The invasive Indian bullfrog *Hoplobatrachus tigerinus* on the Andaman Islands: Evaluating drivers of distribution, density, and trophic impact of an early stage invader

Dissertation presented for the degree of Doctor of Philosophy in the
Faculty of Science at Stellenbosch University

By Nitya Prakash Mohanty

Supervisor: Dr. John Measey

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This dissertation includes two articles published with me as lead author, and one article submitted and under review, and two papers yet to be submitted for publication. The development and writing of the papers (published and unpublished) were the principal responsibility of myself. At the start of each chapter, a declaration is included indicating the nature and extent of any contributions by co-authors.

Nitya Prakash Mohanty

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Abstract

The global spread of humans and their activities change movement patterns of other species, by limiting or enhancing their movement and consequently their distribution. Biological invasions occur when species are moved beyond their natural range by human activities to a new range, where the species reproduce and spread. These biogeographic changes now occur with rapidity on large scales due to accelerating global trade and transport. Amphibians are an emerging group of invaders, with increasing global frequency of invasive populations. Invasive amphibians have considerable ecological impact on the recipient system mediated through toxicity, competition, predation, and probable disease transmission. The level of ecological impact by invasive amphibians is comparable to that of invasive fish and birds. However, only a limited number of species have been well-studied for their invasion dynamics, limiting understanding and management.

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 the bullfrog, based on species-traits and human-interaction, its invasion process has not been assessed. This study aimed to understand four major aspects of the Indian bullfrog's invasion on the Andaman Islands, where it has recently been introduced: i) distribution and dispersal, ii) impact of adults iii) impact of carnivorous tadpoles, and iv) invasion dynamics and efficacy of potential management strategies. Finally, the thesis aimed to assess v) the bullfrog's global invasion potential and status of all extra-limital populations.

I used a novel approach to reconstruct the Indian bullfrog invasion of the Andaman Islands, combining public surveys and field surveys in a formal analytical framework. The bullfrog occurred in at least 62% of the sampled sites spread over six islands, a dramatic increase to the previously known invaded range. The bullfrog was most likely introduced in early 2000s, and its exponential expansion has occurred since 2009. 'Contaminants' of fish culture trade and intentional 'release' were reported to be the primary pathways of introduction and post-introduction dispersal, facilitating introductions from the Indian mainland and inter-island transfers. The use of public surveys in a systematic framework adds a complimentary tool to the existing methods for reconstructing invasions.

I assessed the diet of the invasive Indian bullfrog and two co-occurring native frogs (genus *Limnonectes* and *Fejervarya*) to assess the impact of adult bullfrogs. Vertebrates made up the majority of the bullfrog's diet in terms of volume, whereas, invertebrates were numerically dominant. I only found a significant dietary overlap between the bullfrog and individuals of the genus *Limnonectes*. Prey size electivity was governed by body size of the three species. This intensive study on a hitherto unassessed genus of invasive amphibians contributes to the knowledge on impacts of amphibian invasions.

To assess the impact of the larval (tadpole) stage of the Indian bullfrog on endemic anurans of the Andaman archipelago, I carried out a mesocosm experiment with larval bullfrogs, the Chakrapani's narrow-mouthed frog, *Microhyla chakrapanii,* and the Andaman tree frog, *Kaloula ghosi*. Predation by bullfrog tadpoles resulted in no survival of endemic tadpoles, with all individuals being consumed within a three-week period. In contrast, the single-species treatments of *M. chakrapanii* and *K. ghosi* led to a survival of 90% and 62% respectively. This predation impact is likely to translate to population declines in anurans which co-occur with and breed in similar habitats as the bullfrog. The study is timely as the rapidly expanding invasion is likely to affect other native anurans including many anuran genera that are awaiting formal taxonomic re-assessments. Further, the findings augment the limited existing knowledge on the impact of amphibian invaders with carnivorous larvae.

I developed a model to evaluate the effect of human-mediated translocations, natural dispersal, and demography on the invasion dynamics of the Indian bullfrog. I combined an age-structured demographic model with a gravity model of human influence, in a spatially explicit modelling context. Human influence had a positive effect on spread rates, facilitating both between island and within island movement of the bullfrog. Interestingly, the model predicted an overriding effect of human influence on origin of the invasion. Based on the modelled predictions, I recommend immediate deployment of screening mechanisms between islands (especially for the hitherto uncolonized Baratang and Long Island). Understanding invasions with frequent human-mediated translocations in the extra-limital range, can benefit from the modelling approach developed in this study, which allows for utilization of surrogates of human influence.

Finally, I assessed the profile of the Indian bullfrog as a potentially emerging invasive species. Apart from the focal study area of the Andaman archipelago, I could only confirm another successful invasion on Madagascar. Reported populations on Maldives and Laccadive Islands do not have recent substantive records for validation; Thailand and Cuba have captive individuals and do not have confirmed populations in the wild. An environmental niche model identified isothermality, high precipitation, and human modification as factors conducive for bullfrog occurrence. I assigned the species a standardized score of ‘Moderate’ for ‘socio-economic impact’, on account of reduction in human activities of poultry keeping and threat to aquaculture. Similarly, ‘environmental impact’ was assigned a score of ‘Moderate’, based on documented population extirpations of native anurans under experimental conditions.

Overall, the Indian bullfrog is likely to increase it extra-limital range by spreading to the Nicobar Islands and in new locations of Madagascar and the Andaman Islands. I identified the Nicobar Islands, Mascarene Islands, Malaysia and Indonesia, and East Africa to be likely recipients of new introductions. Screening at points of entry is likely to be effective for small islands, such as the Andaman and Nicobar archipelagos, due to the relatively low human traffic they experience.

The thesis used a suit of methodological approaches to understand the invasion dynamics of the Indian bullfrog and generated novel insights that are transferable to other taxonomic groups and contexts. The findings have theoretical and applied implications for biological invasions and population ecology in general.

Opsomming

Die wêreldwye verspreiding van mense en hul aktiwiteite verander bewegingspatrone van ander spesies, deur die beperking of bevordering van hul beweging en gevolglik hul verspreiding. Biologiese invalle kom voor wanneer spesies oor hul natuurlike bevolkingsreeks verplaas word deur menslike aktiwiteite na 'n nuwe reeks, waar die spesies voortplant en versprei. Hierdie biogeografiese veranderinge vind op groot skaal plaas teen haas as gevolg van versnelde wêreldhandel en vervoer. Amfibieë is ŉ groep wat toenemend op ŉ globale vlak indring in nuwe omgewings Uitheemse amfibieë het aansienlike ekologiese impak op die inheemse ekostelsel wat deur toksisiteit, kompetisie, predasie en waarskynlike siekteoordrag veroorsaak word. Die vlak van ekologiese impak deur indringende amfibieë is vergelykbaar met dié van indringende visse en voëls. Slegs 'n beperkte aantal spesies is egter goed bestudeer vir hul indringdinamika, wat begrip en bestuur beperk.

Die Indiese brulpadda, *Hoplobatrachus tigerinus*, 'n groot dicroglossid padda (neus tot kloaka lengte: tot 160 mm), is inheems aan die Indiese subkontinent. Ten spyte van die hoë waarskynlikheid van indringersukses vir die brulpadda, gebaseer op spesie-eienskappe en menslike interaksie, is sy invalproses nie geassesseer nie. Hierdie studie het ten doel om vier hoofaspekte van die Indiese brulpadda se inval op die Andaman-eilande te verstaan, waar dit onlangs bekendgestel is: i) rangskikking en verspreiding, ii) die impak van volwassenes iii) die invloed van karnivoor paddavisse, en iv) indringdinamika en doeltreffendheid van potensiële bestuur strategieë. Uiteindelik het die proefskrif gemik op die evaluering van v) die brulpadda se wêreldwye invalpotensiaal en status van alle buite-limietbevolkings.

Ek het 'n nuwe benadering aangewend om die Indiese brulpadda inval van die Andaman-eilande te herbou, en die opname van openbare opnames en veldopnames in 'n formele analitiese raamwerk te analiseer. Die brulpadda is teenwoordig in minstens 62% van die steekproewe wat oor ses eilande versprei is, 'n dramatiese toename in die inval streek. Die brulpadda is waarskynlik vroeg in die 2000's bekendgestel, en die eksponensiële uitbreiding het sedert 2009 plaasgevind. 'Verontreiniging' van viskultuurhandel en doelbewuste 'vrylating' is aangewys as die primêre paaie van indringing en na-indrining verspreiding, fasiliteer dus van die indringing uit die Indiese vasteland en tussen-eiland oordragte. Die gebruik van openbare opnames in 'n sistematiese raamwerk voeg 'n komplimentêre instrument by die bestaande metodes om invalle te herbou.

Ek het die dieet van die uitheemse indringende Indiese brulpadda en twee mede-voorkomende inheemse paddas (genus *Limnonectes* en *Fejervarya*) geëvalueer om die impak van volwasse brulpaddas te bepaal. Vertebrate het die grootste deel van die brulpadda se dieet in terme van volume uitgemaak, terwyl ongewerwelde diere numeries oorheersend was. Ek het net 'n beduidende dieet oorvleueling tussen die brulpadda en individue van die genus *Limnonectes* gevind. Prooi grootte en tipe is bepaal deur die liggaam grootte van die drie spesies. Hierdie intensiewe studie oor 'n tot dusver onbeoordeelde genus van indringende amfibieë dra by tot die kennis oor die impak van amfibiese invalle.

Om die impak van die larwe (paddavis) stadium van die Indiese brulpadda op endemiese amfibieë van die Andaman-eilandgroep te assesseer, het ek 'n mesokosm-eksperiment uitgevoer met brulpadda larwe, die Chakrapani se smalmondige padda, *Microhyla chakrapanii*, en die Andaman boompadda, *Kaloula ghosi*. Predasie deur brulpaddas het gelei datgeen endemiese paddavisse oorleef nie, al die paddavisse was binne ʼn tydperk van drie weke opgeëet. In teenstelling hiermee het die enkel-spesies behandelings van *M. chakrapanii* en *K. ghosi* gelei tot 'n oorlewing van onderskeidelik 90% en 62%. Die bevolkingsdalings van die inheemse amfibieë is moontlik as gevolg van kombinasie van dìe predasie impak en soortgelykte broeihabitatte. Die studie is tydig, aangesien die vinnig groeiende inval waarskynlik ander inheemse amfibieë sal beïnvloed, insluitende baie Anuran genera wat op formele taksonomiese herbeoordelings wag. Verder bevind die studie die beperkte bestaande kennis oor die impak van amfibiese indringers met karnivoor larwes.

Ek het 'n model ontwikkel om die effek van mensgemedieerde translokasies, natuurlike verspreiding en demografie oor die indringdinamika van die Indiese brulpadda te evalueer. Ek het 'n ouderdom gestruktureerde demografiese model gekombineer met 'n

swaartekragmodel van menslike invloed, in 'n ruimtelike eksplisiete modelleringskonteks. Menslike invloed het 'n positiewe uitwerking gehad op verspreidingsyfers, wat beide tussen eiland en binne die eilandbeweging van die brulpadda fasiliteer. Interessant genoeg het die model 'n oorheersende uitwerking van menslike invloed op die oorsprong van die inval voorspel. Op grond van die gemodelleerde voorspellings, beveel ek aan onmiddellike implementering van siftings meganismes tussen eilande (veral vir die tot dusver ongekoloniseerde Baratang en Long-eiland). Die verstaan van invalle met gereelde mensgemiddelde translokasies in die buite-limietreeks kan baat vind by die modelleringsbenadering wat in hierdie studie ontwikkel is, wat die gebruik van surrogate van menslike invloed moontlik maak.

Uiteindelik het ek die profiel van die Indiese brulpadda beoordeel as 'n tot dusver onbekende en moontlik ontluikende indringerspesie. Afgesien van die fokusarea van die Andaman-eilandgroepl, kon ek net nog 'n suksesvolle inval op Madagaskar bevestig. Gerapporteerde populasies op Maldive en Laccadive-eilande het nie onlangse inhoudelike rekords vir bevestiging nie; Thailand en Kuba het gevangenes en het nie bevolkings in die natuur bevestig nie. 'n Omgewing-nismodel het isotermie, hoë neerslag en menslike aanpassing geïdentifiseer as faktore wat bevorderlik is vir die voorkoms van brulpaddas. Ons het die spesie 'n gestandaardiseerde telling van 'Gematigde' vir 'sosio-ekonomiese impak' toegeken aan die hand van die vermindering van menslike aktiwiteite van pluimvee en bedreiging vir akwakultuur. Net so is 'n omgewingsimpak 'n telling van 'Matig' toegeken, gegrond op gedokumenteerde bevolkings uitdrywings van inheemse amfibieë.

Gevolglik, die Indiese brulpadda sal waarskynlik die buite-limietreeks verhoog deur na die Nicobar-eilande en op nuwe plekke van Madagaskar en Andaman-eilande te versprei. Ek het die Nicobar-eilande, Mascarene-eilande, Maleisië en Indonesië geïdentifiseer, en Oos-Afrika is waarskynlik ontvangers van nuwe inleidings. Sifting by intreepunte sal waarskynlik effektief wees vir klein eilande, soos die Andaman- en Nicobar-eilandgroepe weens die relatief lae menslike verkeer wat hulle ervaar. Die proefskrif het 'n variasie metodologiese benaderings gebruik om die indringdinamika van die Indiese brulpadda te verstaan en nuwe insigte te skep wat oordraagbaar is aan

ander taksonomiese groepe en kontekste. Die bevindings het teoretiese en toegepaste implikasies vir biologiese indringers en populasie-ekologie in die algemeen.

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List of published and submitted articles

[CHAPTER 2]
Mohanty NP, Measey J. (*in press*). Reconstructing biological invasions using public surveys: a new approach to retrospectively assess spatio-temporal changes in invasive spread. *Biological Invasions* DOI: 10.1007/s10530-018-1839-4.

[CHAPTER 3]
Mohanty NP, Measey J. (2018) What's for dinner? Diet and potential trophic impact of an invasive anuran *Hoplobatrachus tigerinus* on the Andaman archipelago. *PeerJ* DOI: 10.7717/peerj.5698.

[CHAPTER 4]
Mohanty NP, Measey J. (*accepted*). No survival of native larval frogs in the presence of invasive Indian bullfrog *Hoplobatrachus tigerinus* tadpoles. *Biological Invasions*.

Conference presentations of the PhD work

Mohanty NP, Measey J. Reconstructing biological invasions using public surveys: a new approach to retrospectively assess spatio-temporal changes in invasive spread. Oral Presentation at *10th International Neobiota Conference*, Dublin, Ireland, 2018.

Mohanty NP. Invasions in isolation: a review of distribution, dispersal pathways, and management of faunal invasions on Indian islands. Invited lecture at *Workshop on economic and ecological impacts of invasive alien species*, Kolkata, India, 2018.

Mohanty NP, Sachin A, Selvaraj G, Vasudevan K, Measey GJ. Using key informant surveys to rapidly and reliably estimate distributions of invasive species. Poster at *Island Invasives Conference* (II17), Dundee, Scotland, 2017.

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1 Introduction

BIOLOGICAL INVASIONS

The pan-global spread of the human population and activities alter dispersal patterns of other species, by limiting or enhancing their movement and consequently their distribution (Trakhtenbrot et al., 2005). This alteration of species' dispersal has behavioural, genetic, and biogeographic consequences. Biological invasions occur when species are moved beyond their natural range by human activities to a new range, where the species reproduce and spread (Blackburn et al., 2011). These biogeographic changes now occur with rapidity on large scales due to accelerating global trade and transport (Hulme, 2009), where species are moved through a variety of intentional and unintentional pathways over a range of distances (Wilson et al., 2009).

For an invasion to take place, individuals of a species must move through a series of stages while overcoming barriers to dispersal, survival, and reproduction (Blackburn et al., 2011). Such extra-limital populations may impact the native biodiversity on a hierarchy of levels, from changes in individual fitness to ecosystem processes (Blackburn et al., 2014). Impact mechanisms are diverse, encompassing processes such as predation, competition, disease transmission, and habitat alteration (Simberloff et al., 2013). Simultaneously, economic impacts can occur in the recipient system, influencing human activities and wellbeing (Bacher et al., 2018).

The intrinsic link of invasions to humans make the study of biological invasions more than just an ecological one. 'Invasion science' has evolved to address questions arising from this interaction of ecological and anthropogenic processes (Hui & Richardson, 2017). It is highly inter-disciplinary, borrowing from diverse fields such as population biology, community ecology, economics, sociology, restoration and conservation biology, and often involves multiple stakeholders (Vaz et al., 2017). A range of hypotheses have been put forward to explain patterns in invasion success and impact

(Catford et al., 2009; Jeschke, 2014), based broadly on the key aspects of species traits, propagule pressure, and recipient system traits (Kueffer et al., 2013).

AMPHIBIAN INVASIONS

Amphibians are an emerging group of invaders, with increasing global frequency of invasive populations (Kraus, 2009; Capinha et al., 2017). Globally, 78 non-native species of amphibians are known to have at least one established or invasive population (Capinha et al., 2017); a less conservative estimate records a total of 104 non-native amphibians (Measey et al., 2016). As with other taxonomic groups, there is no saturation in accumulation rates of invasive populations of amphibians worldwide (Seebens et al., 2017), driven by active pathways such as the pet trade (Kraus, 2009). Current patterns of invasions are partly driven by historical introductions (‘invasion debt’) and similarly current trade will likely influence future invasions (Essl et al., 2011). Amphibian invasions are further complicated by a range of dispersal modes, ranging from unintentional dispersal in the nursery trade or as stowaway in cargo to intentional pathways of pet trade and release (Kraus, 2007; Christy et al., 2007; Garcia-Diaz and Cassey et al., 2014; Measey et al., 2017). These pathways can also display taxonomic and life-history stage bias. Invasive amphibians have considerable ecological impact on the recipient system mediated through toxicity, competition, predation, and probable disease transmission (Kraus, 2015; Kumschick et al., 2017 a, b). The level of ecological impact is comparable to that of invasive fish and birds (Measey et al., 2016), whereas economic impacts are also markedly high (Bacher et al., 2018). Several global assessments of invasive amphibians have evaluated factors influencing success in stages of introduction (Tingley et al., 2010), establishment (Bomford et al., 2009; Rago et al. 2012) and spread (Liu et al. 2014).

However, taxonomic biases in assessments of amphibian invasions still limit generalizations and risk assessments (Measey et al., 2016; van Wilgen et al., 2018). For example, only three species, the cane toad *Rhinella marina*, the American bullfrog *Lithobates catesbeianus*, and the African clawed frog *Xenopus laevis* account for 82% of the studies on amphibian invasions (van Wilgen et al., 2018). This bias is probably compounded by the limited studies in developing countries on invasion science (Nuñez &

Pauchard, 2010). Further, a significant knowledge gap exists for the processes governing the early stages of invasions (Puth & Post, 2005), which lead to exponential expansion (van Wilgen et al., 2014).

THE INDIAN BULLFROG

The Indian bullfrog *Hoplobatrachus tigerinus*, a large dicroglossid frog (snout to vent length: up to 160 mm), is native to the Indian sub-continent (Dutta, 1997). Given the common occurrence of the frog in the Indian sub-continent (Padhye et al., 2008), many autecological and experimental studies have focussed on the species, especially on its larval stage (e.g. Dutta & Mohanty-Hejmadi, 1976; Dash & Hota, 1980; Hota & Dash, 1981; Marian & Pandian, 1985). Tadpoles of *H. tigerinus* are known to be carnivorous, preying upon other anuran larvae and zooplankton (Khan, 1996; Grosjean et al., 2004), along with records of cannibalism (Dash & Hota, 1980; Mohanty-Hejmadi & Dutta, 1981; Hota & Dash, 1983). Although, reproductive biology and feeding ecology of *H. tigerinus* is broadly understood, population ecology is not well studied (but see Gramapurohit et al., 2004). A key aspect of the species is its history of human use. The species was harvested and exported as part of the ‘frog leg trade’ until late 1980s (Abdulali, 1985). Following apparent population decline, trade was banned, and the species accorded protection under the Schedule IV of the Indian Wildlife Protection Act (Oza, 1990).

Its body size, association with human-modified landscapes (e. g. paddy fields; Daniels, 2005), and utilization for consumption (Oza, 1990) make *H. tigerinus* a likely candidate for human-mediated introduction outside its native range (Tingley et al., 2010). Further, the species has high fecundity (ca. 6000 eggs) and can breed successfully in ephemeral pools of human-modified habitats. An ‘intentional’ mode of introduction and climate matching can confer advantages at the establishment stage for anurans (Rago et al. 2012), along with large clutch sizes; a ‘fast’ life history trait (Allen et al., 2017). Within the non-native range, intentional or unintentional transfers of propagules can accelerate spread rates of invasive amphibians (Liu et al., 2014). Further, large bodied amphibians with high reproductive potential are likely to have higher environmental impacts (Measey et al., 2016). Post-metamorphic individuals of *H. tigerinus* consume a broad range of invertebrates and small vertebrates (Padhye et al., 2008) and are likely to have predatory and competitive impacts in extra-limital regions (Harikrishnan & Vasudevan, 2013).

Indian bullfrogs have been introduced to the Maldives (Dutta, 1997) and Madagascar (Vences et al., 2003). Though there are reports of the bullfrog from the Laccadive Islands (Sinha, 1994), its successful establishment still requires verification. Introduced populations of the frog were reported from the Andaman Islands only very recently, with the suggestion that they were possibly introduced in 2009 or 2010 from the Indian mainland (Harikrishnan & Vasudevan, 2013).

THE ANDAMAN ISLANDS

The Andaman Islands, in the Bay of Bengal, are situated 1200 km to the east of the Indian mainland, and only 600 km south of Myanmar. The Islands range from 10°30’N to 13°40’N, and from 92°10’E to 93°10’E. This tropical island group, comprising of ca. 300 islands, is a part of the Indo-Burma global biodiversity hotspot (Myers et al., 2000). The south-west monsoon commencing in May and the north-east monsoon commencing in November, account for the majority of the annual rainfall ranging from 3000 mm to 3500 mm. Forest types include evergreen, semi-evergreen, moist deciduous, littoral and mangrove forests; forests cover nearly 89% of the entire archipelago, with varying levels of protection. Tribal reserves, which host Jarawa, Great Andamanese, Sentinelese, Onges and other small tribes are restricted areas located on South Andaman, Middle Andaman, Little Andaman, Strait, and North Sentinel Islands. The human population on the archipelago is approximately 344 000, distributed across eight islands with major human habitations; settlements mostly comprise of villages along with one or more towns on each island. Agriculture and aquaculture are widely practised in the archipelago, with artificial ponds for aquaculture and sustenance. Roughly 40% of the reptiles and amphibians (n = 53) are endemic to the Andaman Islands (Harikrishnan et al., 2010). Several introduced vertebrates also occur, including fishes, mammals, birds and reptiles; the Indian bullfrog is the first non-native amphibian to be reported (Mohanraj et al., 1997; Harikrishnan & Vasudevan, 2013). With minimal biosecurity measures in place, invasions on these islands are mostly unmanaged (Mohanty & Ravichandran, 2017), leading to large spread extents and impacts (Ali, 2004; Mohanty et al., 2016; Mohanty et al., 2018).

