009, the population spread to six of the eight major human-inhabited islands of the Andaman archipelago, with established populations occurring in at least 58 of 91 villages by 2017 (see Mohanty and Measey 2019a). Pathways contributing to the invasive spread included propagules as ‘contaminants’ of fish culture and intentional ‘release’ for consumption and novelty (Hulme et al. 2008; Mohanty and Measey 2019a). Tadpoles of *H. tigerinus* were likely to be transported accidentally with fish fingerlings, which are used for aquaculture; adult *H. tigerinus* were intentionally released, with frequent human-mediated

transfers (47.48 ± 11.81 km, range 6.2–188 km; Mohanty and Measey 2019a) within and between islands. Importantly, dispersal hubs (sites that served as the origin of multiple dispersals in the invaded range) were influential in exacerbating spread and could be targeted for management (Mohanty and Measey 2019a). We therefore consider this population to be fully invasive on the Andaman Islands (Category E, Blackburn et al. 2011).

Post-metamorphic *H. tigerinus* prey upon small vertebrates (including many endemic species of the archipelago), which constitute a majority of its diet by volume, whereas invertebrates are numerically higher (Mohanty and Measey 2018). Significant dietary overlap occurs with *Limnonectes* spp., indicating a potential for competition (Mohanty and Measey 2018). It is important to note that *Limnonectes* spp. on the Andaman archipelago may harbor multiple undescribed species (Harikrishnan and Vasudevan 2018) facing competition from *H. tigerinus*. Economic loss to household-level poultry and aquaculture has also been reported (Mohanty and Measey 2019a). Predation by larval *H. tigerinus* has been documented to cause zero survival of endemic *Microhyla*

chakrapanii and *Kaloula ghoshi* tadpoles (under mesocosm conditions), a mechanism that could lead to population extirpations (Mohanty and Measey 2019b). No management action is in effect for the invasive *H. tigerinus* population on the Andaman Islands, as the species is protected under the Schedule IV of the Indian Wildlife Protection Act (1972) which applies to the entire geopolitical region of India.

Madagascar

The first published record of *H. tigerinus* on Madagascar comes from Guibé (1953), where the author reported a specimen that was collected by R. Paulian in Mahajanga region, in the northwest of the island (Vences et al. 2003). Guibé identified the specimen as *Rana t. tigrina* and suggested a ‘recent’ introduction (Guibé 1953). The taxonomic identity of this specimen was supported by Blommers-Schlösser and Blanc (1991), and a subsequent molecular study confirmed that specimens collected on Madagascar belong to *H. tigerinus* (Kosuch et al. 2001). Guibé (1953) also noted that *H. tigerinus* is common in its native range and is consumed by humans, suggesting that the species might have been intentionally introduced to support the protein intake of local communities (Vences et al. 2003). Another possible reason for the introduction could have been its use as biocontrol of rodents and mosquito larvae (Vences et al. 2003). However, precise information on the introduction event(s) continues to be unclear (Guibé 1953; Kosuch et al. 2001; Vences et al. 2003).

Populations of *H. tigerinus* are widely distributed at low altitude sites in the north and northwest of Madagascar, with confirmed records from the wild at several sites (see SI 2 for detailed list). Recently, *H. tigerinus* has also been reported from Ivoloina and Tamatave, on the eastern coast of Madagascar (AC unpublished data). Overall, the species is expanding its range at low altitudes in the northwest, in the eastern coast and apparently also on the island of Nosy Be (Andreone et al. 2003; Padhye et al. 2008). The species is known to be sold live in city markets of Antananarivo and Toliara in south-west Madagascar (Gardner and Jasper 2009; AC unpublished data) but it is unclear if the species is harvested at these locations or elsewhere. Given the synanthropic nature of this species, it may be useful to conduct public surveys to gain more information on the invasion history,

especially in the eastern coast of Madagascar where the species most probably expanded its range in recent years. Such surveys in human-modified areas of Madagascar could reveal a larger distribution than is currently known, as herpetofaunal surveys have mostly focused on natural areas of forests. Based on this spread, we consider this population to be fully invasive on Madagascar (Category E, Blackburn et al. 2011).