Apart from initial records of distribution, the invasion of the Indian bullfrog on the Andaman Islands remains completely unstudied. Critical information for its management, such as, distribution and dispersal, is missing. Further, the impact of its larval and adult stage on native biodiversity remains unquantified. Bullfrogs were reportedly introduced for consumption (Harikrishnan & Vasudevan, 2013), though accidental introduction through the aquaculture trade is also possible (Christy et al., 2007). Bullfrogs had been reported from one site each on Middle and South Andaman Island (Harikrishnan & Vasudevan, 2013) and later from the islands of Neil and Havelock (Rangaswamy et al., 2014).

THESIS STRUCTURE AND AIMS

This study aims to understand four major aspects of the Indian bullfrog's invasion on the Andaman Islands: i) spatio-temporal patterns in distribution and dispersal, ii)) trophic impact of post-metamorphic stage, iii) impact of larval stage, and iv) invasion dynamics and efficacy of potential management strategies. Finally, the thesis aims to assess v) the bullfrog's global invasion potential, status of all extra-limital populations, and assign standardized impact scores for environmental and socio-economic impacts.

In doing so, the study intends to contribute towards addressing specific knowledge gaps in invasion biology. As research on emergent or early stage invasions are limited (Puth & Post, 2005), this investigation could inform the factors governing the initial stage of invasions. Given that knowledge on amphibian invasions are based on a very limited subset of species (van Wilgen et al., 2018), this work can potentially add significantly to the existing knowledge. Being set in an archipelago system, the study can elucidate aspects of invasive spread in scenarios of disjunct populations. Further, the lack of research on invasion biology of vertebrates in the Indian subcontinent can be addressed with the study. Finally, the use of multiple approaches such as modelling of public survey data on invasive species, diet assessments, mesocosm experiments, combined use of age-structured and connectivity models, and environmental niche models is likely to yield transferable insights for ecology in general.

2 Reconstructing biological invasions using public surveys: a new approach to retrospectively assess spatio-temporal changes in invasive spread

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AUTHOR CONTRIBUTIONS

NPM and JM conceived the idea of the study; NPM collected the data; NPM and JM analysed the data; NPM wrote the manuscript, JM contributed to the writing.

ABSTRACT

Management of biological invasions increasingly relies on the knowledge of invasive species' dispersal pathways that operate during introduction and post-introduction dispersal. However, the early stages of biological invasions (introduction, establishment, and initial spread) are usually poorly documented, limiting our understanding of post-introduction dispersal and the role of humans in invasive spread. We aim to assess a new approach to retrospectively understand spatio-temporal patterns of introduction, establishment, dispersal, and spread in biological invasions, using the case study of an ongoing invasion of the Indian bullfrog (*Hoplobatachus tigerinus*) on the Andaman archipelago, Bay of Bengal. We sampled 91 villages on eight human inhabited islands of the Andaman archipelago from 2015-2016. We assessed the occurrence of the bullfrog using visual encounter surveys and recorded the invasion history (year of establishment, source site, and dispersal pathway) for each site by surveying 892 key informants (farmers, plantation workers, and aqua-culturists). We sought to corroborate the reconstructed invasion history with false positive occupancy modelling, using site specific covariates that corresponded to hypotheses on specific dispersal pathways. The bullfrog occurred in at least 62% of the sampled sites spread over six islands, a dramatic increase to the previously known invaded range. The bullfrog was most likely introduced in early 2000s, and its exponential expansion has occurred since 2009. ‘Contaminants’ of fish culture trade and intentional ‘release’ were reported to be the primary pathways of introduction and post-introduction dispersal, facilitating introductions from the Indian mainland and inter-island transfers. False-positive occupancy modelling confirmed that three sites on the archipelago influenced the invasion disproportionately by acting as dispersal hubs. The study elucidates the efficacy of using public surveys to identify dispersal pathways and hubs, and to understand invasive spread, when such information is typically unavailable otherwise. The proposed approach is scalable to other systems and species.

INTRODUCTION

The role of humans in species dispersal is of interest to both conservation biology and invasion biology (Trakhtenbrot et al., 2005). With globally accelerating rates of biological invasions (Seebens et al., 2017) and their consequent negative impacts (Simberloff et al., 2013), it is imperative to understand the processes governing human mediated introduction of species and subsequent dispersal within their non-native range (Hulme, 2009; Wilson et al., 2009). The success of risk assessment, biosecurity, early detection, eradication and control actions depend on the knowledge of invasive species dispersal pathways (Hulme 2015; Essl et al., 2015; Pergl et al., 2017). Acknowledging this, global and regional strategies aiming to manage invasions now aim to identify, prioritize, and manage human mediated introduction and dispersal pathways (CBD 2014; Genovesi et al., 2015).

The early stages of invasions (e.g. introduction, establishment, and initial spread) are often not well documented (Puth & Post 2005) in comparison to the latter stage of invasive dominance, where impacts often become apparent (Blackburn et al., 2011), and in turn generate research attention. As an invasion progresses towards the latter stages, information regarding spatio-temporal patterns of distribution and dispersal in the early stages may be lost. This is particularly relevant for invasions resulting from accidental dispersal pathways. Nevertheless, understanding the processes leading up to exponential invasive spread could lead to better management of potential new invasions. To this end, several approaches have been formulated to study invasions retrospectively, relying on genetic tools (Fitzpatrick et al., 2012), individual based models (Vimercati et al. 2017), herbarium/museum specimens (Loo et al., 2007), and more frequently on published or unpublished 'first observation' records (Zhulidov et al., 2010; Nunes et al., 2015; Horvitz et al., 2017). However, there are limitations to each of these approaches. Although genetic information can help determine source populations, it may have limited power to elucidate invasion history (see Barun et al., 2013); individual based models may be highly data intensive; museum/herbarium records and literature may be subject to bias (e.g. taxonomic or sampling bias, McGeoch et al., 2012; or bias in time of collection and detection, Aikio et al., 2010). New approaches such as geographic profiling can provide leads on likely source populations using sightings of the species by various sources (including passive observations by members of the public, Faulkner et al., 2016). Historical ecology is also seen as a potential window to understand the spatio-temporal dynamics of long-term invasions (Clavero & Villero, 2014; Van Sittert & Measey, 2016).

Public surveys have been used in invasion science to assess distribution (Goldstein et al., 2014; Crall et al., 2015), public attitude towards management (Bremner & Park 2007), risk assessment (Chown et al., 2012), and the ability of the public to identify invasive species (Somaweera et al., 2010). Li et al. (2011) determine residence time of invasive American bullfrogs *Lithobates catesbeianus* in 65 water bodies using interviews of local residents, albeit with a small sample size (1-3 interviews per site). Positive public perception may lead to intentional introductions (e.g. the introduction of "pretty" plants as ornamentals, Reichard and White 2001 or "cute" animals as pets, Kikillus et al., 2012) and negative perception may lead to voluntary management (Somaweera et al., 2010). Assessing this perception is also essential for management in human inhabited landscapes (Sharp et al., 2011).

Public surveys can be a potential tool to reconstruct invasion history but should be corroborated with field observations to ensure reliability. False-positive occupancy modelling can incorporate both field observations and key informant data (Miller et al., 2011; Pillay et al. 2014; Chambert et al., 2015) and can be applied to reliably and rapidly estimate distributions of invasive species (Mohanty et al., 2018). In the present study, we combine key informant and visual encounter surveys using multi-method false positive occupancy models (Miller et al., 2011; Mohanty et al., 2018), such that the visual encounter surveys are used to validate key informant responses on both detection/non-detection and spatial information on the invasion.

We explore this approach with the case study of an anuran amphibian invasion on the Andaman Islands, Bay of Bengal. In doing so, we also aim to contribute to the relatively understudied subject of amphibian invasions (Pyšek et al., 2008), which have considerable impact on native biodiversity (Kraus, 2015), comparable to that of invasive freshwater fish and birds (Measey et al., 2016). Common introduction pathways (and probable post-introduction dispersal pathways) in amphibians are cargo and the nursery trade, along with intentional pet trade and culture for human consumption (Kraus, 2007). Although studies on amphibian invasions have increased noticeably in the last decade, three species (the cane toad *Rhinella marina*, the American bullfrog *Lithobates catesbeianus*, and the African clawed frog *Xenopus laevis*) account for nearly 80% of published research; knowledge on dispersal is lacking for most amphibian invasions.

The invasion of the Indian bullfrog *Hoplobatrachus tigerinus* on the Andaman Islands was reported recently (Harikrishnan & Vasudevan, 2013). This ‘first report’ identified an introduction in 2009-10 from the Indian mainland. This large dicroglossid frog is expected to have impacts, through predation and competition, on small vertebrates of the Andaman archipelago (Mohanty and Measey, 2018), part of the Indo-Burma global biodiversity hotspot (Myers et al., 2000). In this study, we aimed to assess our novel approach to reconstruct spatio-temporal patterns of introduction, establishment, dispersal, and spread using the case study of the ongoing invasion of the Indian bullfrog. We aimed to i) assess the current distribution of the invasive bullfrog population on the Andaman archipelago using a combination of key informant surveys and field surveys, ii) determine its introduction and post-introduction dispersal pathways based on key informant surveys, and iii) assess temporal changes in distribution and dispersal using both key informant surveys and field surveys. In addition, we evaluate the public perception of the species in the local community. We use this case study to explore the use of public surveys as a complementary tool in generating invasion history, especially for dispersal and spread.

METHODS

Study Species

The Indian bullfrog, *Hoplobatrachus tigerinus* (Daudin, 1802), has its native range on the Indian sub-continent encompassing low to moderate elevations in Nepal, Bhutan, Myanmar, Bangladesh, India, Pakistan, and Afghanistan (Dutta, 1997). This large bodied frog (up to 160 mm) has high reproductive potential (up to 5750 eggs per clutch, once per year; Oliveira et al., 2017) and is uncommon or absent in forested and coastal regions, but occurs as a human commensal (Daniels, 2005). The bullfrog has been introduced to Madagascar (Glaw & Vences, 2007), and possibly to the Maldives (Dutta, 1997) and Laccadive Islands (Gardiner, 1906). It was reported to occur in two sites on Middle Andaman and South Andaman Island (Webi and Wandoor; Harikrishnan & Vasudevan, 2013), followed by observations on Havelock and Neil islands (Rangaswamy et al., 2014). Intentional human-assisted dispersal reportedly occurred within the Andaman archipelago, along with confirmed establishment in at least two locations, indicating the beginning of an invasion (Harikrishnan & Vasudevan, 2013). Since these initial reports, no systematic studies have been carried out into the bullfrog invasion and there is a lack of critical information on distribution and dispersal of the species on the Andaman Islands. Moreover, museum specimens and citizen science records are unavailable.

Study Area

The Andaman Islands, in the Bay of Bengal, are situated 1200 km to the east of the Indian mainland, ranging from 10°30’N to 13°40’N, and from 92°10’E to 93°10’E. This tropical island group, comprising of ca. 300 islands, is part of the Indo-Burma global biodiversity hotspot (Myers et al., 2000). The majority of the landmass is accounted for by eight islands with major human habitations (Table 2.1) and the mostly uninhabited Interview and Rutland islands (Forest Statistics, 2013). Primary and secondary forests encompass nearly 87% of the entire archipelago, falling under several protection regimes of Protected Areas and Tribal Reserves (Forest Statistics, 2013). Roughly 40% of the reptiles and amphibians (n = 53) are endemic to the Islands (Harikrishnan et al., 2010). Several introduced invertebrates and vertebrates also occur, including fishes, mammals, birds and reptiles (Mohanraj et al., 1997; Rajan & Pramod, 2013); the Indian bullfrog was the first non-native amphibian to be reported (Harikrishnan & Vasudevan, 2013). The human population on the archipelago is approximately 344,000 people (Directorate of Economics and Statistics, 2013), distributed across the eight islands with major human habitations; settlements are mostly comprised of villages along with one or more towns on each island. Agriculture and aquaculture (subsistence and commercial) are widely practised in the archipelago; most villages have artificial ponds for aquaculture and sustenance.

Study Design

The reconstruction approach involves three key components: i) false-positive occupancy modelling of current invasive distribution using key informant and visual encounter surveys, ii) generating information on ‘time of establishment’ (and consequently spread rate) and dispersal pathways from only key informant surveys, and iii) using spatial information (‘source sites’) obtained from key informant surveys in false-positive occupancy models to corroborate key informant data with field observations.

The first report of the bullfrog on the Andaman Islands described populations occurring in two villages of Middle and South Andaman Islands (Harikrishnan & Vasudevan, 2013), and no occurrence on uninhabited islands (Rangaswamy et al., 2014; Harikrishnan & Vasudevan, 2015). Given the synanthropic nature of the species (Daniels, 2005), we assume that the bullfrog would most likely occur in human-modified areas if they were present in a region. For example, if a region containing the bullfrog encompasses forests and adjoining villages, we assume that individuals will at least be present in the villages. Under this assumption, we defined a village with natural boundaries (forests, and not administrative boundaries) as the observational unit to sample for occurrence and invasion history. This strategy was further informed by the probable intentional dispersal of the bullfrog, from one village to another, in the region (Harikrishnan & Vasudevan, 2013). We identified 101 villages on the archipelago, but we were unable to sample in ten villages due to poor accessibility. Overall, we sampled 91 villages on eight human inhabited islands of the archipelago from 2015-2016. Sampling consisted of two components: i) visual encounter surveys to determine occurrence and ii) key informant surveys to generate invasion history.

Two personnel carried out visual encounter surveys in the evenings (starting any time between 1800h-2000h), searching for bullfrogs near water bodies, agricultural fields, and plantations (preferred habitats; Daniels, 2005). In those cases where bullfrogs were not detected on the first survey, we sampled again on a second evening. The survey ended upon confirming presence or continued for a minimum of 1 hour. We could carry out visual encounter surveys in 84 villages (92% of total; Table 2.1), due to logistical constraints of sampling in the evening at certain locations.

We conducted 892 key informant surveys in all 91 selected villages (with an average of ca. 9.8 participants (SD = 1.38, range: 4–15) per village; Table 2.1). Our aim was to survey ten respondents per site (given that most villages are small with 50-100 households) in order to attain convergence in responses. Key informants were defined as farmers, plantation workers, and aqua-culturists, i.e. those who engage with outdoor work on a daily basis and are likely to encounter the target species. We found and selected key informants by searching for people working in ponds, agricultural fields, and plantations or by enquiring for their profession on visiting their household. We conducted surveys individually and attempted to cover most areas of a village, in order to avoid clustered samples. The surveys aimed to obtain information on bullfrog occurrence, invasion history (e.g. time of first observation, vector and source of introduction/post-introduction dispersal), and perception of the species (e.g. beneficial, harmful; Supplementary Information 1) for each site. To avoid cross-contamination of responses, we sought answers only regarding the village of the respondent. When participants provided information on the introduction of bullfrogs through intentional release, we attempted to follow up with the personnel involved in the actual introduction to gather further details. The median age of the participants was 42 (17-85); the survey included 123 females (14%) and 18 anonymous respondents, which reflected the existing gender bias of the categories of key informants targeted. The surveys were a combination of structured and semi-structured questions and carried out in the local languages (Hindi, Bengali, and Tamil). We showed respondents photographs of the Indian bullfrog (adult) to assist with the question ‘Have you sighted this frog in this particular village?’ (Supplementary Information 1). Verification was carried out based on the local name, morphological features, and behaviour in order to avoid bias in species identification. As the bullfrog’s large body size, greenish-brown colouration, and guttural vocalizations are markedly different from that of native frogs, respondents were provided further information to aid in identification, only upon request.

Table 2.1 Sampling effort for key informant surveys and visual encounter surveys on the Indian bullfrog *Hoplobatrachus tigerinus*, at 91 sites on eight human inhabited islands of the Andaman archipelago, from 2015 to 2016.

Island	**Size (km^2)**	**Sites**	**Respondents/Site (SD)**	**Sites with Field Survey**	**Sites Detected**
North Andaman	1375.99	29	9.66(1.54)	27	23
Middle Andaman	1535.5	27	10.19(1.11)	27	26
Long	17.9	1	7	0	-
Baratang	297.6	5	9(2.35)	4	0
Havelock	113.93	5	10.8(1.79)	5	5
Neil	18.9	2	10.5(0.71)	2	2
South Andaman	1348.2	13	9.62(1.26)	13	1
Little Andaman	734.39	9	9.44(1.13)	6	0

Data Analysis

For analyses on invasion history, we did not include sites with only one report of presence by key informants (n = 4), to reduce uncertainty. We also did not consider responses where the participant answered a question with a rider of ‘uncertain’. We generated invasion history for each site from key informant surveys with respect to time of first observation, introduction/dispersal vector, and source site, by obtaining modal responses to each question (Supplementary Information 1). We considered the modal value (instead of the average; Li et al., 2011) of first observations per site to indicate time of establishment of the bullfrog in that site. Based on the time of establishment, we assigned each site to one of five time periods, each of three years duration (i.e. 2001-03, 2004-06, 2007-09, 2010-12, and 2013-15). We evaluated the increase in the number of sites with bullfrogs, across the five time periods, using linear, exponential, and logistic growth curves.

Information on introduction/dispersal vector and source site were classified as 'uncertain' if more than 50% of the respondents did not answer the question on introduction/dispersal vector (Fig. 2.3). As the question on source site was nested within introduction/dispersal vector, the proportion of respondents for each question was analysed step-wise. We also extracted independent introduction events from public surveys by considering the reported source site and recipient site, and the reported personnel involved; this information was validated with the actual personnel who carried out the introduction. We analysed the responses on perception toward the bullfrog by considering each response as an individual datum; we compared responses across two time periods signifying relatively old (2001-2009) and new invasions (2010 onwards) using a Wilcoxon signed rank test in the statistical software R 3.4.1 (R Core Team, 2017). Even though, two questions regarding the perception were semi-structured, we categorized similar responses post hoc. All GIS based analyses were carried out on ArcGIS 10.3.1 (ESRI, 2012).

We constructed occupancy models to estimate site-specific occupancy and to test for the likelihood of potential dispersal pathways. Following Mohanty et al. (2018), we addressed the possibility of false positive detections in the public surveys using multi-method false positive occupancy models (Miller et al., 2011) along with the standard McKenzie models (MacKenzie et al., 2002), in the program PRESENCE 6.4 (Hines, 2010). We built a detection/non-detection matrix consisting of both key informant observations (uncertain data) and one field observation (certain data) per site. All detection/non-detection observations used for the occupancy models belonged to the same time period (2015-16). For false-positive models, we assumed that 'certain data' did not contain false-positives. To model this assumption, we fixed the parameter 'b' (probability that a detection is classified as certain when the site is occupied, and the species is detected) for all occasions to 0; 'P_{10}' (probability of detecting the species at a site when the site is unoccupied) was fixed to 0only for field observations. We did not estimate differential true-positive detection probability (P_{11}) for key informant and field surveys, as we did not carry out multiple field surveys of the same site. We estimated occupancy rate (ψ), true-positive probability, false-positive probability, and associated 95% confidence intervals.

We included seven site specific covariates in the models, representing dispersal pathways (sensu Hulme et al., 2008), to model occupancy; the covariates included distances to the nearest port (stowaway in shipping), major road (stowaway in transport and unaided), town (stowaway in trade), and three ‘dispersal hubs’, individually and together (local influence through any dispersal pathway). A ‘dispersal hub’ (see Results) was defined as a site that served as the origin of multiple dispersals in the invaded range, based on the reported source (modal response) of each site. Dispersal hubs were defined to be distinct from ‘introduction hubs’, which were defined as sites with multiple introductions originating from them, located outside the invaded range of the Andaman archipelago. In all, we built 16 candidate models and used the Akaike information criterion (AIC; Burnham & Anderson, 2002) to select suitable models.

RESULTS

From visual encounter surveys (2015-16), we detected the Indian bullfrog in 57 villages, located on five of the eight sampled islands, with no detections obtained from Baratang, Long, and Little Andaman Islands (Table 2.1). A new population of Indian bullfrog was observed on Little Andaman Island in 2018. Of the 16 candidate models, the false positive multi-method model with the covariate ‘distance to nearest dispersal hub’ was chosen as the most suitable (Table 2.2). Site-specific occupancy estimates were higher on North and Middle Andaman as compared to Neil, Havelock, and South Andaman Islands (Fig. 2.1). Models which accounted for false positive detection performed better in terms of AIC, although the overall occupancy rate overlapped between the standard constant detection model and the standard false positive model (Table 2.2). The best model estimated a true positive detection probability (P_{11}) of 0.93 (0.90-0.95) and a false positive detection probability (P_{10}) of 0.04 (0.02-0.08; Table 2.2).

Respondents reported presence of the bullfrog on the Andaman archipelago as far back as 2000-01, and establishment in seven sites up to 2009. A further 29 sites were reported from 2010-12, and another 23 sites from 2013-15 (Fig. 2.2, Fig. 2.3). An exponential curve ($R^2 = 0.77$, $y = 0.47e^{0.83x}$) best fitted the increase of sites with bullfrogs over the five time periods. *Contamination* of fish stocks with bullfrog propagules (eggs and tadpoles; hereafter ‘fish culture’) was reported to be a major mode of introduction and post-introduction dispersal within the archipelago. Intentional capture-release of post-metamorphic individuals (hereafter, ‘*release*’) was reported to operate only as a major mode of post-introduction dispersal (Fig. 2.2, Fig. 2.3). Post-introduction, natural dispersal through flood-waters and stowaways in transport of cargo was also mentioned. Fish culture was reported in more sites than release, which was only noted in sites post 2009 (Fig. 2.2, Fig. 2.3). Respondents suggested that private traders were the source of fish stocks from the Indian mainland, as well as the Department of Fisheries, and local self-government organizations (*Panchayat*).

The public surveys detected 17 independent releases to 14 sites (Fig. 2.3), from a total of 38 responses. The release events moved the bullfrog over an average distance of 47.48 km (SE = 11.81, range: 6.2 – 188 km). The stated purpose behind five such releases was consumption (3 events, including one escape) and novelty (2 events), while information about the others were unavailable. We recorded release events in four sites where the majority of respondents claimed fish culture as the source.

Figure 2.1 Site-specific occupancy estimates of the invasive Indian bullfrog *Hoplobatrachus tigerinus* at 91 villages on the Andaman archipelago. Colour gradient (green to red) denotes the occupancy estimates ranging from 0 to 1. Best predictor of occupancy is distance to nearest 'dispersal hub', defined as sites acting as sources for multiple transfers within the archipelago (labelled).

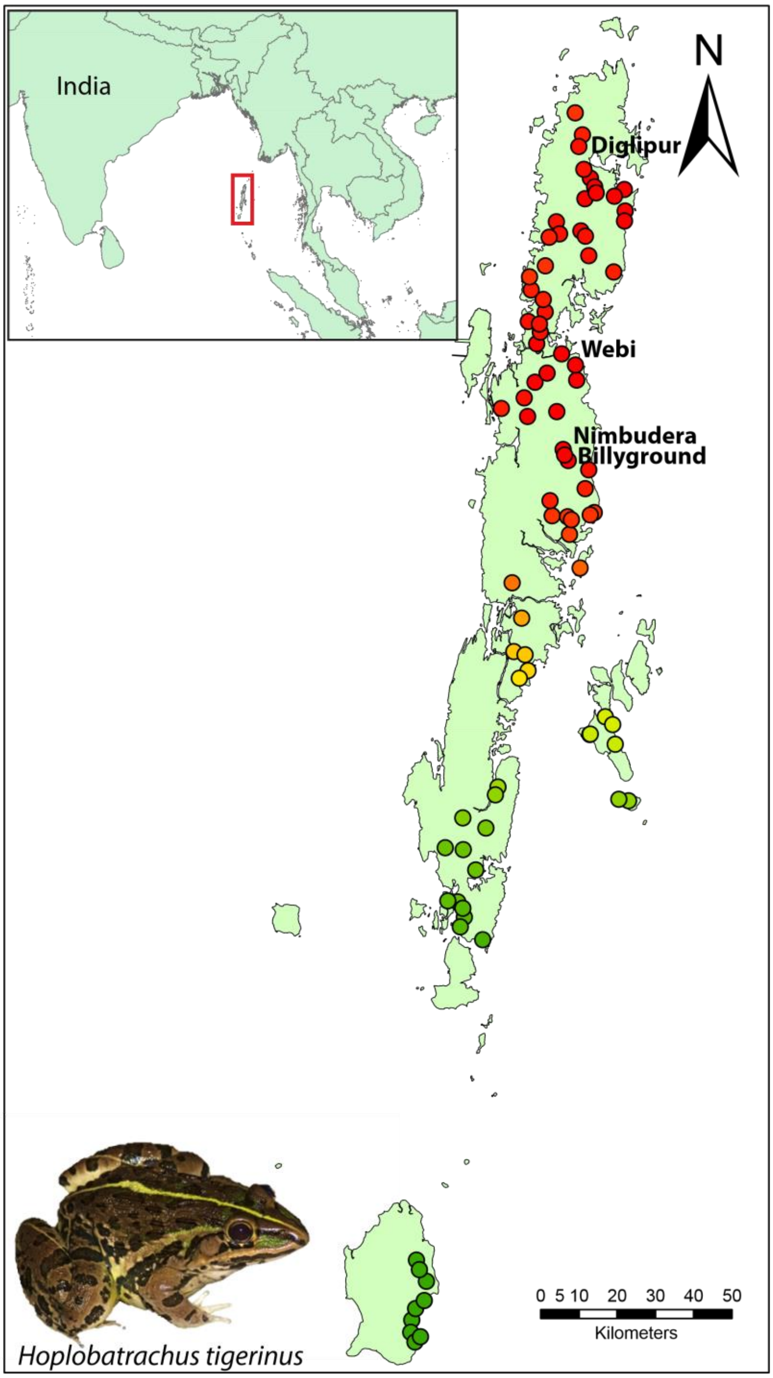
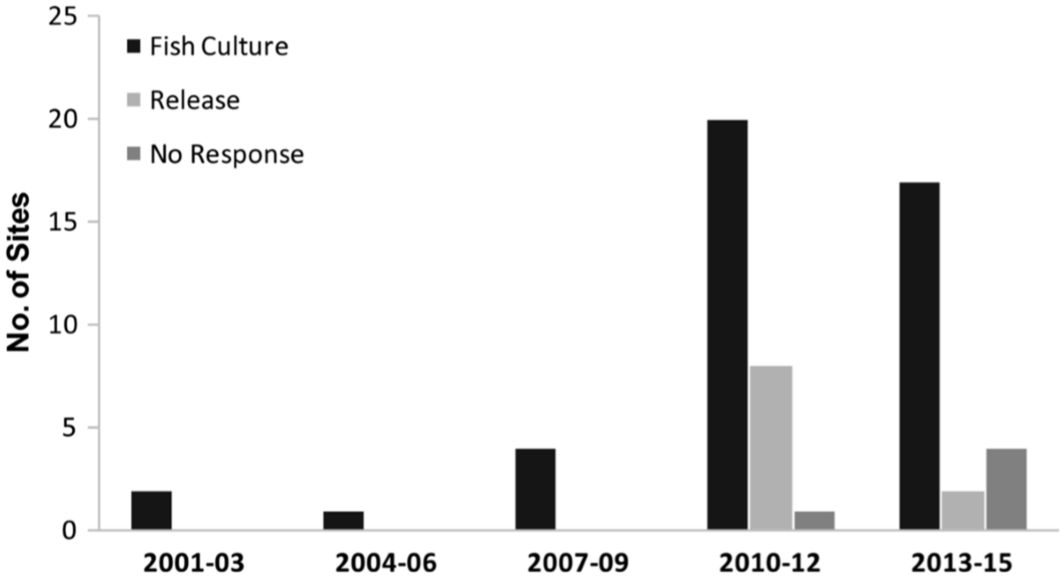


Figure 2.2 Number of villages with established populations of the Indian bullfrog *Hoplobatrachus tigerinus* on the Andaman Islands across five time periods (from 2001 to 2015), as reported by key informants. Columns for each time period separated based on the reported dispersal pathway; pre-metamorphic bullfrogs as contaminant of fish culture (‘fish culture’), post-metamorphic bullfrogs capture-released (‘release’), and sites with no responses on dispersal.



‘Introduction hubs’ included West Bengal and unidentified locations on the Indian mainland and were reported for the fish culture pathway only. We identified three ‘dispersal hubs’ on the Andaman archipelago - Billyground-Nimbudera cluster, Diglipur, and Webi (Fig. 2.3); Webi was reportedly associated with the release pathway, while the remaining two sites acted as sources of both the fish culture and release pathways. Based on the selected occupancy model (Table 2.2), villages nearer to any of the dispersal hubs had higher site specific-occupancy as compared to sites farther from the hubs (Fig. 2.1).

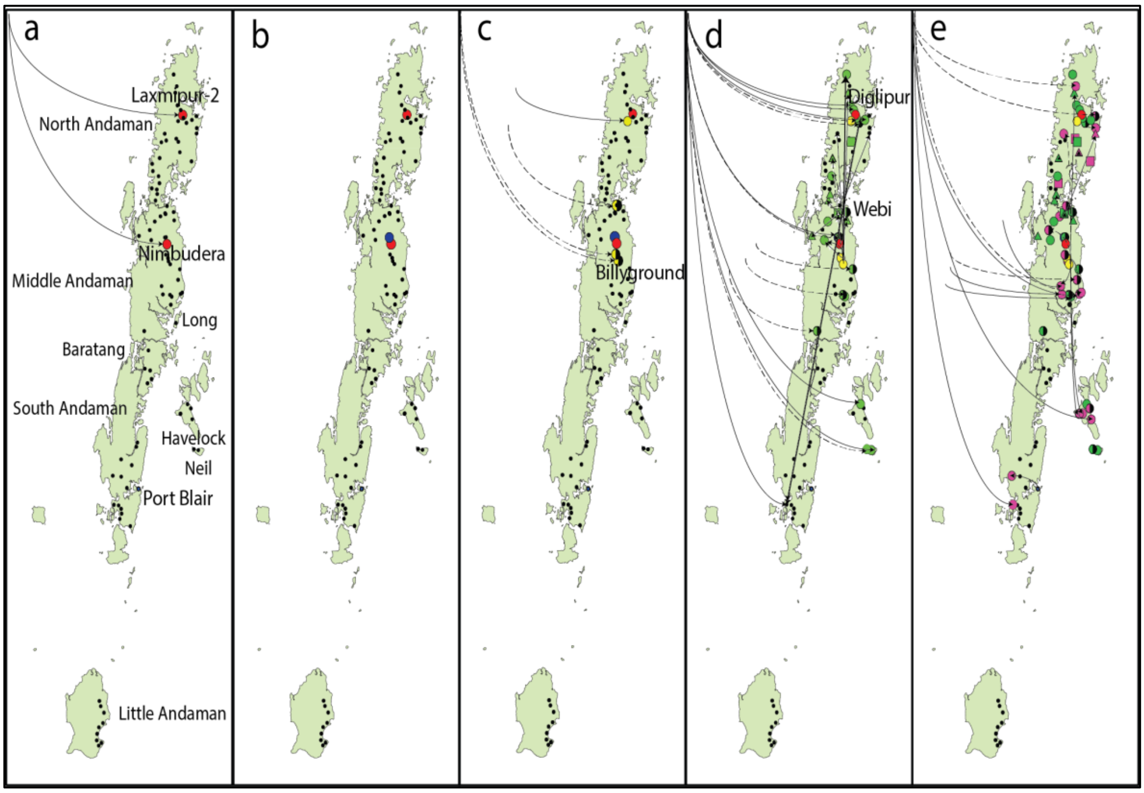
The majority of respondents reported only negative impacts of the bullfrog, followed by those who reported both negative impacts and benefits, those who were neutral, and finally those who only reported benefits (Fig. 2.4). Perception of respondents was not found to differ in sites with old and new invasions (V ~ 0, p = 0.99; Fig. 2.4). The most frequently reported negative impact was that the bullfrog preys on poultry and aquaculture fish (though water contamination was reported once). Predation on centipedes (*Scolopendra* spp.), snakes, and crop pests was also cited as a benefit. Of the 510 respondents we questioned on whether they consumed the bullfrog, 82.7% said no, 15.8% said yes, and 1.4% did not answer; most of those who reportedly consumed the bullfrog were concentrated in Middle Andaman. On the question of whether the respondent culled the bullfrog (n = 477), 66.8% said no, 32.8% said yes, and 1.3% did not answer.

Table 2.2. Models explaining the occurrence of the Indian bullfrog *Hoplobatrachus tigerinus* at 91 sites on the Andaman archipelago, with estimates of occupancy (psi or ψ), true positive detection probability, and false positive detection probability along with 95% confidence intervals.

Model	**AIC**	**Occupancy (ψ)**	**True-positive (p_{11})**	**False-positive (p_{10})**
psi(source),p(.),p_{10}(.),b(.)**	507.71	site-specific	0.93 (0.90 - 0.95)	0.04 (0.02 - 0.08)
psi(Webi),p(.),p_{10}(.),b(.)	512.11	site-specific	0.93 (0.91 - 0.95)	0.04 (0.03 - 0.08)
psi(Diglipur),p(.),p_{10}(.),b(.)	513.54	site-specific	0.93 (0.90 - 0.95)	0.04 (0.02 - 0.08)
psi(BG-ND),p(.),p_{10}(.),b(.)	514.41	site-specific	0.93 (0.91 - 0.95)	0.04 (0.03 - 0.08)
psi(port),p(.),p_{10}(.),b(.)	551.66	site-specific	0.93 (0.91 - 0.95)	0.04 (0.03 - 0.07)
psi(town),p(.),p_{10}(.),b(.)	551.66	site-specific	0.93 (0.91 - 0.95)	0.04 (0.03 - 0.07)
psi(.),p(.),p_{10}(.),b(.)	554.01	0.63 (0.52 - 0.72)	0.93 (0.91 - 0.95)	0.04 (0.03 - 0.08)
psi(road),p(.),p_{10}(.),b(.)	582.75	site-specific	0.92 (0.89 - 0.94)	0.04 (0.03 - 0.08)
psi(source),p(.)	705.23	site-specific	0.84(0.81 - 0.87)	-
psi(Diglipur),p(.)	705.54	site-specific	0.84(0.81 - 0.87)	-
psi(Webi),p(.)	706.71	site-specific	0.84(0.81 - 0.87)	-
psi(BG-ND),p(.)	709.98	site-specific	0.84(0.81 - 0.87)	-
psi(.),p(.)	720.03	0.71 (0.61 - 0.80)	0.84(0.81 - 0.87)	-
psi(port),p(.)	728.95	site-specific	0.84(0.81 - 0.87)	-
psi(town),p(.)	728.97	site-specific	0.84(0.81 - 0.87)	-
psi(road),p(.)	749.84	site-specific	0.83(0.80 - 0.86)	-

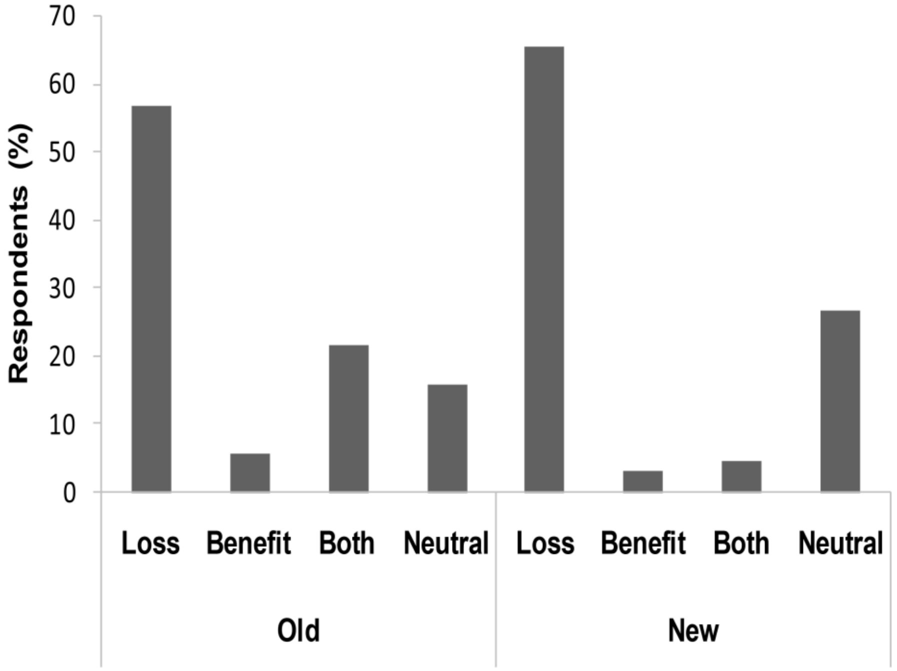
Site-specific covariates include distance to nearest – port, town, major road, three dispersal hubs individually and in combination. Dispersal hubs are defined as source sites for more than one introduction and include BG-ND (Billyground-Nimbudera cluster), Webi, and Diglipur; 'source' denotes distance to nearest dispersal hub. *b – probability that a detection is classified as certain when the site is occupied, and the species is detected; **best model based on AIC values.

Figure 2.3 Villages with established populations of the Indian bullfrog *Hoplobatrachus tigerinus* on the Andaman Islands, as reported by key informants, in a) 2001-03, b) 2004-06, c) 2007-09, d) 2010-12, and e) 2013-15.



Coloured symbols indicate new populations reported in each time period, with colours of each time period being fixed in the following periods. Circles denote fish culture as the most reported pathway, triangles denote release, and squares denote no response. Half-filled symbols indicate uncertainty in dispersal information (less than 50% responses). The direction of introduction and dispersal pathways is marked with arc line (fish culture) and straight line (release), where dotted lines indicate uncertainty in source. Arc lines with from the top-left corners represent West Bengal, India as the source and lines with uncertain origins indicate unknown location on the Indian mainland as the source. Dispersal hubs, sites which serve as origins for multiple dispersals, are labelled as Diglipur, Webi, and Billyground-Nimbudera.

Fig. 2.4 Perceptions of key informants on benefit and/or negative impacts incurred due to the Indian bullfrog *Hoplobatrachus tigerinus*, in sites where established bullfrog populations up until 2009 (old) and after (new).



DISCUSSION

We found our novel approach to reconstruct invasion history to be effective in the case of the Indian bullfrog's invasion on the Andaman Islands. Our approach helps define the processes underlying introduction (introduction pathways) and the expansion phases (specific dispersal pathways and hubs), which are rarely documented (Puth & Post, 2005). The approach enabled us to estimate the current distribution of the invasive bullfrog based on both key informant and visual encounter surveys (Fig. 2.1), to reconstruct the spread of the bullfrog over five time periods (Fig. 2.2) and describe dispersal pathways (Fig. 3) using key informant surveys, and finally corroborate the significance of 'dispersal hubs' in facilitating the invasion (Table 2.2; Fig. 2.1) by integrating spatial information from the key informant data into occupancy models. The reconstruction provides insights into the multi-faceted nature of spread in the early stages through human aided dispersal. This approach also circumvents the scarcity of museum records and publications, which may be the case with relatively new invasions or as a result of taxonomic and geographic biases in invasion science (Pyšek et al., 2008).

The overall occupancy rate of 0.63 (0.52 - 0.72), obtained from the false-positive occupancy model (Table 2.2) is highly similar to field survey data which find the bullfrog to occur in at least 62% of the sampled villages spread over six islands. This is a dramatic increase on the previously known invaded range (reported only in Harikrishnan & Vasudevan, 2013; Rangaswamy et al., 2014) and is due to the fact that the previous studies were broad herpetofaunal assessments, focussing mostly on forested areas, whereas we specifically chose human modified areas based on existing literature describing the synanthropic nature of the species (Daniels, 2005). However, invasive populations may occupy a broader niche as compared to their native range (Pearman et al., 2008) and the occurrence of the bullfrog in primary and secondary forests still needs to be assessed. The observations of a few individuals along forest streams (Harikrishnan & Vasudevan, 2013) must also be validated.

The low probability of false positive detections at 4% (2 – 8%; Table 2.2) indicate the suitability of the selected participants (Mohanty et al., 2018). The bullfrog’s distinctly large size as compared to native amphibians (three to five times larger), its use of human modified habitats and interactions with the public (positive and negative) is likely to positively influence the accuracy of identifications (Mohanty et al., 2018). It is important to note that high identification accuracy may not always be the case; Somaweera et al. (2010) found that 20.5% of the general public failed to distinguish between invasive cane toad (*Rhinella marina*) and native frogs in Australia. Identification was more accurate in the case of adult males, when the respondent lived in areas invaded by the cane toad or the respondent had prior training (Somaweera et al., 2010). Therefore, the suitability of respondents, preferably key informants who are most likely to encounter the species, must be validated. It is not necessary for the invasive species in question to be restricted to human modified areas, as selection of appropriate respondents can address the issue of sampling coverage (e.g. wildlife personnel, Pillay et al., 2014).

We reconstructed the time of establishment of the bullfrog at each site using the data obtained with the public surveys. A critical issue to consider while undertaking such surveys is recall bias, which could arise out of a combination of cognitive processes (Connelly et al., 2000; Beaman et al., 2005). The longer back in time a respondent is asked to recall events, the greater the chances of inaccuracy (Coughlin, 1990). Additionally, dramatic events (such as the December 2004 tsunami that had great impact in the region) may alter recall patterns and lead people to gravitate towards such events. We addressed the issue of accuracy by making our comparison categories broad (of three years instead of one). Though we encouraged people to assign a year or period (instead of stating how many years ago) to their first observation of the bullfrog, we had no control over the potential tendency to gravitate towards the tsunami as a temporal reference. However, we find no evidence of distortion of recall by the tsunami, probably because the invasion occurred in most sites only after 2009. It is important to assess the applicability of our approach in moderately old invasions (up to one human generation) and address recall bias.

The invasion of the bullfrog on the Andaman Islands displays a lag phase (2000-09) followed by an exponential expansion phase after 2009, a curve typical of biological invasions (van Wilgen et al., 2014). It is noteworthy that the first published record of the bullfrog on the Andaman Islands was in 2013 (by the time 40% of the sites were invaded, Harikrishnan & Vasudevan, 2013), even though the local community was aware of it much earlier. Similar observations have been made in the case of invasions elsewhere (Wells, 1974), and indicate the difficulty of directly studying invasions in the early stages (Hyndman et al., 2015).

Unintentional human-mediated dispersal of amphibians is common (García-Díaz & Cassey, 2014) and can accelerate invasions (Kraus & Campbell, 2002). The role of the fish culture pathway (a known pathway in amphibian invasions; Christy et al., 2007) in the introduction and post-introduction dispersal of the bullfrog is plausible given the widespread practice of fish culture for commercial and sustenance purposes in the Islands, and that the identified dispersal hubs export fish fingerling stocks. However, we do not have direct evidence of contamination and cannot confirm the reported spatio-temporal prevalence of the fish culture pathway. This purported fish culture pathway is associated with uncertainty, since it is based on respondents' interpretation of appearance of the bullfrog at a site in conjunction with low fish turnover per unit fingerling stock released. Such a perception could be a ‘shared narrative’ (Middleton, 2012) across the Islands, though it is unlikely to operate at the large extent over which we carried out the study.

The deliberate release for consumption and novelty is known to operate frequently as a pathway in amphibian invasions (Kaiser et al., 2002; Measey et al., 2017), and vertebrate invasions in general (Hulme, 2009). Similar to our findings, Ficetola et al. (2007) describe the significant role of ‘personal initiatives’ in the invasion of the American bullfrog (*Lithobates catesbeianus*) in Europe. Such intentional releases can move individuals over long distances (Ficetola et al., 2007; Nunes et al., 2015) and increase the likelihood of establishment (Liu et al., 2012).

Overall, the combination of these two pathways occurring frequently is likely to have resulted in the initial spread (2001-09), where after a few sites served as dispersal hubs for new introductions triggering the exponential expansion phase. The role of dispersal hubs is particularly likely upon considering the parallel evidence from respondents and occupancy analysis. Floerl et al. (2009) theoretically demonstrated the importance of such ‘hubs’ in rapidly propagating invasions to secondary sites. Lakes serving as hubs for non-native zooplankton and zebra mussel invasion to secondary lakes and streams have been identified to inform better management (Kraft et al., 2002; Muirhead and MacIsaac, 2005). The chosen best model (Table 2.2) suggests that villages which were closer to any one of the three dispersal hubs were more likely to have the bullfrog than villages farther away (e.g. South Andaman and Little Andaman). Further, the models which specified a dispersal hub performed better than the models representing other common pathways such as *stowaway* and *unaided* dispersal due to trade and habitat disturbance. The future of the currently unmanaged invasion may depend on new dispersal hubs for the hitherto uninvaded sites (Murray et al., 2015) on Baratang, South Andaman, and the Nicobar archipelago and on the recently invaded Little Andaman Island (ca. 2018). South Andaman has only one site with confirmed bullfrog presence (Wandoor), which may serve as a source for the release pathway, but not for the fish culture pathway given that no commercial aquaculture is practised in the village.