Within Madagascar, the live trade of *H. tigerinus* for human consumption is likely to result in the expansion and establishment of new populations. *H. tigerinus* is among the most common species of amphibians sold as food both in street markets and restaurants of urban centers, such as Antananarivo and Toliara (Glaw and Vences 2007; Jenkins et al. 2008; Gardner and Jasper 2009), and at least in northern Madagascar this species is sourced from the wild rather than being farmed for the food trade (Jenkins et al. 2008). The consumption of this species has become increasingly important, with collection and trade reaching a significant volume (for production of the popular “cuisses de nymphe”). A large number of people are currently involved in this business, including collectors in the field, intermediate traders, restaurants and consumers (Jenkins et al. 2008). As *H. tigerinus* has been present for a relatively long time on Madagascar, it has proved difficult to disentangle its dispersal pathways. But it is worth noting that there has been little research on the spread and impacts of this invasive population.

No management against the spread and proliferation of this frog on Madagascar is in effect. While harvesting adults might help population control, the food trade has almost certainly helped facilitate introduction and establishment in new locations. In the 1990s, this species was collected intensively in rice paddies of the Marovoay area (northwestern Madagascar), apparently leading to a strong proliferation of rodents (Vences et al. 2003). This incident convinced regional authorities that the species had to be considered beneficial rather than a threat and a community-based effort to reduce the harvesting was put in place (Vences et al. 2003). However, we lack information to know if this program is still active.

Maldives and Lakshadweep (*Laccadives*)

Dutta (1997) recorded introduced *H. tigerinus* on the Maldivian Islands, but recent records confirming establishment and spread are missing. *H. tigerinus* has also been reported from Minicoy Island in the Lakshadweep archipelago, Arabian Sea (Sinha 1994). Our recent attempts to validate this record through local researchers did not confirm current presence of *H. tigerinus*; the only amphibians reported from both Maldives and Lakshadweep by researchers were of bufonids, most likely *Duttaphrynus melanostictus* (from photographic ID).

Captive populations

H. tigerinus populations are present in captivity, intended for farming, in Cuba (Borroto-Páez et al. 2016; Category B1, Blackburn et al. 2011) and Thailand (Timsina 2013; Category B2, Blackburn et al. 2011), with no records of populations occurring in the wild. The species has been recorded in the pet trade (Carpenter et al. 2014), in Brazil (Fonseca et al. 2019) and the USA (Mohanty and Measey 2019c).

Species distribution modelling

The ensemble species distribution model for *H. tigerinus*, reflecting the median across all cross-validations and pseudo-absence runs, was ‘good’ in performance in the native range (AUC = 0.89, range 0.58–0.90; TSS = 0.66, range 0.31–0.70; see SI 1 Fig. 4 for the results for single-models). Sensitivity of the ensemble model was 87.5%, indicating high true positive detection. Model transferability to new geographical areas was high, as indicated by the results of spatially-subset k-fold cross validation (mean Boyce index = 0.65, range 0.34–0.92; SI 1 Table 1). Independent evaluation of the ensemble model using non-native range occurrences resulted in Boyce index values of 0.77 for Madagascar and 0.90 for the Andaman Islands, indicating good predictive power. The mean precipitation of wettest quarter had relatively high importance in the ensemble model (21.7%), followed by HII (19.5%), maximum temperature of the warmest month (18.3%), and minimum temperature of the coldest month (17.3%). While mean precipitation and HII had sigmoidal relationships with suitability, maximum and minimum

temperature had bell-shaped response curves (SI 1 Fig. 5). Overall, extrapolation maps suggested that most high-suitability regions, globally and in the confirmed invaded range (Andaman and Madagascar), had predictor values within the range of the training values, allowing us to place higher confidence in these results (SI 1 Fig. 6). Model uncertainty was similarly low in regions with higher suitability values (SI 1 Fig. 7).