Though leading-edge dispersal may occur between sites, alone it does not explain the spread across multiple islands (Liu et al., 2014), the short lag phase, and the continuing exponential expansion phase (Suarez et al., 2001). Under a scenario of only natural dispersal, assuming that salt water barriers between islands are overcome (e.g. by vegetation rafts; Bell et al., 2015), the origin point in new islands should be closest to the nearest point across the barrier. However, the observed pattern of spread does not support this notion (Fig. 2.3). Further, the recorded release events moved the bullfrog over long distances (48 km on an average), some of which may have resulted in establishment. We infer that multiple human mediated jump dispersals, both intentional and accidental, have occurred (and probably continue to occur) within and between islands, possibly combined with an active pathway (fish culture) between the Indian mainland and the Andaman Islands. The influence of human mediated dispersal is particularly strong in the case of herpetofauna in archipelagos, where natural salt water barriers are frequently breached by human assistance (Liu et al., 2014).

The reported negative perception of the bullfrog among the majority of the respondents reflects apprehensions of its negative impact on two household level economies, aquaculture and poultry. This potential impact must be quantified and considered while assessing the overall economic impact of the species (Bacher et al., 2018). The stated reasons for benefit (pest control) and negative impact (threat to economy) are not unfounded, as there are records of the bullfrog preying on fish, poultry, crop pests, and scolopendian centipedes in the region (Mohanty & Measey, 2018). Voluntary culling of the bullfrog by private citizens reflect the perceived negative impact (as with *Rhinella marina*, Somaweera et al., 2010), whereas the geographic concentration in consumption pattern may be due to local cultural factors.

CONCLUSION

Biological invasions, by definition, encompass humans as a key component. Yet the potential of using human knowledge to aid in reconstruction of invasions has been underappreciated. We show the utility of public surveys in identifying pathways, dispersal hubs, and understanding spatio-temporal changes in invasive spread. In addition, such surveys provide an opportunity to assess economic impacts and human perceptions for impact assessments (Bacher et al., 2018). We believe that our approach is scalable to other systems and species, as long as the subject is easily identified by the public (or a subset of key informants) and the invasion being reconstructed is relatively recent.

SUPPLEMENTARY INFORMATION 1

Questionnaire used for key informant survey, to assess the invasion history of the Indian bullfrog *Hoplobatrachus tigerinus* on the Andaman Islands.

1. Have you sighted this frog (photograph of Indian bullfrog) in this particular village?
2. Which frog is this? (photograph of Indian bullfrog; verification to be done based on local name, morphology, and mating call)

If identified correctly,

Structured

3. When did you first see the bullfrog in this village? [time of introduction]
4. How did the bullfrog arrive in this village? [mode of introduction]

If by human mode,

5. Where was the bullfrog brought to this village from? [dispersal distance]
6. Who brought it to this village?
7. How many individuals were brought?

Semi-structured

8. Do you incur any benefit due to the bullfrog’s presence in this village? If yes, please explain the benefit.
9. Do you incur any loss due to the bullfrog’s presence in this village? If yes, please explain the loss.
10. Do you kill bullfrogs for any reason? If yes, state the purpose.

3 What's for dinner? Diet and potential trophic impact of an invasive anuran *Hoplobatrachus tigerinus* on the Andaman archipelago

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AUTHOR CONTRIBUTIONS

NPM and JM conceived the idea of the study; NPM collected the data; NPM and JM analysed the data; NPM wrote the manuscript, JM contributed to the writing.

ABSTRACT

Amphibian invasions have considerable detrimental impacts on recipient ecosystems. However, reliable risk analysis of invasive amphibians still requires research on more non-native amphibian species. An invasive population of the Indian bullfrog, *Hoplobatrachus tigerinus*, is currently spreading on the Andaman archipelago and may have significant trophic impacts on native anurans through competition and predation. We carried out diet analyses of the invasive *H. tigerinus* and native anurans, across four habitat types and two seasons; we hypothesized that i) small vertebrates constitute a majority of the *H. tigerinus* diet, particularly, by volume and ii) the diet of *H. tigerinus* significantly overlaps with the diet of native anurans, thereby, leading to potential competition. We assessed the diet of the invasive *Hoplobatrachus tigerinus* (n = 358), and individuals of the genera *Limnonectes* (n = 375) and *Fejervarya* (n = 65) and found a significant dietary overlap of *H. tigerinus* with only *Limnonectes*. Small vertebrates, including several endemic species, constituted the majority of *H. tigerinus* diet by volume, suggesting potential impact by predation. Diets of the three species were mostly governed by the positive relationship between predator-prey body sizes. Individuals of *Hoplobatrachus tigerinus* and *Fejervarya* chose evasive prey, suggesting that these two taxa are mostly ambush predators; individuals of *Limnonectes* chose a

mixture of sedentary and evasive prey indicating that the species employs a combination of 'active search' and 'sit and wait' foraging strategies. All three species of anurans mostly consumed terrestrial prey. This intensive study on a genus of newly invasive amphibian contributes to the knowledge on impacts of amphibian invasions, and elucidates the feeding ecology of *H. tigerinus*, and species of the genera *Limnonectes* and *Fejervarya*. We also stress the necessity to evaluate prey availability and volume in future studies for meaningful insights into diet of amphibians.

INTRODUCTION

Accelerating rates of biological invasions (Seebens et al., 2017) and their consequent negative impacts (Simberloff et al., 2013) have led to increased efforts towards pre-invasion risk assessment and prioritization based on impacts (Blackburn et al., 2014). Amphibian invasions have considerable detrimental impacts on recipient ecosystems (Pitt et al., 2005; Kraus, 2015), the magnitude of impact being comparable to that of invasive freshwater fish and birds (Measey et al., 2016). Impact mechanisms of amphibian invaders remain relatively understudied (Crossland et al., 2008) and are varied. Impact via predation and competition (*sensu* Blackburn et al., 2014) has been documented on invertebrates (Greenlees et al., 2006; Choi & Beard, 2012; Shine 2010), fishes (Lafferty & Page, 1997), amphibians (Kats & Ferrer, 2003; Wu et al., 2005; Measey et al., 2015; Liu et al., 2015; but see Greenlees et al., 2007) and birds (Boland, 2004), though other taxa may also be affected (Beard & Pitt, 2005). Amphibian invaders may carry diseases (e.g. *Batrachochytrium dendrobatidis*; Garner et al., 2006; Liu et al., 2013) and cause reproductive interference (D'Amore et al., 2009), apart from several other ecological impacts (see Kraus, 2015 and Measey et al., 2016 for detailed assessments).

However, reliable risk analysis of invasive amphibians still requires research on more non-native amphibian species, as the existing knowledge on impacts is mostly based on the cane toad *Rhinella marina* and the American bullfrog *Lithobates catesbeianus* (Measey et al., 2016). Comparisons of impact across taxonomic groups for management prioritization (Blackburn et al., 2014; Kumschick et al., 2015) may also be impeded by the relatively understudied category of amphibian invasions as compared to other vertebrate invasions (Pyšek et al., 2008). This knowledge gap is further compounded by geographic biases in invasion research, with limited coverage in Asia and Africa (Pyšek et al., 2008); developing countries also have relatively less invasion research (Nunez & Pauchard 2010; Measey et al., 2016).

An invasive population of the Indian bullfrog, *Hoplobatrachus tigerinus* (Daudin, 1802), is currently spreading on the Andaman archipelago, Bay of Bengal (Mohanty & Measey, *in press*). The bullfrog was most likely introduced in early 2000s and its exponential expansion has occurred since 2009, resulting in invasive populations on six out of the eight human inhabited islands of the Andaman archipelago (Mohanty & Measey, *in press*). ‘Contaminants’ of fish culture trade and intentional ‘release’ are likely to be the primary pathways of introduction and post-introduction dispersal, facilitating introductions from the Indian mainland and inter-island transfers (Mohanty & Measey, *in press*). The bullfrog has its native range on the Indian sub-continent encompassing low to moderate elevations in Nepal, Bhutan, Myanmar, Bangladesh, India, Pakistan, and Afghanistan (Dutta, 1997). The bullfrog has previously been introduced to Madagascar (Glaw & Vences, 2007), and possibly to the Maldives (Dutta, 1997) and Laccadive Islands (Gardiner 1906). This large bodied frog (up to 160 mm) has high reproductive potential (up to 5750 eggs per clutch, Oliveira et al., 2017) and is uncommon or absent in forested and coastal regions but occurs as a human commensal in plantations and agricultural fields (Daniels 2005). It is considered a dietary generalist, feeding on invertebrates and even large anurans such as *Duttaphrynus melanostictus* (Padhye et al., 2008; Datta & Khaledin, 2017); however, quantitative diet assessment with adequate sample size across habitats and seasons is lacking (but see Khatiwada et al., 2016 for diet of *H. tigerinus* in rice fields of Nepal).

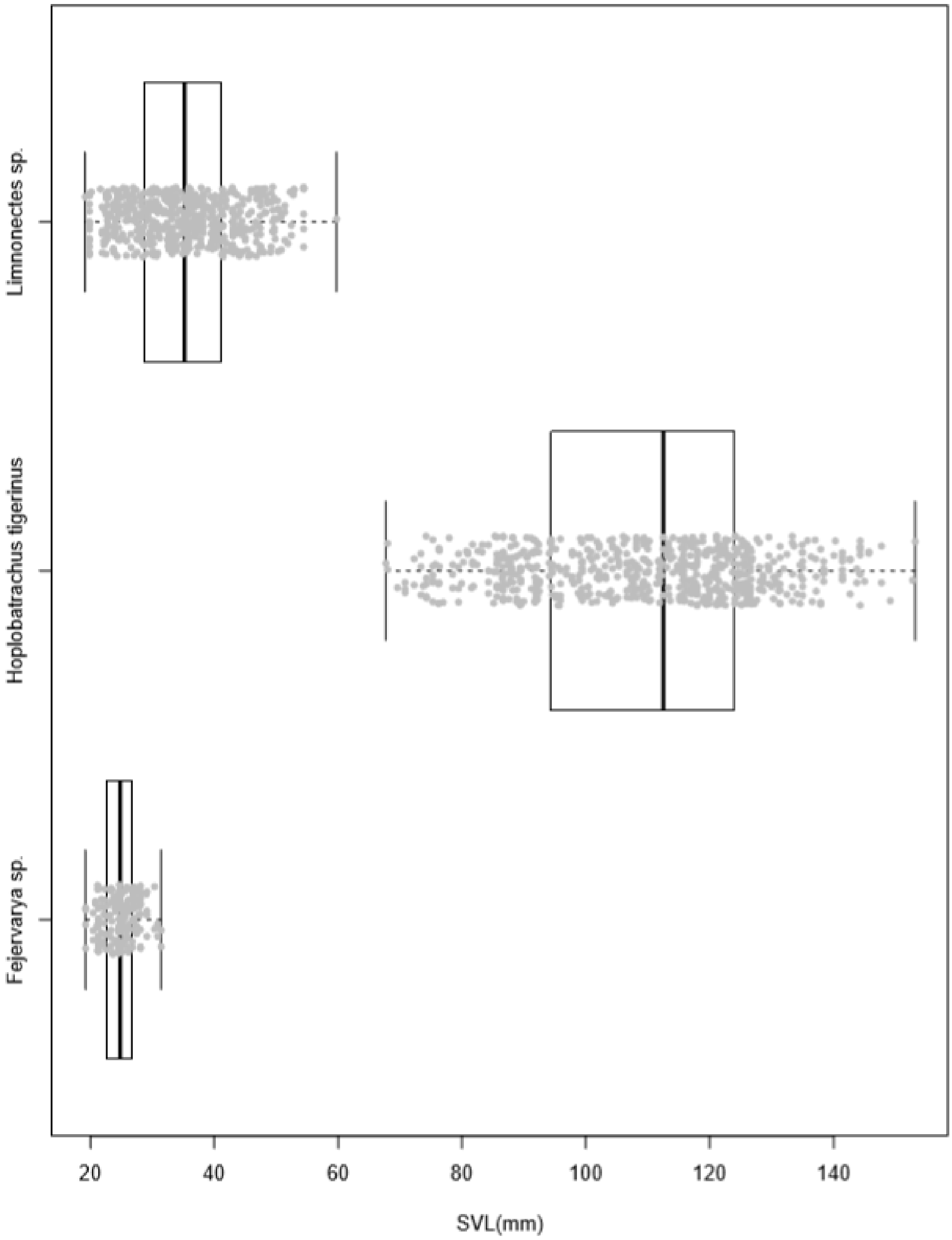
Hoplobatrachus tigerinus on the Andaman archipelago co-occurs with native anurans of the genera *Duttaphrynus*, *Fejervarya*, *Limnonectes*, and *Microhyla* (NPM unpublished data; Harikrishnan et al., 2010). Given the large size of *H. tigerinus,* it is likely to feed on proportionately large prey, including amphibians and other vertebrates (Datta & Khaledin, 2017; Measey et al., 2015). The high volume of prey consumed by *H. tigerinus* (Padhye et al., 2008) may lead to direct competition with native anurans, especially under relatively high densities of *H. tigerinus* in human modified areas

(Daniels, 2005). Although the diet of native anurans has not been assessed on the Andaman Islands, *Fejervarya limnocharis* is considered to be a generalist forager on terrestrial invertebrates (Hirai & Matsui, 2001), *Limnonectes* spp. are known to feed on vertebrates in addition to arthropods (Emerson, Greene & Charnov 1994). This leads us to expect a high diet overlap of native frogs belonging to *Fejervarya* and *Limnonectes*, with the generalist *H. tigerinus*. In terms of size, *H. tigerinus* is much larger than native anurans of the Andaman archipelago (Fig. 3.1) and may impact the native anurans through both predation and competition.

Niche overlap, in combination with prey availability (electivity), can be used to assess trophic competition between species (e.g. Vogt et al., 2017). In addition to taxonomic evaluation and enumeration of the prey consumed, it is crucial to consider prey volume and frequency of prey occurrence to ascertain overall importance of a particular category of prey (Hirschfeld & Rödel, 2011; Boelter et al., 2012; Choi & Beard, 2012). Classification by functional type (hardness and motility of prey) is useful in understanding predator behaviour (Toft 1980; Vanhooydonck et al., 2007; Carne & Measey 2013). Further, seasonality in prey availability may influence diet in amphibians (Hodgkison & Hero 2003; de Oliveira & Haddad, 2015), therefore, there is also a need to assess diet across seasons, to fully capture the range of prey. Another important driver of prey choice may be the positive relationship between predator-prey body sizes (Werner et al., 1995; Wu et al., 2005).

We aimed to assess the trophic impact of the invasive *Hoplobatrachus tigerinus* on the native anurans of the Andaman Islands through predation and potential competition. We carried out diet analyses of the invasive *H. tigerinus* and native anurans, across four habitat types and two seasons, to ascertain the nature and magnitude of trophic impact. We hypothesized that i) small vertebrates constitute a majority of the *H. tigerinus* diet, particularly, by volume and ii) the diet of *H. tigerinus* significantly overlaps with the diet of native anurans, thereby, leading to potential competition. Additionally, we aimed to characterize the predation behaviour of these anurans in terms of electivity and predation strategy (ambush or active search).

Figure 3.1 Snout-vent length of three species of anurans used for dietassessment. Individuals belong to the invasive Indian bullfrog *Hoplobatrachus tigerinus* and the native *Limnonectes* spp. and *Fejervarya* spp., sampled at three locations on the Andaman archipelago.



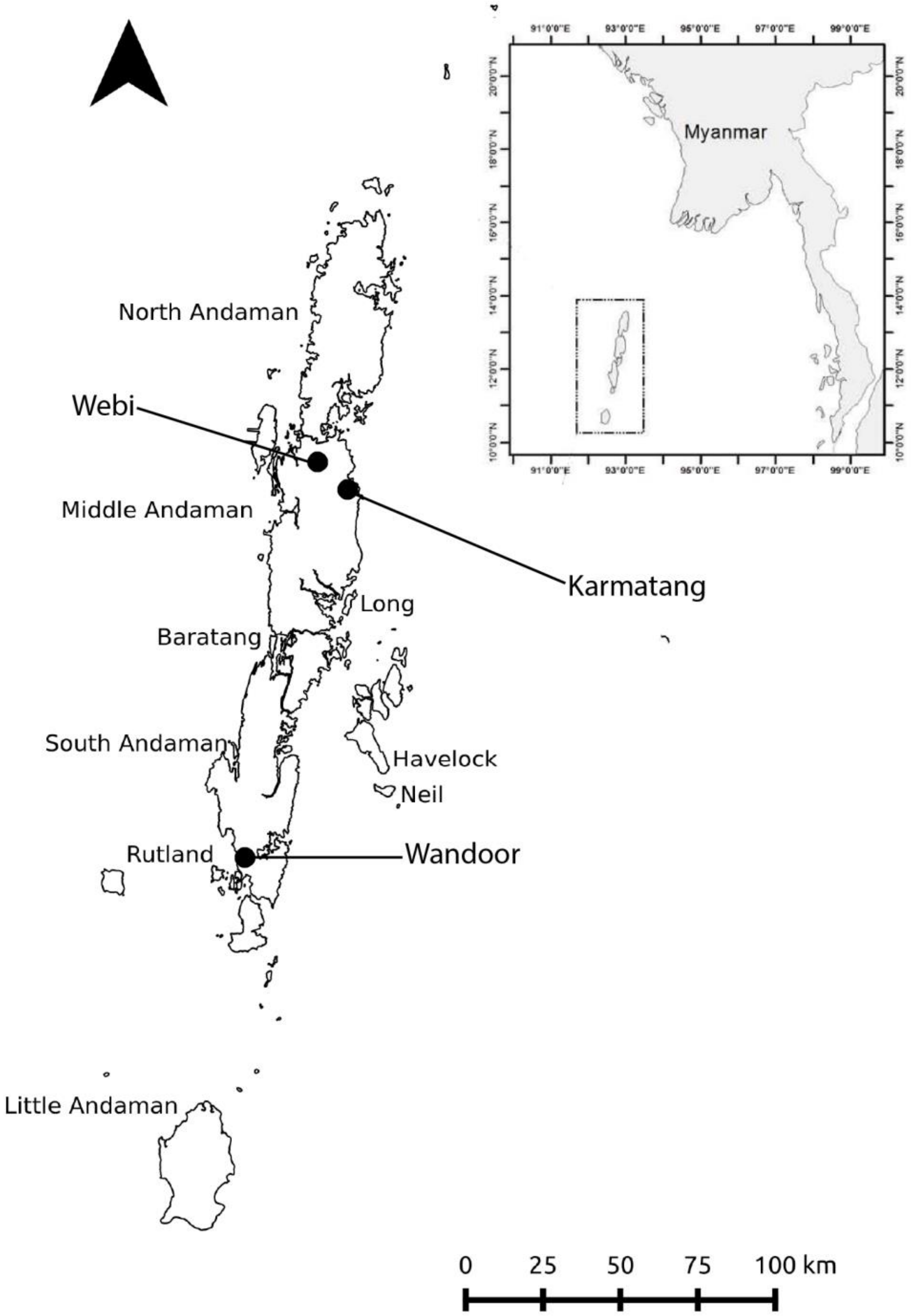
METHODS

We carried out the study in the Andaman archipelago for six months, from February to July 2017. The Andaman archipelago comprises nearly 300 islands (ca. 6400 km^2) is situated between 10°30’N to 13°40’N and 92°10’E to 93°10’E (Fig. 3.2), which are part of the Indo-Burma biodiversity hotspot (Myers et al., 2000) with a 40% endemism level in herpetofauna (Harikrishnan et al., 2010). The tropical archipelago receives an annual rainfall of 3000 mm to 3500 mm (Andrews and Sankaran 2002); primary and secondary forests encompass nearly 87% of the entire archipelago (Forest Statistics 2013), whereas the remaining human modified areas comprise of settlements, agricultural fields, and plantations. Of the nine species of native amphibians recorded, five species (*Ingerana charelsdarwinii*, *Blythophryne beryet*, *Microhyla chakrapanii*, *Kaloula ghoshi* and *Fejervarya andamanensis*) are endemic to the Andaman Islands (Das 1999; Harikrishnan et al., 2010; Chandramouli et al., 2016; Chandramouli et al., 2018), however, taxonomic uncertainties still persist (Chandramouli et al, 2015; Harikrishnan & Vasudevan, 2018). Post-metamorphic frogs of the range restricted *I. charlesdarwinii*, the semi-arboreal *B. beryet*, the arboreal *Kaloula ghosii* and the littoral *F. cancrivora* are unlikely to co-occur with *H. tigerinus* at present (Das 1999; Chandramouli 2016; Chandramouli et al., 2016). Thus, we constrained our choice for comparative species to those which were strictly syntopic. As the taxonomy of the Andaman amphibians remains in flux, we limited our identifications to the genus level for species belonging to the genera *Fejervarya* and *Limnonectes*, which are pending formal re-assessments (Chandramouli et al., 2015). Currently, *L. doriae*, *L. hascheanus*, *Fejervarya limnocharis*, *F. andamanensis*, and *F. cancrivora* are considered members of these two genera in the Andaman Islands (Harikrishnan et al., 2010; Harikrishnan & Vasudevan, 2018). Hereafter, *Fejervarya* spp. and *Limnonectes* spp. are referred to as *Fejervarya* and *Limnonectes*, respectively.

We conducted the study at two sites (Webi and Karmatang) on Middle Andaman Island and at one site (Wandoor) on South Andaman Island (Fig. 3.2). We chose sites with moderately old invasions of *H. tigerinus* (more than 3 years since establishment; Mohanty & Measey, *in press*), assuming that a relatively longer time since establishment would indicate an adequate population to sample from. In each site, we established four 1 ha plots with varying land use-land cover types: agriculture, plantations (Areca nut and Banana), disturbed (logged) and undisturbed forest (minimal use). To capture the variation in diet with respect to seasons, we carried out the sampling in both dry (January to April) and wet (May to July) seasons, the latter coinciding with the south-westerly monsoon.

Our protocol was approved by the Research Ethics Committee: Animal Care and Use, Stellenbosch University (#1260) and permission to capture anurans, was granted under the permit of the Department of Environment and Forests, Andaman and Nicobar Islands (#CWLW/WL/134/350). Diet of anurans was determined using stomach flushing, a standard and low-risk technique to determine prey consumed (Solé et al., 2005). Anurans were hand-captured between 1800 to 2200 hrs; stomach flushing was carried out within 3 h of capture. We consciously avoided capture bias towards any particular size class, by actively searching for anurans of all size classes. As our sampling focussed on sub-adult and adult *H. tigerinus* and was completed in July (presumably before breeding and emergence of metamorphs) we did not examine the diet of metamorphs. In order to avoid mortality, we did not stomach flush individuals below 20 mm SVL and hence, individuals of co-occurring *Microhyla chakrapaniii* (ca. 10-30 mm SVL; Pillai, 1977) were not sampled After excluding native anurans which did not co-occur with *H. tigerinus*, our samples included *Duttaphrynus melanostictus* (although its taxonomic and geographic status is uncertain, Das 1999), *Limnonectes* and *Fejervarya*. We conducted stomach flushing using a syringe (3 ml to 10 ml for anurans of 20 mm-50 mm SVL and 60 ml for anurans >60 mm SVL), soft infusion tube, and water from site of capture. In addition to SVL, we measured head width (HW) and lower jaw length (LJL) of the anurans, using a Vernier calliper (0.01 mm precision) and noted the sex. The stomach flushed individuals were toe-clipped (following Grafe et al., 2011) to record the total number of recaptures (n = 54). Individuals were released back to the capture site post completion of the procedure.

Figure 3.2 Study area map showing the major islands of theAndaman archipelago and the three sampling locations. Diet assessment of *Hoplobatrachus tigerinus*, *Limnonectes* spp., and *Fejervarya* spp. were carried out from February 2017 – July 2017.



We collected the expelled prey items in a transparent beaker and sieved the contents using a mesh of 0.5 mm. Prey items from each individual were classified up to a minimum of order level, and further characterized by functional traits (hardness and motility, following Vanhooydock et al., 2007). Length and width of intact prey were measured under an 8x magnifying lens to the nearest 0.01 mm using a Vernier calliper and recorded along with the prey's life stage (adult/larvae). We preserved all prey items in 70% ethanol.

We also determined electivity of prey, based on prey consumption as compared to prey availability. Terrestrial prey were measured using five pitfall traps in each 1 ha plot, which were visited twice daily for a duration of three days (total of 30 trap occasions). Within each 1 ha plot, the pitfalls were arranged in the four corners and one in the centre of the plot. We used plastic traps, 80 mm in diameter and 300 mm high. A wet cloth was kept at the bottom to provide refuge to trapped animals, so as to prevent any predation before sample collection. We used chloroform-soaked cotton balls to euthanize the invertebrate prey, prior to collection. These prey items were also identified up to the order level and measured for length and width. Our approach of estimating prey availability excludes flying evasive orders (e.g. adult lepidopterans) and vertebrate prey.

Data analyses

We did not obtain adequate numbers of *Duttaphrynus melanostictus* (n = 4) individuals and hence they were not included in the analyses. We pooled samples from the three sites to examine diet at the species level for *H. tigerinus* and genus level for *Limnonectes* and *Fejervarya*. We assessed the number, volume, and frequency (number of individuals with a given prey item in their stomach) of consumed prey under each taxonomic category. Volume was calculated using the formula of an ellipsoid, following Colli and Zamboni (1999),

$$\text{volume } = \frac{4}{3}\pi\left(\frac{l}{2}\right)\left(\frac{w}{2}\right)^2 ,$$

where, l is prey length and w is prey width. Prey items for which volume could not be calculated due to lack of measurement data (i.e. fragmented prey) were assigned the median prey volume for that order. We carried out a generalized linear model to test the relationship between body size of anurans (SVL) and prey volume, after accounting for taxonomic identity of anurans. We log transformed SVL to adhere to the assumption of normality and cube root transformed prey volume, prior to the analysis.

In order to assess the overall importance of a prey category, based on the percentage of number, frequency and volume, we used the Index of Relative Importance (IRI, Pinkas et al., 1971). To test for diet overlap, we employed the MacArthur and Levins' index *Ojk* (MacArthur & Levins, 1967) in the pgirmess package (Giraudoux, 2016); we built null models using the 'niche_null_model' function of the EcoSimR package (Gotelli et al., 2015) to test for statistical significance of *Ojk*. We also assessed prey availability for each site across both dry and wet seasons, using the Simpson's diversity index (Supplemental Information 1). We determined electivity of terrestrial invertebrate prey by the anurans, using the Relativized Electivity Index (Vanderploeg & Scavia, 1979). Following Measey (1998), we computed electivity for only those prey taxa with $n \geq 10$ prey items for *H. tigerinus* and *Limnonectes*; given the low sample size for *Fejervarya* (Table 3.1), we fixed the cut-off at $n \geq 5$. Further, electivity for *H. tigerinus* was calculated only for agriculture and plantations; electivity for *Fejervarya* was considered only for one site with adequate sample size: Wandoor (Table 3.1). All analyses were carried out in the statistical software R 3.4.1 (R Core Team, 2017).

Table 3.1 Sampling effort for diet assessment of the invasive *Hoplobatrachus tigerinus* and native *Limnonectes* spp. and *Fejervarya* spp. Sampling carried out in four habitat types across two seasons, at three sampling locations on the Andaman Islands.

	Agriculture		**Plantation**		**Disturbed Forest**		**Undisturbed Forest**	
	dry	wet	dry	wet	Dry	wet	dry	wet
H. tigerinus								
Karmatang	41	35	29	29	0	0	0	0
Webi	32	35	48	38	0	0	0	0
Wandoor	0	0	38	33	0	0	0	0
Limnonectes								
Karmatang	0	17	5	26	0	25	0	22
Webi	14	17	19	26	13	17	13	17
Wandoor	7	21	17	29	19	11	30	10
Fejervarya								
Karmatang	0	0	0	0	0	0	0	0
Webi	1	0	0	0	1	0	0	0
Wandoor	19	17	13	2	10	0	2	0

RESULTS

Overall, we sampled 798 individuals of the two native anurans and the invasive *Hoplobatrachus tigerinus* (Table 3.1). We obtained 1478 prey items (*H. tigerinus*: 687, *Limnonectes*: 618, *Fejervarya*: 173) belonging to 35 taxonomic categories in the stomach of 688 anurans (Table 3.2). Vacuity index (i.e. proportion of empty stomachs) was higher in the dry season (19.68%) as compared to the wet season (8.67%). Less than 4% of prey items remained unidentified, mostly due to advanced levels of digestion. *Hoplobatrachus tigerinus* consumed prey items under most of the taxonomic categories (29), followed by *Limnonectes* (25), and *Fejervarya* (14). Vertebrates were consumed by both *H. tigerinus* and *Limnonectes*, although the numeric and volumetric percentage of vertebrates consumed was higher for *H. tigerinus* (2.62%, 58.03%) than

Limnonectes (0.48%, 5.16%; Table 3.2). Based on IRI, coleopterans and orthopterans constituted the major prey of *H. tigerinus* and *Limnonectes*, whereas, formicids and coleopterans formed the majority in the diet of *Fejervarya* (Table 3.2).

The diet of *H. tigerinus* overlapped significantly with that of *Limnonectes* ($Ojk = 0.87$, lower-tail $p > 0.999$, upper-tail $p < 0.001$) but there was no significant overlap with *Fejervarya* ($Ojk = 0.35$, lower-tail $p = 0.919$, upper-tail $p = 0.08$). The diet of the two native anurans overlapped significantly ($Ojk = 0.58$, lower-tail $p = 0.967$, upper-tail $p = 0.03$).

Based on availability of terrestrial invertebrates, prey electivity of all three anurans indicated a positive relationship between predator-prey body sizes (Fig. 3.3). While the largest species, *H. tigerinus*, strongly selected larger prey (≥ 100 mm^3), the smallest anuran, *Fejervarya*, selected for prey items smaller than 10 mm^3; the medium sized *Limnonectes* chose small and medium-sized prey items (10 mm^3 – 500 mm^3), although the magnitude of electivity (positive or negative) was lowest for this species (Fig. 3.1; Fig. 3.3). We found a positive correlation between prey volume and body size of *H. tigerinus* ($\beta = 1.93$, $SE = 0.21$, $p < 0.001$) and *Limnonectes* ($\beta = 0.88$, $SE = 0.25$, $p < 0.001$), but found no such relationship in case of *Fejervarya* ($\beta = -0.07$, $SE = 0.33$, $p = 0.83$).The majority of prey consumed by the three anurans was hard, and evasive, although diet of *Limnonectes* included a relatively higher proportion of soft and sedentary prey (Table 3.3). Terrestrial prey were the dominant type in the diet of *H. tigerinus* (91.29%), *Limnonectes* (93.18%), and *Fejervarya* (99.34%).

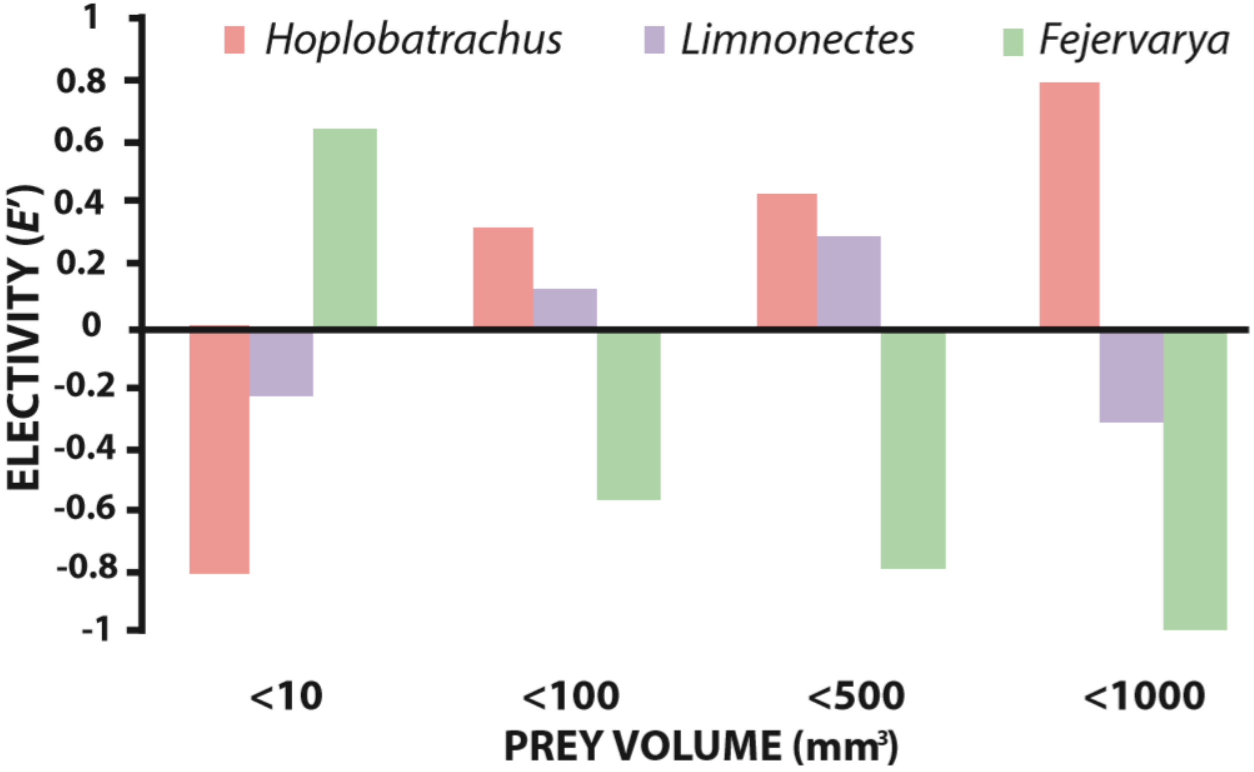
Table 3.2 Diet of *Hoplobatrachus tigerinus* (n = 687), *Limnonectes* (n = 618) and *Fejervarya* (n = 173), described in terms of percentage N – prey abundance, V – volume, F – frequency of occurrence in anurans, and IRI – Index of relative importance.

	Hoplobatrachus tigerinus (n = 687)				***Limnonectes*** (n = 618)				***Fejervarya*** (n = 173)			
Prey	N%	V%	F%	IRI	N%	V%	F%	IRI	N%	V%	F%	IRI
Acari	0	0	0	0	0.32	0.006	0.39	0.12	0.57	0.14	0.84	0.61
Agamidae	0.43	50.44	0.57	29.07	0	0	0	0	0	0	0	0
Amphipoda	0	0	0	0	0.48	0.07	0.58	0.32	0	0	0	0
Anura	0.87	4.95	1.14	6.65	0.32	5.12	0.39	2.12	0	0	0	0
Aranae	3.20	0.73	4	15.74	7.60	2.27	8.59	84.93	7.51	7.75	10.16	155.23
Arthropoda	6.55	0	8.57	56.22	5.50	0	6.64	36.53	0.57	0	0.84	0.48
Blattaria	1.45	0.33	1.90	3.42	1.29	0.71	1.56	3.14	0	0	0	0
Chilopoda	3.35	6.15	2.85	27.15	3.23	2.75	3.9	23.41	1.15	7.62	1.69	14.88
Coleoptera	29.73	12.14	24.57	1029.14	15.85	10.34	15.42	404.29	9.24	20.50	12.71	378.16
Brachyura	0.58	2.40	0.76	2.27	0.16	0.81	0.19	0.19	0	0	0	0
Dermaptera	0.14	0.009	0.19	0.02	1.61	0.20	1.95	3.55	0	0	0	0
Diplopoda	0.87	0.07	0.76	0.72	3.55	0.73	3.12	13.41	0	0	0	0
Diptera	1.89	0.56	1.52	3.74	4.04	0.09	3.9	16.15	14.45	3.38	14.40	256.95
Formicidae	3.93	0.37	3.80	16.42	10.19	0.24	8.00	83.58	38.72	5.80	23.72	1056.60
Gastropoda	4.22	0.71	4	19.76	3.23	1.5	3.32	15.72	0	0	0	0
Geckonnidae	0.14	0.45	0.19	0.11	0	0	0	0	0	0	0	0
Hemiptera	0.58	0.19	0.76	0.59	2.10	0.35	2.34	5.77	5.20	10.96	5.08	82.18

Hymenoptera	0.14	0.004	0.19	0.02	0	0	0	0	1.15	0.86	0.84	1.70
Insecta	1.45	0	1.90	2.77	1.29	0	1.36	1.76	6.35	0	9.32	59.27
Isoptera	2.62	0.24	2.09	6.01	7.44	1.88	4.49	41.89	2.31	0.87	3.38	10.81
Lacertidae	0.29	0.90	0.38	0.45	0	0	0	0	0	0	0	0
Lepidoptera	1.31	0.24	1.33	2.07	0.48	0.14	0.39	0.24	0	0	0	0
Leplarva	6.26	3.01	7.42	68.95	6.63	5.95	6.64	83.59	3.46	15.08	4.23	78.61
Mantodea	0.29	0.72	0.38	0.38	0	0	0	0	0	0	0	0
Odonata	0.72	0.07	0.95	0.76	0.16	0.04	0.19	0.04	0	0	0	0
Oligochaeta	1.31	0.77	1.52	3.18	4.69	54.54	4.10	242.95	0	0	0	0
Opilionida	0	0	0	0	0	0	0	0	0	0	0	0
Orthoptera	24.48	12.62	24.19	897.74	13.26	9.45	14.84	337.34	3.46	20.01	5.08	119.39
Rodentia	0.14	0	0.19	0.02	0	0	0	0	0	0	0	0
Scincidae	0.14	0.62	0.19	0.14	0	0	0	0	0	0	0	0
Serpentes	0.58	0.67	0.76	0.95	0.16	0.04	0.19	0.04	0	0	0	0
Siphonaptera	0	0	0	0	0	0	0	0	0.57	0.075	0.84	0.55
Gastropoda	0.29	0.27	0.38	0.21	0.80	1.97	0.78	2.17	0	0	0	0
Unidentified	1.89	0.26	2.47	5.35	5.33	0.69	6.44	38.87	5.20	6.92	6.77	82.19
Zygentoma	0	0	0	0	0.16	0.01	0.19	0.03	0	0	0	0

Figure 3.3 Prey electivity in terms of volume, by the invasive *Hoplobatrachus tigerinus* and native *Limnonectes* spp. and *Fejervarya* spp.

Prey electivity based on prey consumption and availability, at three sites on the Andaman archipelago.



We observed several endemic vertebrate species in the diet of *H. tigerinus*, including the Andaman emerald gecko *Phelsuma andamanensis* (n = 1), Chakrapanii's narrow mouthed frog *Microhyla chakrapanii* (2), the Andaman skink *Eutropis andamanensis* (1), and Oates's blind snake *Typhlophs oatesii* (3). We also found *Limnonectes* (4), unidentified rodent (1), *Lycodon* sp. (1) and the invasive *Calotes versicolor* (3) in the diet of *H. tigerinus* (Supplemental Information 2). *Limnonectes* preyed upon a conspecific on one occasion and an unidentified anuran in another instance.

Table 3.3 Prey electivity (E') of the invasive *Hoplobatrachus tigerinus* and native *Limnonectes* and *Fejervarya* based on prey hardness and motility, following Vanhooydonck et al. (2007). Sampling carried out in four habitat types across two seasons, at three sampling locations on the Andaman Islands.

H. tigerinus					
	dry	wet		dry	wet
soft	-0.10	-0.31	sedentary	-0.12	-0.22
medium	0.80	-0.07	medium	-0.70	0.20
hard	-0.59	0.32	evasive	0.85	-0.01
Limnonectes					
	dry	wet		dry	wet
soft	0.52	0.14	sedentary	0.41	0.15
medium	0.15	-0.09	medium	-0.46	-0.11
hard	-0.52	-0.09	evasive	0.31	-0.06
Fejervarya					
	dry	wet		dry	wet
soft	0.14	-0.18	sedentary	0.01	-0.33
medium	-0.45	-0.43	medium	0.10	0.49
hard	-0.01	0.38	evasive	-0.34	-0.45

DISCUSSION

We expected the diet of invasive *Hoplobatrachus tigerinus* to overlap significantly with the diet of the two native anurans considered. However, we found a significant overlap only with *Limnonectes*, such that when prey is limited competition may arise. As expected, small vertebrates constituted a majority of *H. tigerinus* diet by volume, suggesting potential impact by predation on a large proportion of the endemic island fauna. Volume of prey elected was positively related to predator size (Fig. 3.3); within species, volume of prey consumed was positively correlated with predator size for *H. tigerinus* and *Limnonectes* only.

We observed 86% niche overlap between *H. tigerinus* and *Limnonectes*, which was statistically significant in comparison to the constructed null model; whereas, niche overlap of *H. tigerinus* with *Fejervarya* was not significant. On the other hand, prey electivity suggests that *H. tigerinus* strongly elected for medium-sized and larger prey whereas small and medium-sized prey were elected by *Limnonectes* (Fig. 3.3). This may result in competition for prey ranging from 10 – 500 mm^3 between the two anurans, under the conditions of limited prey. Trophic competition in amphibians may lead to a decrease in fitness (e.g. growth rate) and affect population level processes (Benard & Maher, 2011). Impact of invasive amphibians (post-metamorphic) via trophic competition has been documented in fewer studies as compared to predation (Measey et al., 2016), but this mechanism may affect taxa at various trophic levels (Smith et al., 2016). Metamorphs of *H. tigerinus* may also compete with both *Fejervarya* and *Limnonectes* as they would fall under the same size class (20 mm-60mm; Daniels, 2005). The observed positive correlation between body size and prey volume in the case of both *H.* tigerinus and *Limnonectes*, also supports the notion that metamorphs of these species may compete for small prey. Although our sampling did not evaluate the diet of *H. tigerinus* metamorphs, we think this may be relevant as competition between juvenile *Lithobates catesbeianus* and small native anurans has been previously documented on Daishan Island, China (Wu et al., 2005).

Evaluating dietary overlap is a pre-cursor to determining trophic competition due to invasive populations, which do not have shared evolutionary history with native species. Dietary overlap in co-occurring species may be independently influenced by prey availability (Kuzmin, 1995), prey taxa (Lima, 1998), prey size (Toft, 1981; Vignoli et al., 2009; Crnobrnja-Isailović, 2012) and a combination of these factors. Therefore, it is essential to design studies and interpret dietary patterns with reference to all three factors, in order to arrive at meaningful inferences on prey consumed, dietary overlap, and probable subsequent competition (Kuzmin, 1990; but see Kuzmin, 1995 regarding criteria for competition). Further, prey size should ideally be measured in terms of volume, as it is known to be a better dietary descriptor (Vignoli & Luiselli, 2012).

Hoplobatrachus tigerinus preyed upon three classes of vertebrates (Amphibia, Reptilia, and Mammalia), which accounted for a significant proportion of its diet by volume, although vertebrate prey was numerically inferior to invertebrates in the diet. Such major contribution to the volume of prey by vertebrates (despite numerical inferiority) has been observed for *Lithobates catesbeianus* and *Xenopus laevis* (Boelter et al., 2012; Vogt et al., 2017); anurophagy may also contribute significantly to the diet of many amphibians (Measey et al., 2015; Courant et al., 2017). We observed several endemic species in the diet of *H. tigerinus*, which may become threatened if frequently preyed upon. *Limnonectes* was also consumed by *H. tigerinus*, thereby, indicating a potential two-pronged impact through predation and competition. However, demographic change (if any) in *Limnonectes*, due to predation and competition by *H. tigerinus*, was not evaluated in this study. The invasive *H. tigerinus* on the Andaman Islands reportedly consume poultry (Manish Chandi pers comm., Mohanty & Measey, *in press*) and stream fish (NPM unpublished data), resulting in a potential economic impact. We expect the invasive *H. tigerinus* on Madagascar (Glaw & Vences, 2007) to similarly consume a large proportion of vertebrates in its diet and consider the invasion to be a threat to the highly diverse small vertebrates of Madagascar.

Despite the presence of a large portion of vertebrates in the diet of *H. tigerinus*, its trophic position (consistency of vertebrate prey consumption) can only be ascertained with stable isotope analyses (Huckembeck et al., 2014). Although, diet analysis of invasive species can identify vulnerable taxa and confirm at least ‘minimal’ to ‘minor’ levels of impact through predation and competition (*sensu* Blackburn et al., 2014; Hawkins et al., 2015), such analysis must be complimented with evidence of trophic level effects to evaluate the degree of impact (Smith et al., 2016).