In non-native areas, most regions on the Andaman Islands were predicted as suitable for *H. tigerinus* occurrence, and lowland areas on Madagascar were particularly suitable (Fig. 1). From the perspective of environmental suitability, the population on the Andaman archipelago has the potential to establish in at least two more human inhabited islands hitherto uncolonized (Long and Baratang). On Madagascar, new areas along the east and the west coast were predicted as environmentally suitable for establishment (Fig. 1). Pearson (2015) inferred a similar potential distribution for the invasive population of *D. melanostictus* on Madagascar, another anuran native to South-East Asia; however, Vences et al. (2017) identified higher suitability mostly along the eastern coast. The predicted range for *H. tigerinus* (Fig. 1) should be considered as a hypothesis to inform further field surveys in the non-native range (Jarnevich et al. 2015).

Globally, our models predicted higher suitability in the tropical parts of Central and South America (including Brazil), Africa, Madagascar, South-East Asia and Australia (Fig. 2). However, this prediction does not necessarily translate into invasion risk. The only regions at risk are those with a potential for introduction through translocation for food or

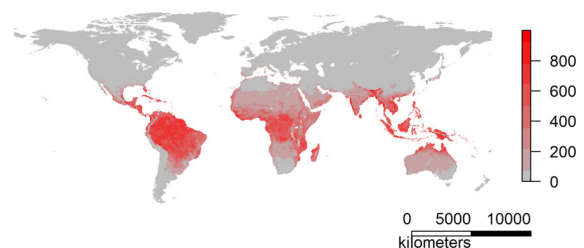


Fig. 2 Global environmental suitability (median ensemble projection) for *Hoplobatrachus tigerinus*, based on ensemble species distribution modelling for the native range, projected at a resolution of 2.5 arc minutes. See SI 1 Fig. 6 and Fig. 7 for the associated extrapolation and uncertainty maps

biocontrol, pet trade, and contamination of fish culture (Mohanty and Measey 2019a, c). The species was listed in Appendix II of Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES; www.cites.org) in 1985, as a result of its harvest for the international ‘frog leg trade’ (Abdulali 1985; Oza 1990). Due to this listing, its export (and not import) requires permissions from relevant authorities. Permission is conditional on the assessment if such trade will be detrimental to the survival of the species in the wild. Further, any collection or export of *H. tigerinus* for commercial purposes is prohibited under the Indian Wildlife Protection Act. However, unintentional introductions, within-country trade, and illegal trade are likely to go undocumented. Under the current trade climate, intentional release is highly likely in the Nicobar archipelago, although environmental suitability is low. Similarly, bridgehead introductions are possible to the climatically suitable regions of Malaysia, Indonesia, Mascarene Islands and eastern Africa. As new occurrence data in the invaded range become available, future modelling efforts for this species should quantify niche dynamics during the invasion process and include both the native and non-native ranges in the training step.

Impact scoring

Based on the experimental documentation of *H. tigerinus* impact on tadpoles of the endemic *Microhyla chakrapanii* and *Kaloula ghoshi* on the Andaman archipelago (Mohanty and Measey 2019b), we assigned a score of ‘moderate’ environmental impact to the species, with a ‘medium’ confidence score due to the limited scale of the experiment (Table 1). Interview data from key informants (farmers, plantation workers, and pond owners; see Mohanty and Measey 2019a) record population declines in native anurans; we scored this environmental impact as ‘moderate’ with ‘low’ confidence due to the inferred nature of the information (Table 1). Socio-economic impact was also scored as ‘moderate’ based on the same set of key informant interviews, which recorded cessation of poultry keeping by many households, due to predation by *H. tigerinus* (Table 1). We assigned a confidence score of ‘medium’ due to possible ambiguity given that the data resulted from semi-structured questionnaire surveys, lacking a directed question at abandonment of activity (Mohanty and Measey

2019a). These impact scores were based solely on the invasive population on the Andaman archipelago, in the absence of published information on impacts on Madagascar.

Based on the evaluation of non-native populations, we provide a species summary of *H. tigerinus* describing key aspects of its invasion process, including dispersal pathways, environmental suitability, and impact (Table 2). Apart from known impact mechanisms for *H. tigerinus*, impacts of other invasive large Ranoid frogs (superfamily Ranoidea; Novoa et al. 2020) indicate the possibility of competition for acoustic niche (Both and Grant 2012), disease transmission (Mutnale et al. 2018), facilitative interaction with non-native species (Adams et al. 2003). Indirect exacerbation of predation on native species by predator supplementation (Woolbright et al. 2006), and hybridization (Dufresnes et al. 2015), are also probable mechanisms that require future evaluation (Table 1).