The large proportion of ants in the diet of *Fejervarya* does not necessarily prove specialization for myrmecophagy. Hirai and Matsui (2000) inferred relatively weaker avoidance of ants by *Glandirana rugosa* as compared to other anurans. Although we found the same pattern for *Fejervarya* based on prey electivity (*E*= -0.02), it does not prove weak avoidance either. As social insects, ants may be disproportionately captured in the pitfall traps; therefore, it is necessary to compliment diet studies on potentially myrmephagous predators with additional evidence (e. g. cafeteria experiments). *Hoplobatrachus tigerinus* and *Fejervarya* chose evasive prey, suggesting that these two species are mostly ambush ('sit and wait') predators; *Limnonectes* elected sedentary prey along with other prey types, indicating a combination of 'active search' and 'sit and wait' foraging (Table 3.3; Huey & Pianka, 1981; Vanhooydonck et al., 2007). Generally, soft bodied prey are considered to provide more nutrition by size as compared to hard prey and therefore, it is hypothesized that species will select soft prey more often than hard prey, which in turn is dependent on prey availability by season (Measey et al., 2011; Carne & Measey 2013). However, we find that diet does not appear to vary considerably across the seasons and is governed more by size than hardness of prey (Fig. 3.3; Werner et al., 1995).

Although our sampling for diet analysis by stomach flushing was adequate (Table 3.1), our assessment of prey availability did not include flying invertebrates and vertebrates, which prevents us from carrying out electivity analyses on these taxa.

CONCLUSION

Diet analyses of *Hoplobatrachus tigerinus* confirmed our first hypothesis, i.e. significant predation of *H. tigerinus* on endemic vertebrates (hypothesis 1) and partially supported the second hypothesis of a high diet overlap with native anurans (hypothesis 2) indicating potential competition; overlap was significant only for the large-bodied *Limnonectes*. Given the observed high density of *H. tigerinus* in human modified habitats on the Andaman archipelago (NPM unpublished data), trophic competition and predation by *H. tigerinus* may have a significant impact on native anuran populations in these habitats. Pursuing our additional aim of characterizing anuran foraging modes, we determined the foraging strategy of *H. tigerinus* and *Fejervarya* as ambush foraging (‘sit and wait’) and that of *Limnonectes* to be a combination of ‘active search’ and ‘sit and wait’ foraging. In addition to quantifying the trophic niche of anurans belonging to three genera, we stress the necessity to evaluate prey availability and volume in future studies for meaningful insights into diet of amphibians.

4 No survival of native larval frogs in the presence of invasive Indian bullfrog *Hoplobatrachus tigerinus* tadpoles

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AUTHOR CONTRIBUTIONS

NPM and JM conceived the idea of the study; NPM collected the data; NPM and JM analysed the data; NPM wrote the manuscript, JM contributed to the writing.

ABSTRACT

Invasive amphibians have considerable negative impacts on recipient ecosystems, however, impact has been assessed for only a few species, limiting risk assessments. In particular, the impact of invasive anurans with carnivorous tadpoles have not been examined thoroughly. The Indian bullfrog (*Hoplobatrachus tigerinus*), native to the Indian sub-continent, is rapidly invading the Andaman archipelago, Bay of Bengal after its recent introduction. We aimed to evaluate the effect of carnivorous *H. tigerinus* tadpoles on two species of endemic anuran tadpoles *Microhyla chakrapanii* and *Kaloula ghosi*, in a mesocosm experiment. Rapid predation by larval *H. tigerinus* resulted in no survival of endemic frog tadpoles. Survival of *H. tigerinus* larvae was density-dependent. The study is timely in elucidating the impact of invasive larval *H. tigerinus* on native anurans and helps substantiate the need to manage invasive populations (or potential incursions) of the species on the Andaman archipelago and elsewhere.

INTRODUCTION

Invasive amphibians have considerable negative impacts on recipient ecosystems with the magnitude of impact being similar to that of invasive birds and fishes (Measey et al., 2016). However, amphibians remain a relatively understudied taxon in invasion science (Pyšek et al., 2008), despite the increasing number of established non-native amphibian species and populations globally (Capinha et al., 2017). Amphibian invaders, with biphasic life-histories, require assessment of their effect on native species in both terrestrial and aquatic environments (Greenlees et al., 2014), as the outcome of interactions in the aquatic stage may have carry over effects influencing the terrestrial stage (Chelgren et al., 2006). Invasive larval anurans are known to have negative effects on survivorship or performance of native larval anurans through competition (Kupferberg, 1997; Smith, 2005a) and toxicity (see Shine, 2010), however, impact of carnivorous larvae have not been well studied. Although the number of studies on the impact of larval amphibians are greater than those on post-metamorphic amphibians (Measey et al., 2016), there is considerable bias in the species assessed. Three species (the cane toad *Rhinella marina*, the American bullfrog *Lithobates catesbeianus*, and the African clawed frog *Xenopus laevis*) account for greater than 80% of published research on amphibian invasions (van Wilgen et al., 2018).

The Indian bullfrog (*Hoplobatrachus tigerinus*, Daudin 1802), native to the Indian sub-continent (Dutta, 1997), is currently invading the Andaman archipelago, Bay of Bengal (Mohanty and Measey, *in press*). The Andaman archipelago, comprising of nearly 300 islands (ca. 6400 km^2), is situated between 10°30’N to 13°40’N and 92°10’E to 93°10’E. The archipleago is a part of the Indo-Burma biodiversity hotspot with a 40% endemism level in herpetofauna (Harikrishnan et al., 2010). Introduced in early 2000s, the invasive range of *H. tigerinus* (Dicroglossidae) in the archipelago has expanded exponentially since 2009, resulting in established populations on six out of the eight human inhabited islands of the Andaman archipelago (Mohanty & Measey, *in press*). *Hoplobatrachus tigerinus* is uncommon or absent in forested and coastal regions but occurs as a human commensal in plantations and agricultural fields (Daniels, 2005). This large bodied frog (up to 160 mm) is known to prey upon a host of small endemic vertebrates on the archipelago and its diet overlaps significantly with larger native anurans, indicating a potential for competition (Mohanty & Measey, 2018). The species is also established on Madagascar and is reported from the Maldives and Laccadive Islands (see references in Mohanty and Measey, *in press*).

Hoplobatrachus tigerinus has a high reproductive potential (up to 5750 eggs per clutch) with egg survival of ca. 40% (Dash and Hota, 1980). Given the common occurrence of the frog in the Indian sub-continent, many autecological studies have described its breeding biology and the larval stage (reviewed in Saidapur, 2001). Tadpoles of *H. tigerinus* are known to be carnivorous, feeding on zooplanktons, other anuran larvae and even display cannibalism (Saidpaur, 2001). The bullfrog on the Andaman archipelago co-occurs with native anurans of the genera *Microhyla*, *Kaloula*, *Duttaphrynus*, *Fejervarya* and *Limnonectes* (NPM unpublished data; Harikrishnan et al., 2010). In human-modified areas, the invasive *H. tigerinus* and all the syntopic native anurans breed in ephemeral pools in waterlogged agricultural fields and plantations. While the breeding phenology has not been systematically evaluated for all anuran species of the archipelago, all the syntopic native species likely breed at the onset of the south-west monsoon (in May), with the continued breeding of native anurans being relatively longer when compared to the explosive breeding *H. tigerinus* (NPM *pers. obs.*). Given its high reproductive potential and carnivorous tadpoles, the impact of larval *H. tigerinus* on native larval anurans requires urgent evaluation.

We aim to evaluate the effect of invasive Indian bullfrog tadpoles on two species of endemic anuran tadpoles, in a mesocosm experiment. We hypothesise that, 1) predation by bullfrog tadpoles decreases the survival of both endemic anuran tadpoles and 2) bullfrog tadpoles benefit from preying upon native anuran larvae, leading to increased survival, growth rates and metamorph size, and a reduced larval period.

METHODS

We conducted the study in and around the Andaman and Nicobar Environment Team (ANET) field station, located in Wandoor, South Andaman Island. We selected two endemic anurans, *Microhyla chakrapanii* and *Kaloula ghosi* (both Microhylidae), which breed syntopically and synchronously with the invasive bullfrog (NPM *pers. obs.*). We excluded the other syntopic anurans, as we did not obtain a minimum number of clutches (n = 4) to start the experiment. Following heavy rains, breeding commenced on the night of May 12th, 2017. Four clutches of eggs belonging to invasive *H. tigerinus* were collected from waterlogged paddy fields and plantation moats. Similarly, four clutches from each of the two endemic species were collected. Upon emergence of tadpoles, we mixed the clutches and assigned individuals to treatments randomly, to avoid any parental bias (Dash & Hota, 1980). We started the experiment on May 16th for 21 pools and on May 19th for the remaining four pools. All tadpoles had reached Gosner stage 25 at the onset of the experiment.

Our experiment comprised seven treatments: three with single-species, three with two-species, and one with three-species. We replicated each treatment three times for single-species (3 x 3), and four times each for two-species (4 x 3) and three-species (4 x 1) treatments, with a total of 25 pools (Table 4.2). The circular plastic pools (125 cm in diameter x 40 cm in depth) were filled with ca. 150 litres of untreated pond water. We kept the total tadpole density of pools constant across all treatments, at 30 tadpoles (two-species pools: 15 tadpoles/species; three-species pools: 10 tadpoles/species). This density is equivalent to the 'high density' (0.213 larvae/litre) treatments for larval *Lithobates catesbeianus* mesocosm experiments (following Kiesecker et al., 2001), and closely resembles the natural assemblages observed in the area. We provided uniform food resources (40 g of leaf litter and algae per week) collected from the ephemeral pools in the study site used for breeding by the three species. The pools were cleaned once a week, with the tadpoles (segregated by species) being held temporarily in plastic buckets filled with water. Cleaning involved draining of used water and scrubbing of the pool manually to remove any sediments, followed by restocking with fresh water (including zooplanktons) and food. A nylon net was used to cover each pool to avoid external predation, as the pools were placed outdoors to experience a natural photoperiod. Mean temperature (measured by Davis-Vantage Pro 2 weather-station) of the study area during the experiment was 27.52 °C (SD = 1.95; range: 23.2 – 33.3 °C).

We recorded survival of tadpoles in each pool weekly and photographed five tadpoles (or fewer if unavailable due to mortality), haphazardly selected from each pool, on a gridded sheet (10 mm x 10 mm) thrice a week. The experimental setup was monitored daily to detect metamorphosing tadpoles (and dead tadpoles), which were removed at Gosner stage 42 (emergence of forelimbs). We provided a floating *Colocasia* leaf in each pool to enable metamorphosing individuals to avoid drowning. Upon completing metamorphosis, individuals were photographed on the gridded sheet; we processed the photographs in the image analysis software 'ImageJ' and obtained body length (BL) and total length (TL) for all tadpoles and snout-vent length (SVL) for metamorphs. Time to metamorphosis was recorded in days for all individuals, with the start set at the night of spawning (May 12th).

We obtained the final proportion of survival for each species per pool based on the initial number of allocated tadpoles. Time to metamorphosis was computed as the median value of the number of days to metamorphosis for all tadpoles in a pool. Body length and total length were measured up until the median date of metamorphosis for each pool. We fitted linear regressions to both size measurements over time to obtain growth slopes. We removed one pool (*Microhyla-Kaloula* treatment) from all analyses, as there was a mass die-off on the first day, probably due to contamination of the pool. One other pool of the same treatment (*Microhyla-Kaloula*) overflowed 14 days from the start of the experiment, hence no statistical tests were carried out for survival, time to metamorphosis, and metamorph size on this treatment. However, we were able to estimate growth rates for three pools of the *Microhyla-Kaloula* treatment.

A Shapiro-Wilk test was carried out to test for normality of all response variables, failing which we executed non-parametric tests. We performed a Kruskal-Wallis one-way analysis of variance on survival, growth slopes, time to metamorphosis and metamorph size, for the three species separately (i.e. four treatments per species). A Dunn's test of multiple comparisons using rank sums, was carried out as a post-hoc test to determine pair-wise differences between treatments per species, using the 'dunn.test' package in the statistical software R (Dinno, 2017).

RESULTS

Microhyla chakrapanii was the first species to reach metamorphosis (median: 21 days), followed by *Hoplobatrachus tigerinus* (32 days) and *Kaloula ghosi* (38 days; Table 4.1). Growth was fastest for *H. tigerinus* and resulted in the largest metamorphs (ca. 20 mm; Table 4.1). Survival for both endemic anurans, *M. chakrapanii* and *K. ghosi*, reduced to zero in the presence of invasive *H. tigerinus*, as compared to 0.89 (SE = 0.04) and 0.62 (SE = 0.11) in their respective single species treatments (Fig. 4.1). In the three-species treatment, all individuals of *M. chakrapanii* and *K. ghosi* were also preyed upon (Fig. 4.1). Both endemic anurans were completely consumed by *H. tigerinus* within the first week, in 10 out of 12 pools (83.33%); the remaining two pools had no surviving endemic anurans by the third week.

We found no significant difference between treatments with and without endemic anurans, in terms of *H. tigerinus* growth in body length (Kruskal-Wallis $\chi^2 = 0.95$; $p = 0.81$) and total length (Kruskal-Wallis $\chi^2 = 0.78$; $p = 0.86$), time to metamorphosis (Kruskal-Wallis $\chi^2 = 0.38$; $p = 0.94$), and metamorph size (Kruskal-Wallis $\chi^2 = 3.48$; $p = 0.32$). Mean number of *H. tigerinus* surviving across treatments was 2.80 tadpoles (SE = 0.48; range: 1 to 6; Table 4.2) and did not differ significantly between treatments (Kruskal-Wallis $\chi^2 = 1.06$, $p = 0.79$). However, proportion of *H. tigerinus* surviving was significantly greater in the presence of both endemic anurans ($p = 0.012$; n =15; Fig. 4.1).

Table 4.1 Species-wise growth rates (mm/day), time to metamorphosis (days), and metamorph size (snouth-vent length in mm) for larval invasive *Hoplobatrachus tigerinus* (Dicroglossidae) and the native *Microhyla chakrapanii* and *Kaloula ghosi* (Microhylidae), in the mesocosm experiment. Values reported as mean ± Standard Error, except for time to metamorphosis shown as the median value ±SE.

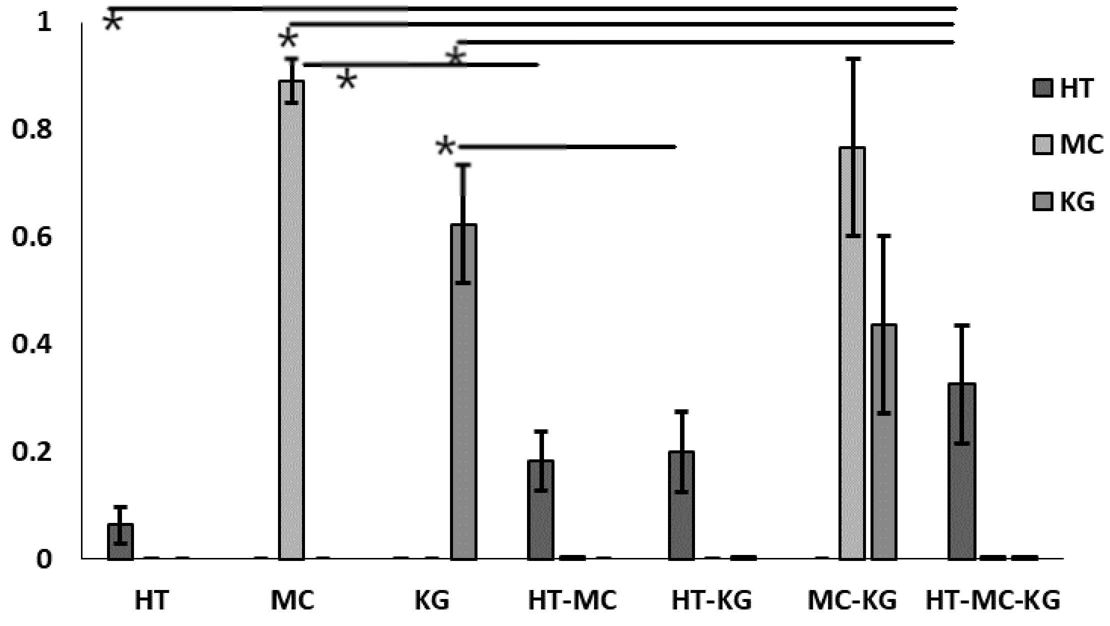
Species	**Growth (Body length)**	**Growth (Total length)**	**Time to metamorphosis**	**Metamorph size**
Hoplobatrachus	0.53 ± 0.06	1.58 ± 0.19	32.00 ± 2.86	19.82 ± 0.48
Microhyla	0.27 ± 0.03	0.88 ± 0.11	21.00 ± 1.44	6.88 ± 0.17
Kaloula	0.17 ± 0.02	0.48 ± 0.05	38.00 ± 2.64	9.86 ± 0.43

Table 4.2 Number of tadpoles surviving (mean ± SE) of the invasive *Hoplobatrachus tigerinus* (HT) and the native *Microhyla chakrapanii* (MC) and *Kaloula ghosi* (KG) across seven treatment types, in the mesocosm experiment.

Treatment	**N**	**HT**	**MC**	**KG**
HT	3	2 ± 1	-	-
MC	3	-	26.67 ± 2.50	-
KG	3	-	-	18.33 ± 3.28
HT-MC	4	2.75 ± 0.85	0	-
HT-KG	4	3 ± 1.15	-	0
MC-KG	2*	-	11.5 ± 1.20	6.5 ± 2.5
HT-MC-KG	4	3.25 ± 1.11	0	0

* Loss of two replicate pools due to contamination and overflow

Figure 4.1 Proportion of survival to metamorphosis in larval invasive *Hoplobatrachus tigerinus* (HT) and native *Microhyla chakrapanii* (MC) and *Kaloula ghosi* (KG), across seven treatments in a mesocosm experiment. Lines with asterix (*) denote statistically significant differences in species-specific survival between pairs of treatments, based on Kruskal-Wallis one-way analysis of variance tests and Dunn's test of multiple comparisons using rank sums.



DISCUSSION

Our findings support the hypothesis on reduction in survival of endemic larval anurans due to predation by invasive *H. tigerinus* tadpoles (hypothesis 1), to the extent of no survival of any native tadpoles. However, our hypothesis of *H. tigerinus* benefitting from preying on endemic anurans in terms of growth rate, time to metamorphosis and metamorph size (hypothesis 2), does not find statistical support; number of *H. tigerinus* tadpoles surviving does not vary between treatments. Our study, elucidating the impact of invasive larval *H. tigerinus* on two endemic species of the Andaman archipelago, is timely as the rapidly expanding invasion is likely to affect other native anurans including the many anuran species awaiting formal taxonomic re-assessments (Chandramouli et al., 2015).

Our findings augment the limited existing knowledge on the impact of amphibian invaders with carnivorous larvae (Kiesecker & Blaustein, 1997; Smith, 2005b). However, the complete extermination of native larval anurans by *H. tigerinus* (0 % survival) has not been observed either in the American bullfrog *Lithobates catesbeianus* (87.7% survival of syntopic native tadpoles; Kiesecker & Blaustein, 1997) or the Cuban treefrog *Osteopilus serpentrionalis* (35% survival of syntopic native tadpoles; Smith, 2005b), albeit with variation in experimental design. Apart from *M. chakrapanii* and *K. ghosi*, considered in our mesocosm experiment, the carnivorous larvae of *H. tigerinus* are likely to impact other native anurans breeding in ephemeral pools of human modified areas. Presently, the invading population of *H. tigerinus* is abundant in human modified landscapes and has only been reported from forest streams based on a few observations (Harikrishnan & Vasudevan, 2013). However, its recent exponential range expansion in the Andaman archipelago (Mohanty and Measey, *in press*) can result in substantial reproductive loss to native anurans across habitat types in the near future. Artefacts of landscape modification by humans, such as artificial ponds for aquaculture, facilitate the invasion of *H. tigerinus* in the archipelago (Mohanty and Measey, *in press*). Further, the presence of moats in areca nut and banana plantations serve as suitable habitat for larval *H. tigerinus* (NPM *pers. obs.*). Such facilitation of breeding populations of invasive anurans and their larvae by landscape modification could prove disadvantageous for native anurans.

The invasive population of *H. tigerinus* on the Andaman archipelago bred synchronously with the native anurans, thereby not limiting *H. tigerinus* larvae with size-dependent barriers to predation (Babbitt & Tanner, 1998). The remarkable rapidity of *H. tigerinus* predation on endemic larval anurans in the experiment precluded the possibility of any inter-specific competitive effects. Similarly, any reverse competitive effects on the invasive anuran due to native anurans (Cabrera-Guzmán et al., 2013) were not observed.

The increased survival proportion of *H. tigerinus* larvae in the presence of the two endemic larval anurans is likely a result of strong density-dependent survival than a treatment effect. This is reflected in the similar numbers of *H. tigerinus* surviving across treatments (Table 4.2). Such density-dependence of tadpole survival has been observed in invasive populations of the American bullfrog *Lithobates catesbeianus* (Govindarajulu et al., 2005) and has important implications for management of invasive *H. tigerinus* and similar anuran invaders (Vimercati et al., 2017). Govindarajulu and colleagues (2005) found removal of tadpoles for management to be detrimental to population control as it increased larval survival; instead, they recommended the targeted removal of post-metamorphic anurans (see also Vimercati et al., 2017).

However, inferences from mesocosm experiments have limitations, as the results may not be completely transferable to natural systems (Cabrera-Guzmán et al., 2013). In natural breeding sites of *H. tigerinus* in the Andaman archipelago, a range of additional effects can alter the magnitude of the impact via larval predation. Availability of other prey in the breeding sites (e.g. mosquito larvae; NPM *pers. obs.*) could offset the rapid predation on only larval anurans and consequently offset reduction in survival; conversely, moderate predation can increase survival of native species driven by density-dependence. Further, the presence of cover or refuge due to structural complexity of the natural breeding site could reduce predation rates (Babbitt & Tanner, 1998). Breeding asymmetry, given the likely prolonged breeding by some native anurans as compared to the explosive breeder *H. tigerinus*, may further reduce population-level impacts. Finally, other aquatic predators (e.g. odonates) can add further complexity to the interactions between larval *H. tigerinus* and native larval anurans (Smith, 2006). Despite these potential offsets to *H. tigerinus* impact, the lack of any survival of endemic anurans due to *H. tigerinus* predation points to the possibility of reproductive loss and population declines of native anurans on the Andaman archipelago.

Elucidating the larval impact of the invasive *H. tigerinus* has implications for other invasive anurans with carnivorous larvae, as well as other extralimital populations of this species. This study on larval impact of *H. tigerinus* consolidates the existing knowledge on the impact of its post-metamorphic stage through consumption of small endemic vertebrates and potential competition with larger native anurans for food (Mohanty & Measey, 2018). Our findings substantiate the need to manage invasive populations (or potential incursions) of *H. tigerinus* on Andaman archipelago and elsewhere.

5 Modelling invasion dynamics of an amphibian with frequent human mediated dispersal

Chapter to be submitted to *Ecological Modelling*

Co-authors: John Measey, Cang Hui

AUTHOR CONTRIBUTIONS

NPM, JM, and CH conceived the idea of the study; NPM collected the data; NPM and CH analysed the data; NPM wrote the manuscript, JM contributed to the writing.

ABSTRACT

Human influence on biological invasions is pervasive across the stages of introduction, establishment, and spread. Post introduction, human-mediated translocations (HMT) can alter the course of invasions by accelerating invasive spread. Therefore, modelling of invading organisms requires accounting for HMT along with complexities in demography, spatial context, and natural dispersal. We aim to disentangle these invasion dynamics for the Indian bullfrog, *Hoplobatrachus tigerinus*, on the Andaman archipelago (Bay of Bengal, India) to assess i) the effect of HMT on colonization rates, and ii) the efficacy of two potential management interventions in limiting invasive spread. We combined an age-structured demographic model allowing stage-based dispersal with a gravity model of human influence, in a spatially explicit modelling context. We parametrized the model using life-history and dispersal variables from *H. tigerinus* (or similar species), and remote-sensed variables describing spatial heterogeneity. The modelled invasion dynamics of *H. tigerinus* shows human influence can increase spread rates by a factor of three, as compared to invasion without human influence on spread. Such exacerbation of spread rates is driven by facilitation of both between and within island movements of *H. tigerinus* by humans. The model also predicted an overriding effect of HMTs on the origin of invasion. Of the two simulated management interventions, only constraining movement of *H. tigerinus* between islands was effective in limiting spread, but success was dependent on time elapsed since introduction. Based on model predictions, we find merit in recommending screening at points of entry (e. g. ports) for the hitherto uncolonized Baratang and Long Islands. Although the model provided insights into the human influence on invasive spread in an archipelago context, it did not perform optimally in estimating demographic dynamics and natural dispersal. We demonstrate the suitability of this modelling approach in understanding invasions in human-modified landscapes, especially between discrete units.

INTRODUCTION

Humans influence species dispersal by constraining and facilitating their movement across local, regional, and biogeographic scales (Trakhtenbrot et al., 2005). Biological invasions result from facilitated dispersal of species beyond their natural range, which may include jump and long-distance dispersals (Wilson et al., 2009). These facilitative movements are not limited to the 'introduction' stage but may continue well into the 'spread' stage (Blackburn et al., 2011; Hui & Richardson, 2017). Post introduction, human-mediated translocations (HMT) can alter the course of invasions by accelerating invasive spread (Kot et al., 1996; Wilson et al., 2009). For instance, Liu et al. (2014) demonstrated that these movements increase the spread rates of invasive herpetofauna globally. Human-mediated dispersals can also lead to long distance movements, establishment of satellite populations and help invasions cross climatic and physical dispersal barriers (e.g. the Argentine ant *Linepithema humile*, Suarez et al., 2001; the emerald ash borer *Agrilus* planipennis; Muirhead et al., 2005).

Within their extra-limital range, species may disperse through a combination of natural diffusive spread and HMT (Hui & Richardson, 2017). Further, HMT can operate via multiple pathways, which may be intentional or unintentional (Kraus & Campbell, 2002; Ficetola et al., 2007; Hulme, 2009). These pathways may also operate on different life-stages of invading organisms (Christy et al., 2007). Spatial heterogeneity of the landscape in terms of physical connectivity, human population, and human connectivity are known to influence invasions (e. g. Bossenbroek et al., 2001). Finally, life-history stages may display differential fecundity, survival, and natural dispersal probabilities.

Therefore, modelling of invading organisms requires accounting for complexities in life-history stages, spatial context, natural dispersal and HMTs.

Several models have been developed to assess invasive spread over time and space (see review in Hastings et al., 2005). To model invasive spread between discrete units (e.g. habitat islands), several variants of gravity models, network models and metapopulation models are in use (Hui et al., 2013; Hui & Richardson, 2017). Gravity models are particularly suitable to predict HMTs, as the models can be informed by proxies of human influence (e.g. population density) and connectivity between units (e.g. distance). In general, gravity models develop a matrix that calculates the flow of individuals between units based on distance and attractiveness (Thomas & Hugget, 1980). Several aquatic and terrestrial invasions have been evaluated using gravity models (Schneider et al., 1998; Leung and Mandrak, 2007; Carrasco et al., 2010).

Invasion of amphibians dependent on lentic water bodies can be characterized by a modelling context of discrete units. For example, a ‘ponds as patches’ approach has been used in modelling population dynamics of several amphibians (Skelly, 2001; Vimercati et al., 2017a). Stage-based matrix models are classically used in population ecology to incorporate differential fecundity and survival in each life-history stage (Crouse et al., 1987) and have been used to model invasion dynamics of amphibians with complex life-histories (Govindarajulu et al., 2005; Vimercati et al., 2017b). Natural dispersal is generally characterized by a dispersal kernel, a probability density function explaining the relationship between distance and dispersal probability. It is critical to use accurate kernels as variation in the kernel shape can alter spread rates significantly (Kot et al., 1996).

Modelling invasion dynamics can benefit planning of management interventions by identifying factors which facilitate (or constrain) demography and dispersal. For example, Govindarajulu et al. (2005) recommended targeted removal of metamophs and juveniles, given their high influence on population growth of invasive American bullfrogs *Lithobates catesbeianus*. Using gravity models for zebra mussel invasions, Schneider et al. (1998) recommended aiming prevention efforts not directly at the high-risk habitats but rather at the currently uncolonized but likely future sources of invasions. Spatially explicit modelling of such factors can lead to a better understanding of management constraints (e.g. limited access to ponds, Vimercati et al., 2017a), while conferring flexibility to implement interventions. For example, the disproportionate influence of certain spatial units on invasions can be identified (e.g. ‘transport hubs’; Floerl et al., 2009), and subsequently these sites can be prioritized for management.

We aim to disentangle the invasion dynamics of the Indian bullfrog, *Hoplobatrachus tigerinus*, on the Andaman archipelago (Bay of Bengal, India). This large discroglossid frog (snout-vent length up to 160 mm) has been spreading on human inhabited islands of the archipelago since its introduction in 2000-01, colonizing at least 58 villages on six islands (Mohanty & Measey, *in press*). Movement between islands is presumed to be driven by HMTs as these salt intolerant amphibians cannot cross salt-water channels, over the short span of 18 years. As the frog is synanthropic and seldom occurs in dense forests (Daniels, 2005), its occurrence on the archipelago is currently limited to rural settlements with diffusion into secondary forests. Two major pathways of HMTs occur, with tadpoles moved as ‘contaminants’ of fish culture, and adults intentionally transported and ‘released’ for consumption; ‘stowaway’ in cargo is considered unlikely (Mohanty & Measey, *in press*). Both adults and tadpoles can have ecological impact on small vertebrates, including native anurans (Mohanty & Measey, 2018; *submitted*) and economic impacts on activities such as poultry and aquaculture (Mohanty & Measey, *in press*). *Hoplobatrachus tigerinus* is native to the Indian subcontinent and is protected under Schedule IV of the Indian Wildlife Protection Act. There is currently no management of the invading population on the Andaman archipelago. The autecology of the species is generally well known, especially for its reproductive biology (Saidapur, 2001).

In this study, we aim to evaluate the invasion dynamics of the Indian bullfrog *Hoplobatrachus tigerinus* on the Andaman Islands, using an approach which integrates demographic growth, natural dispersal, and HMT. Specifically, i) we reconstruct the invasion until the present and predict future spread, ii) quantify the effect of HMT on colonization rates, and iii) assess the efficacy of two potential management interventions in limiting invasive spread. Finally, we explore the generality of the model for application in other invasions.

METHODS

We describe a model of *H. tigerinus* invasion dynamics using the overview-design concepts-details framework (Grimm et al., 2006; 2010), which helps to systematically isolate and explain model components.

1. Purpose

The model's purpose is to simulate population dynamics of the invasive *H. tigerinus* on the Andaman archipelago, based on fecundity, survival, and dispersal.

2. Entities, state variables, scales

The age-structure model of integrodifference equations involves 87 potentially colonizable sites as model entities located on eight islands (Fig. 5.3). These sites are interspersed in a matrix of forests, which are only used as transitory patches during dispersal. Each site is characterized by the number of ponds, carrying capacity, geolocation and the number of individuals belonging to each of the four life-history stages (eggs, tadpoles, juveniles and adults). To calculate total number of ponds per site, we used Google Earth imagery taken in November 2016 (observed at a height of 300 m or less) and identified ponds and streams. Streams typically break into a series of ponds in the dry season. Each stream was assumed to be equivalent to 20 ponds; although, the length of a stream flowing through a site could be heterogenous, its equivalence to pond number was fixed for simplicity. Carrying capacity of each site was computed as the product of mean density of individuals per pond (111.5 ± 39.5, $n = 5$; NPM unpublished data) and the total number of ponds. As the density estimate is based on sampling at sites with moderately old invasions (ca. 5-8 years), and they are unlikely to have attained carrying capacity, we augmented the carrying capacity values by 20%.

Number of individuals at each site is influenced by population dynamics at the site and dispersal out of and into sites. Dispersal is either natural and/or human-mediated and occurs at specific life-history stages. All sites are uncolonized at the first time-step in the model, except the initialization site(s).

3. Process overview and scheduling

One time-step in the model is equivalent to one year, within which individuals at the four different life-history stages are processed. We do not consider metamorphs as a separate life-history stage as the duration of this stage in *H. tigerinus* is very short due to fast growth (Gramapurohit et al., 2004), and we assume it to be identical to juveniles in terms of ecology and survival. The life-history stages progress from one to the next sequentially, from eggs to tadpoles to juveniles and finally to adults. All eggs laid in a year become tadpoles and then juveniles within the same time-step. Maturing probability is sex-biased, with a proportion of males maturing in one year and the remaining males along with all females maturing the year after (Gramapurohit et al., 2004). The model runs for 50 time-steps, corresponding to the years 2000 to 2050. Only adults breed and may disperse naturally along with juveniles, whereas eggs and tadpoles do not disperse. Human-mediated dispersal operates through two pathways, with intentional 'release' pathway operating on adults and unintentional 'contaminant' of aquaculture pathway operating in the case of tadpoles only (Mohanty & Measey, *in press*).

4. Design concept

4.1. Emergence of system level phenomena

The number of sites (and islands) colonized and the total number of adults are obtained for each time-step, after undergoing breeding, survival, and dispersal.

4.2. Sensing

Individuals are assumed to know their age and follow the natural dispersal kernel accordingly.

4.3.Interaction

Competitive interaction only take place as adults. As *H. tigerinus* breeds once per year in ephemeral pools formed in heterogenous landscapes adjoining ponds, breeding pairs are assumed to lay eggs uniformly across a site with no density dependent effects on tadpoles. Further, no between-stage interactions are assumed to occur.

4.4. Stochasticity

Most parameters of the model involve no stochasticity, with only propagule size of human-mediated dispersal pathways being stochastic. Propagule size for 'release' pathway is a random number between two to eight adults (Mohanty & Measey, *in press*), whereas, for the 'contaminant' pathway it is between 20 to 40 tadpoles (assumption). The sub-component, gravity model for human-mediated dispersal involves random sampling of sites over a threshold (see below).

4.5.Observation

Total number of sites colonized and corresponding number of islands colonized are calculated by the model for each time-step. We compare colonization rates to existing distribution data from the field up untill 2015-16 (Mohanty & Measey, *in press*).

5. Initialization

We set the initial location of *H. tigerinus* introduction to Nimbudera on Middle Andaman Island and/or Madhupur on North Andaman Island, based on key informant surveys (Fig. 5.3; Mohanty and Measey, *in press*). Twenty adults were considered to be present at model initialization, with a sex ratio of 1:1.

6. Input data

We provided the model with the list of sites and associated islands, number of ponds per site, proportion of population (as adults and juveniles) dispersing out of sites and into other sites based on distance (see natural dispersal), and a gravity matrix containing likelihood of HMT (see *Human-mediated translocations*).

7. Sub-models

7.1. Demographic dynamics

We parameterized the age-structured model with fecundity, survival, and maturity variables (Table 5.1). The number of eggs laid by females is an outcome of clutch size (φ_n), and the adult sex ratio (s). The model differentiates between males and females at each life-history stage. A proportion of eggs survive (σ_e) to become tadpoles, where tadpole survival (σ_t) is derived from mesocosm experiments on *H. tigerinus* (Mohanty & Measey, *submitted*). Juveniles are then subject to survival (σ_j), where a proportion of juvenile males mature early (p) in one time-step; juveniles that mature into adults, experience survival (σ_a) over years (in a loop). Population is constrained by the maximum carrying capacity (k) of each site as,

$$\mathrm{N}_{\mathrm{adufinal}} = \left(\frac{\mathrm{N}_{\mathrm{aduinitial}}}{1 + \mathrm{N}_{\mathrm{aduinitial}}}\right) * k$$

where, $\mathrm{N}_{\mathrm{aduinitial}}$ and $\mathrm{N}_{\mathrm{adufinal}}$ are the number of adults at a site before and after constraining by the carrying capacity respectively. Egg laying at a site is only possible if the number of adults at the site are equal to or greater than a ‘breeding threshold’ (h), regulating establishment.

7.2. Dispersal dynamics

7.2.1. Natural dispersal

Inter-island movement is constrained for natural dispersal. Adults and juveniles disperse following the log normal dispersal kernel obtained from capture-mark-recapture data of *Lithobates catesbeianus* (Raney, 1940), a similar-sized ranid. The kernel describes the proportion of individuals dispersing out of site based on the Euclidean distance to other sites,

$Y = \frac{1}{1.45x2\pi} e\wedge\frac{-(lnx-11.29)}{4.21}$; where, ‘x’ is the distance (in meters).

The proportion of population dispersing between sites is given by the natural dispersal matrix c [i, j]. The matrix is derived from the Y values for each pair of sites i and j. As we adapt this dispersal kernel to a human dominated landscape, a dispersal cost of 0.5 and 0.3, is incorporated for adults and juveniles respectively to account for additional mortality during dispersal (e. g. road kills or increased visibility to predators).

7.2.2. Human-mediated translocations

The movement of adults and tadpoles by humans within sites is simulated with a production-constrained gravity model, adapted from Bossenbroek et al. (2001). The probability of sites exchanging individuals is based on the total number of ponds in both sites, as the number of ponds is assumed to be proportional to the surrounding human population, and consequently to trade and human interaction with *H. tigerinus*. Further, sites with high number of ponds are likely to practise aquaculture of freshwater fish, a major HMT pathway for *H. tigerinus* on the Andaman Islands (Mohanty & Measey, *in press*).

The probability of *H. tigerinus* movement by humans is given by,

$$d\ [i, j] = N_{ponds,j} * N_{ponds,i} * C^{\alpha}\ ;$$

where, N_{ponds} is the number of ponds at a site, 'C' is the connectivity between two sites, and 'α' is a power function related to the relative likelihood of movement over high connectivity and low distances.

Connectivity between two sites is considered proportional to the road type of donor and recipient village (major-major:4, major-minor/minor-major:2, minor-minor:1) and inversely proportional to island connectivity (within island:1, islands connected by bridge/line ferry:2, direct ferry:4, single-stop over ferry:8, double-stop over ferry:16) and Euclidian distance between sites (measured on ArcMap 10.6.2).

In this sub-model, only colonized sites with more than 1000 adults (ca. 10 colonized ponds) are allowed to serve as donors; this accounts for detection and sampling opportunity for humans at colonized sites. Further, each site can donate only once per each time step whereas sites can receive multiple transfers. This constraint stems from the fact that stakeholders participating in *H. tigerinus* dispersal are a subset of the population and would limit the number of transfers (Mohanty & Measey, *in press*). To select HMT events between site pairs, a random number is sampled from a uniform distribution between 0 to $d\ [i, j]$. If the random value is higher than an event probability threshold (m), then dispersal takes place. In each dispersal event, a random number of adults between two to eight and/or tadpoles between 20 to 40 are moved from the donor site to the recipient site. The proportion of individuals being extracted from a site is assumed to be extremely small, such that it has no effect on the remaining population.

Table 5.1 Baseline values of parameters used in the model to evaluate the invasion dynamics of the Indian bullfrog *Hoplobatrachus tigerinus* on the Andaman Islands. Variables marked with * represent values adopted from the American bullfrog *Lithobates catesbeianus*. 'HMT' denotes human-mediated transloctaions.

Parameter	**Baseline value**	**Source**
Clutch size(φ_n)	6000	Oliveira et al., 2017
Sex ratio(s)	0.5	Inferred in Gramapurohit et al., 2004
Egg survival(σ_e)	0.41	Dash & Hota, 1980
Tadpole survival(σ_t)	0.2	Mohanty & Measey, *submitted*
Juvenile survival(σ_j)*	0.08	Govindarajulu et al., 2005
Juvenile maturity(p)	0.4	Gramapurohit et al., 2004
Adult survival(σ_a) *	0.32	Govindarajulu et al., 2005
Breeding threshold(h)	2	Assumption
Initialization site	Nimbudera (Middle Andaman)	Mohanty & Measey, *in press*
Initialization propagule	20	Assumption
HMT threshold(m)	0.01	Assumption
Dispersal cost (adult)	0.5	Assumption
Dispersal cost (juvenile)	0.3	Assumption

We simulate two potential management interventions: i) stopping HMT between islands by screening at entry and exit points and ii) targeted restriction (through awareness generation) of HMT from sites with large number of ponds (> 150, n = 5). Such sites are likely to serve as 'dispersal hubs' by acting as donors and influence invasive spread (Mohanty & Measey, *in press*). These are the two likely 'preventive' interventions which can be considered in the Andaman archipelago, in the absence of policies supporting population management. We test the efficacy of these interventions in limiting colonization rates, on their own and in combination. Further, we model these actions over six different time-steps since the beginning of the model (1, 5, 10, 15, 20 and 30 years) to identify points of interventions which limit spread. Each intervention is modelled to continue from the time-step it is in place until the final time-step. All model variants were scripted in Python (version 2.7).

RESULTS

The model, incorporating both natural dispersal and HMT, predicted spread to begin with a very short lag phase (2000-03), followed by an exponential growth phase (2004-08) and subsequently a dominance phase (2009 onwards; Fig. 5.1). In the absence of human influence, spread remained limited to the island of origin (Fig. 5.2). As compared to only natural dispersal, HMT boosted spread by a factor of 3 for invasions originating on one island (Middle Andaman or North Andaman) and a factor of 1.53 if invasions began on both islands simultaneously. Irrespective of single or multiple origins, invasions with HMTs were modelled to colonize 77.38 ± 0.22 sites out of 87 (88.5%) sites by 2010 (Fig. 5.1).

The effect of HMT on within-island spread varied with origin of invasion (Supplementary Information 1). Spread rates were augmented by HMT for invasions originating on only Middle Andaman and for invasions with origins on both Middle and North Andaman, but not in the case of invasions originating on only North Andaman (Supplementary Information 1). In the two cases of boosted spread, a colonization asymptote was attained in 9 years as compared to 15 years under conditions of only natural dispersal (Supplementary Information 1). The model predicted intentional movement of adults to be the only pathway with any effect on spread rates, whereas unintentional movement of tadpoles was inconsequential.

Figure 5.1 Modelled invasive spread of the Indian bullfrog *Hoplobatrachus tigerinus* on the Andaman Islands, from 2000 to 2050. Both human-mediated translocations and natural dispersal occur in the model, beginning from Nimbudera (Middle Andaman Island) and/or Madhupur (North Andaman Island).

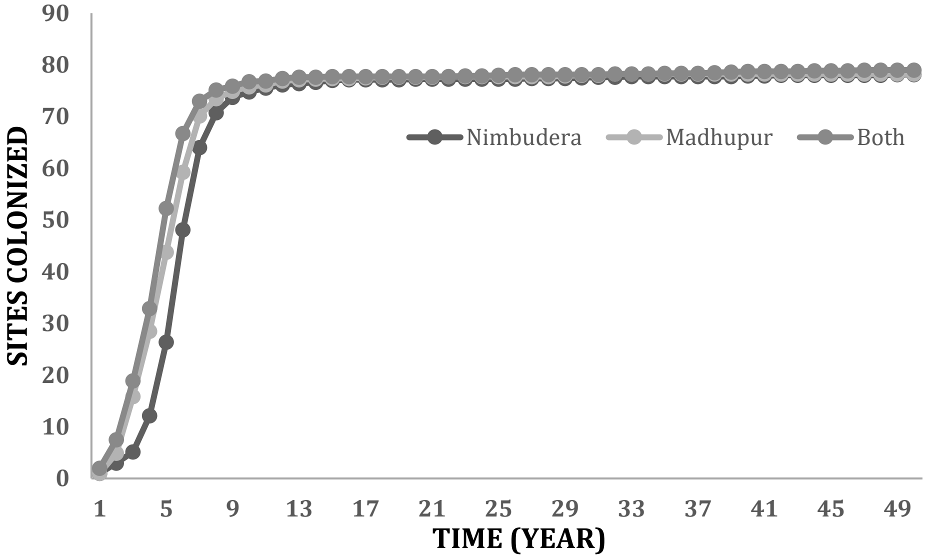
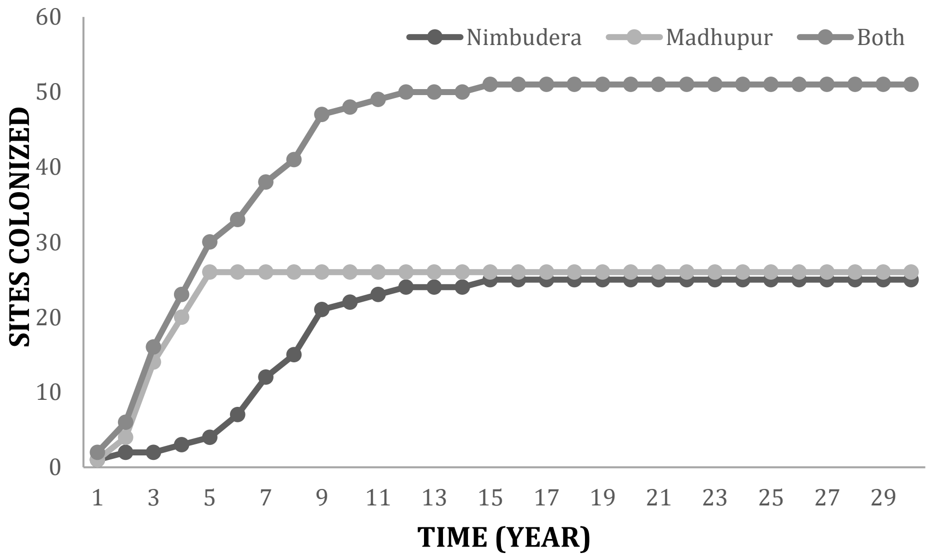


Figure 5.2 Modelled invasive spread of the Indian bullfrog *Hoplobatrachus tigerinus* on the Andaman Islands, from 2000 to 2030. Only natural dispersal occurs in the model, beginning from Nimbudera (Middle Andaman Island) and/or Madhupur (North Andaman Island).