Generalities with other taxa

The five species that currently constitute the genus *Hoplobatrachus* (*H. tigerinus*, *H. rugulosus*—syn. *H. chinensis*, *H. crassus*, *H. occipitalis*, *H. litoralis*; Frost, 2019) share traits that are likely to make them part of an “invasion syndrome” (e.g. Novoa et al. 2020). These large-bodied, semi-aquatic anurans with high fecundity tend to thrive in human-modified environments. Apart from these life-history traits, which promote invasions in amphibians, at least four species are used for human consumption (Carpenter et al. 2014; Mohnke et al. 2009) and three are traded as pets, including the likely illegal trade of *H. tigerinus* due to its CITES listing (Mohanty and Measey 2019c). *Hoplobatrachus rugulosus* (syn. *H. chinensis*), the only other congener with known introductions, has invasive populations on Philippines and Borneo (Pili et al. 2019); the species also shares dispersal pathways with *H. tigerinus* (release for food, contaminant of fish fingerlings; Pili et al. 2019).

The carnivorous nature of tadpoles in the genus *Hoplobatrachus* is hypothesized to have facilitated their historical colonization of arid environments where ponds could be ephemeral (Grosjean et al. 2004). This carnivorous behavior, which drastically reduces survival of co-occurring native tadpoles (Mohanty and Measey 2019b; Table 1), could

Table 2 Summary of invasion dynamics of the Indian bullfrog *Hoplobatrachus tigerinus* with supporting literature and remarks

	Description	Literature	Remarks
Native range	Indian sub-continent	Dutta (1997)	
Non-native range	Andaman Islands, Madagascar	Mohanty and Measey (2019a) and Vences et al. (2003); see SI 2	Distribution on Madagascar updated in current study
Unaided pathways	Contamination of freshwater fish culture by tadpoles	Mohanty and Measey (2019a)	Likely to benefit from farm dams [e.g. Govindarajulu et al. (2005) and Davies et al. (2013)]
Aided pathways	Intentional release for consumption and biocontrol	Harikrishnan and Vasudevan (2013), Mohanty and Measey (2019a) and Guibé (1953)	
Environmental predictors	Maximum temperature of warmest month, Minimum temperature of the coldest month, Human influence index, Mean rainfall of wettest quarter	Current study	
Environmental impact	Predation and competition with anurans by adults; inter-specific predation by carnivorous tadpoles	Mohanty and Measey (2018, 2019b)	Population level declines of native anurans likely
Socio-economic impact	Predation of poultry and fish stocks by adults	Mohanty and Measey (2019a)	May lead to reduction and ceasing of poultry keeping

influence their invasion success by limiting competition. Apart from the predatory impact of the larval stage, adults of the genus may impact native biodiversity similarly to *H. tigerinus* (e.g. predation of native vertebrates, Table 1; Hirschfeld and Rödel 2011; Pili et al. 2019). Similarities in the invasion process of *Hoplobatrachus* to the well-studied model species *Lithobates catesbeianus* (130 publications on its non-native populations; Ficetola et al. 2007a; van Wilgen et al. 2018) belonging to the same “invasion syndrome”, should be leveraged to frame hypotheses and inform management (Novoa et al. 2020).

Conclusion

Non-native populations of *H. tigerinus* are likely to spread to climatically suitable regions that have potential for live trade (consumption and pet trade) and contamination of fish culture. Regions at higher risk for incursions include the Nicobar archipelago, Malaysia, Indonesia, Mascarene Islands and eastern Africa, due to likelihood for bridgehead introductions and climatic suitability. Implementation of biosecurity

measurements (such as the screening of traded goods at seaports and airports) is strongly recommended, along with monitoring of illegal pet trade for emergence of *H. tigerinus* (and other species in this genus) as a species of choice. Risk assessments of the species should be informed by the aspect of human-use which is likely to enhance the likelihood of establishment and spread.

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