The current model did not match field data, which estimated a spread to 63% sites till 2015-16 (Mohanty & Measey, *in press*) and overpredicted spread by 25%. Further, the lag phase of seven years (2001-08) reported in the reconstructed invasion history (Mohanty & Measey, *in press*) was much shorter (three years) in the model output. Spatially, the model predicted colonization of five out of eight islands until 2015-16, leaving out Neil and Long, and Baratang Islands (Fig. 5.3), however, 12.5% iterations of the model colonized Baratang Island (by 2027). Deviating from this pattern, field data observed colonization of Neil but not Little Andaman by 2015-16 and subsequent colonization of Little Andaman in 2017 (Mohanty & Measey, *in press*).

Of the two modelled management interventions, only constraining human mediated movement of frogs between islands reduced spread rates (Fig. 5.4a), whereas stopping transfers from large sites (>150 ponds) had no effect (Fig. 5.4b). Management by constraining movement between islands, was successful in limiting spread to two islands upon intervention in 2005; interventions in later stages of the invasion (2010-2025) could only restrict colonization of one island (Fig. 5.4a). Sensitivity analyses (Supplementary Information 2) demonstrated the spread rate to be indifferent to changes in adult threshold and initial propagule number. Fecundity lower than 1000 (i.e. <2000 eggs), HMT threshold greater than the baseline value of 0.01, tadpole survival lower than the baseline value of 0.2 reduced spread rates; juvenile survival higher than the baseline of 0.08 increase spread rate (Supplementary Information 2).

Figure 5.3 Modelled invasive spread of the Indian bullfrog *Hoplobatrachus tigerinus* to 87 sites on eight islands of the Andaman archipelago.

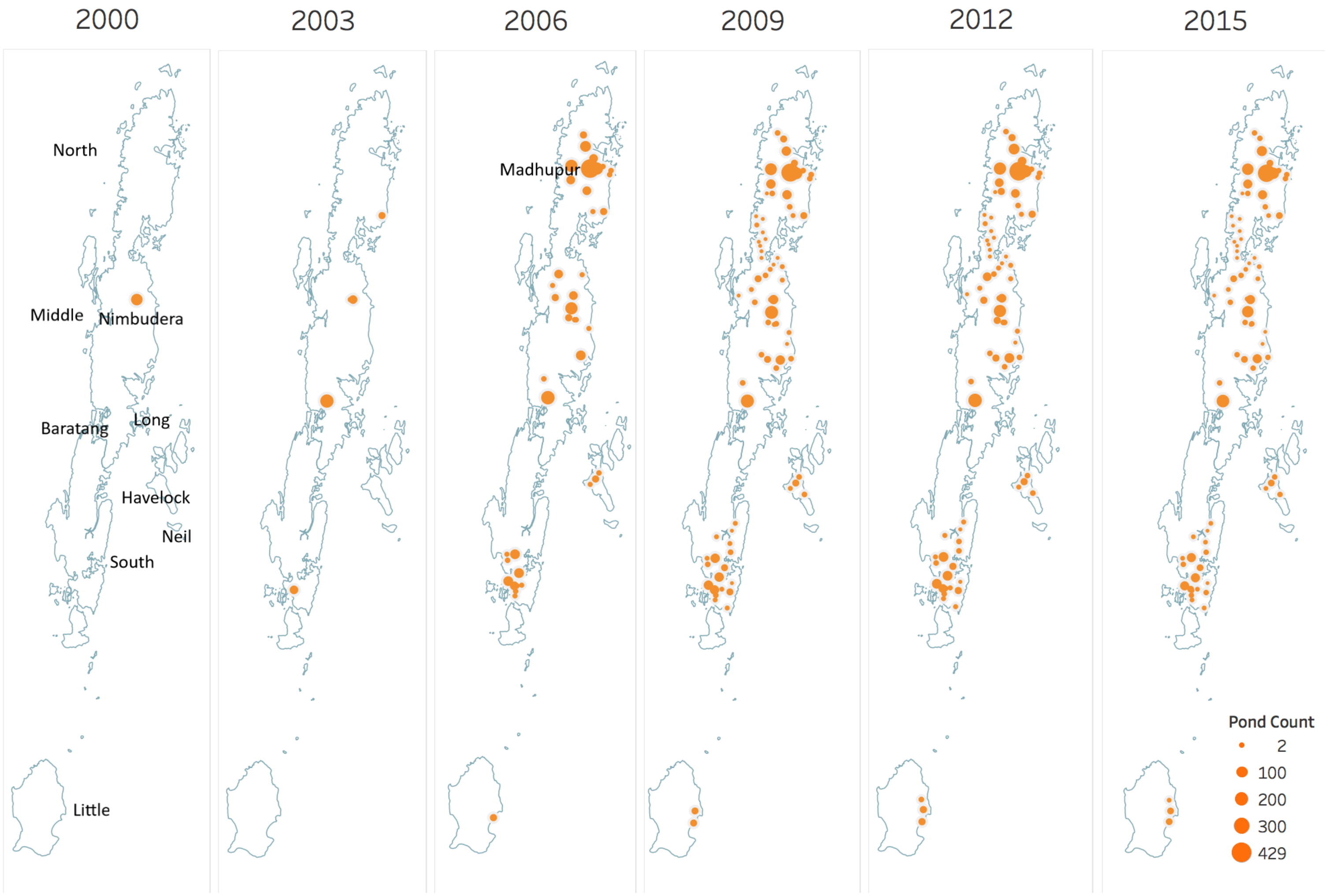
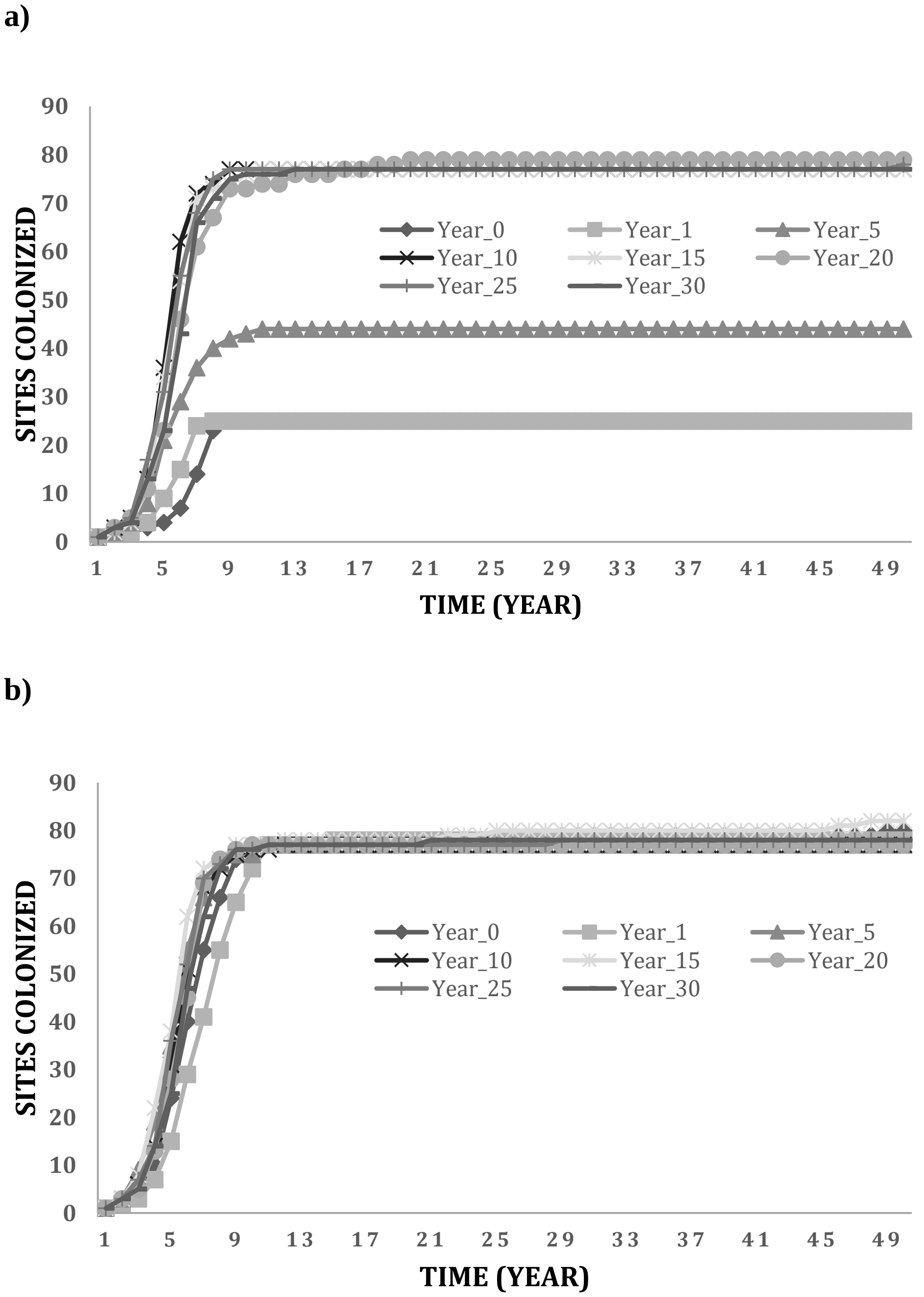


Figure 5.4 Modelled invasive spread of the Indian bullfrog *Hoplobatrachus tigerinus* on the Andaman Islands, from 2000 to 2050. Both human-mediated translocations and natural dispersal occur in the model, with simulated management interventions limiting movement of frogs between islands (a) and from targeted sites (number of ponds > 150). Management is enforced at different years since the beginning of the invasion (0th year to 30th year).



DISCUSSION

In this study, we built a spatially-explicit model incorporating dynamics of demography, natural dispersal, and HMT for an invasive amphibian. We parametrize the model using life-history and dispersal variables from the Indian bullfrog *Hoplobatrachus tigerinus* (or similar species), and remote-sensed variables describing spatial heterogeneity. Our modelling approach attempts to incorporate realism of invasions in human modified landscapes and simulates HMTs of differential life-history stages. We identify a significant role of HMTs in boosting invasive spread, demonstrate the utility of proxies to model human influence, and evaluate the efficacy of potential management interventions.

The modelled invasion dynamics of *H. tigerinus* shows human influence can increase spread rates by a factor of three, as compared to invasion without human influence on spread. As the model context is an archipelago, this enhancement in spread is primarily due to facilitation of between island movements of *H. tigerinus*. The model predicted an overriding effect of human influence on the origin of invasion (beginning on Middle Andaman and/or North Andaman Islands), where spread rates converge for all three origin scenarios (Fig. 5.1). The invading population of *H. tigerinus* on the Andaman archipelago is likely to have multiple introduction events (Mohanty & Measey, *in press*) from the Indian mainland along with frequent HMTs within the archipelago. Multiple introduction events have been demonstrated to alleviate founder effects in invasions (Kolbe et al, 2004; Dlugosch & Parker, 2007; Ficetola et al., 2008). Similarly, secondary translocations may counter founder effects of invasions by promoting gene flow between satellite populations, in addition to boosting spread.

The model predicted the ‘release’ of adults to be the only HMT pathway with influence on spread, rendering the tadpole ‘contaminant’ of aquaculture pathway ineffective. However, this is an artefact of the propagule size for each translocation event for tadpoles (assumed to be 20 to 40). Parametrization of this variable based on field data (as for adults, Mohanty & Measey, *in press*) can lead to a better model that would enable disentangling the relative importance of the two pathways. We inititated the current model with 20 adults (10 of each sex). However, initialization with varying propagule sizes of tadpoles should be considered. This is likely to result in a greater lag in establishment and spread.

The modelled predictions support the role of within island translocations in boosting spread of *H. tigerinus*; colonization asymptotes are reached six time-steps earlier than in the case of only natural dispersal (Supplementary Information 1). This results in a greater number of colonized sites earlier in the invasion which can further accelerate the invasion by enabling more translocations. Apart from facilitating movement across dispersal barriers between islands, within island movements by humans are known to escalate invasions of other amphibians (*Eleutherodactylus coqui* on Hawaii, Kraus & Campbell, 2002; *Duttaphrynus melanostictus* on Madagascar, F. Licata *pers. comm*). Overall, HMT within the extra-limital region is frequent in invasions of many amphibians (Kaiser et al., 2002; Lobos & Jaksic, 2005; Ficetola et al., 2007) and other taxa (Hui & Richardson, 2017). Therefore, human influence on invasive spread must be modelled to achieve realistic predictions.

The modelled invasion dynamics of *H. tigerinus* predicted a faster spread as compared to the field data (Mohanty & Measey, *in press*). This is likely an artefact of the model allowing HMT to occur from the initialization step (in 2000), whereas, such dispersals may be constrained by a lag in human detection and use of the species. The model under predicted island colonization, limiting the invasion to five islands as compared to the observed six (Mohanty & Measey, *in press*). However, model prediction of island colonization experienced stochastic changes and one in eight model iterations colonized Baratang Island. The contrasting influence of connectivity and attraction (number of ponds per site as proxy) on HMT is illustrated with the earlier colonization of the distant Little Andaman Island as compared to Baratang Island, which is closer to the origin of invasion on Middle Andaman Island. Interestingly the site first colonized on Little Andaman in the model corresponds to the only site on Little Andaman where recent field observations (2018) detected the species (Mohanty & Measey, *in press*).

We simulated two preventive management interventions, which constrained translocations between islands and/or limited translocations from likely donor sites (with greater than 150 ponds). The failure of the latter approach to limit spread indicates that several other sites could serve as donors and contribute to HMT. This is supported by field observations where 'Webi' village, with only 32 ponds served as a donor for at least four introductions (Mohanty & Measey, *in press*). Such patterns may arise due to socio-cultural linkages between villages that influence human movement, which are not accounted for in the model. The cost effectiveness of early mitigation is well established for invasions (Simberloff et al., 2013; Van Wilgen et al., 2014) and is reflected in the decreasing efficacy of 'island constrained' management in limiting spread over time. However, we find merit in recommending screening at points of entry (e. g. ports) for the hitherto uncolonized islands of Baratang and Long Islands, and to prevent invasions onto the currently uninvaded Nicobar Islands. Future research must evaluate the efficacy of population control/eradication methods (Loulette et al., 2013) alongside preventive approaches to formulate management strategies (Vimercati, 2017; Vimercati et al., 2017a) for *H. tigerinus*.

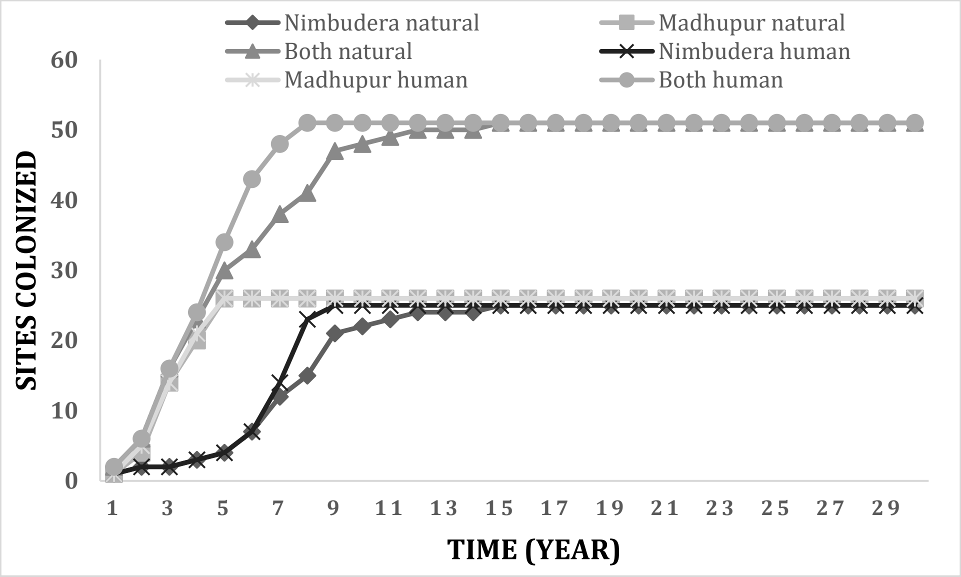
Although the model provided insights into the human influence on invasive spread in an archipelago context, it did not perform well in estimating demographic dynamics and natural dispersal. The model was sensitive to alteration in fecundity and to a lesser extent to changes in juvenile survival (Supplementary Information 2) which should ideally be estimated for the species under field conditions (Biek et al., 2002; Govindarajulu et al., 2005; Vimercati et al., 2017b). As we parameterized the model with several estimates obtained in captivity, and from a different species (*L. catesbeianus*; see Table 5.1), the model is not optimal. Similarly, in the absence of species-specific data for *H. tigerinus* we modelled natural dispersal using a dispersal kernel obtained from mark-recapture data on *L. catesbeianus* (Raney, 1940). Although we controlled natural dispersal by incorporating dispersal costs of moving through human dominated landscapes, the model results indicate over-prediction of spread. For example, an established population of *H. tigerinus* on South Andaman Island is yet to spread to nearby sites, seven years after initial establishment (Mohanty & Measey, *in press*). Variation in dispersal kernels can have significant effects on spread rates (Kot et al., 1996), making it essential to obtain reliable kernels based for the target invasive species (Smith & Green, 2005; De Villiers & Measey, 2017). Further, the model did not incorporate change in natural dispersal and life-history traits, which are known to evolve during range expansion (Phillips et al., 2008; Burton et al., 2010; Shine et al., 2011; Alex Perkins et al., 2013).

The combined modelling of demography, natural dispersal, and HMT is particularly useful for species likely to be translocated intentionally or unintentionally in the extra-limital region (Hui & Richardson, 2017). As amphibians are frequently translocated in their extra-limital region (Liu et al., 2014; Stringham & Lockwood, 2018), modelling the likelihood of such human facilitated events using simple proxies can be highly informative for management. We used the abundance of ponds to model carrying capacities and the likelihood of human facilitations; the positive influence of artificial water bodies on amphibian invasions is well documented (Govindarajulu et al., 2005; Davies et al., 2013; Vimercati et al., 2017b). Several modelling approaches assessing invasion dynamics, incorporate human influence using readily available surrogates (Kizuka et al., 2014). For example, population density of sites (Gilbert et al., 2004) and recreational boat use (Bossenbroek et al., 2001) have been used as proxies for spatial heterogeneity to model invasion risk. Similarly, Rebaudo et al. (2011) used gravity models to include socially induced heterogeneity.

Despite limited success in modelling natural dispersal and demographic dynamics, our model predicted HMT and consequent invasive spread well. We demonstrate the suitability of this modelling approach in understanding invasions in human modified landscapes, especially between discrete units (e. g. island systems). Using data from literature, GIS, and field experiments, we simulate the complex phenomenon of human mediated translocations to predict invasive spread. The model provides a basic framework to further incorporate stochasticity in life history and dispersal variables to better understand the dynamic process of invasions.

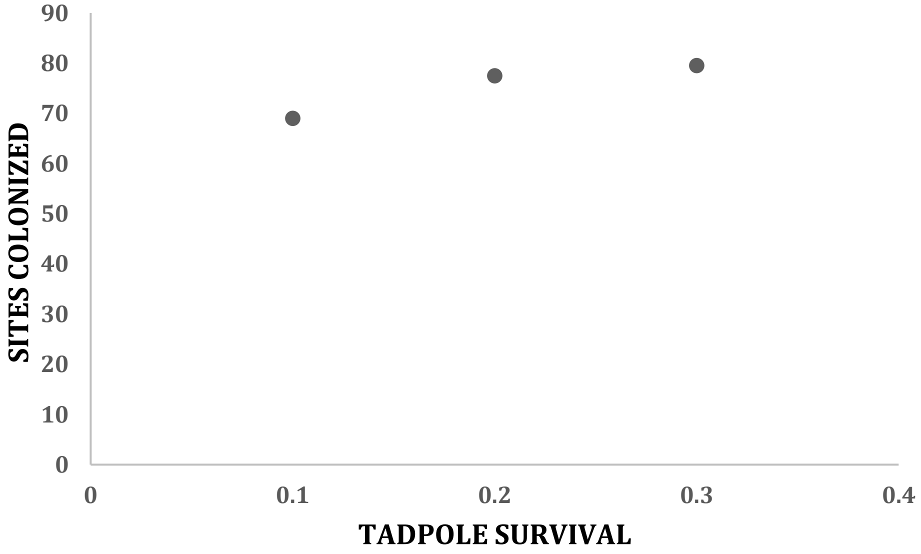
Supplementary Information 1

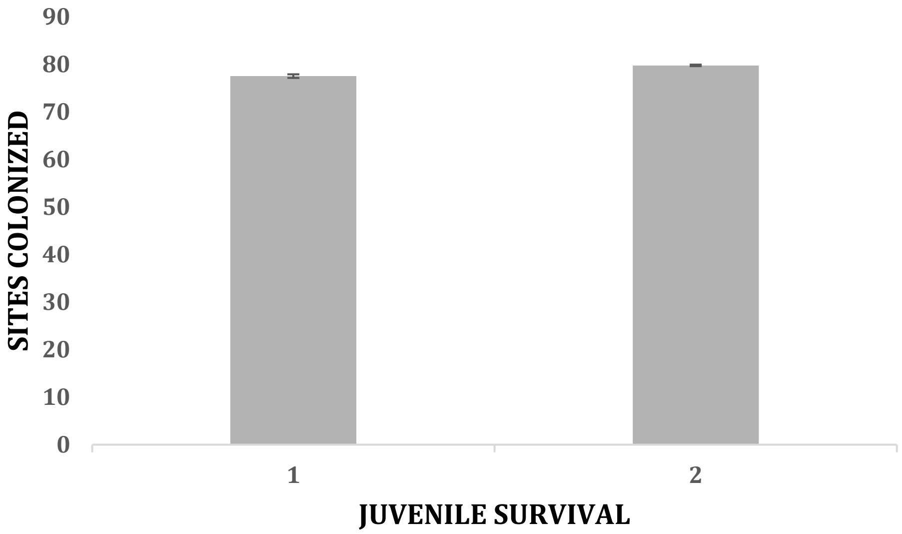
Modelled invasive spread of the Indian bullfrog *Hoplobatrachus tigerinus* on the Andaman Islands, from 2000 to 2030. Natural and human mediated dispersal constrained to within island of origin on Middle Andaman (Nimbudera) and/or North Andaman (Madhupur).



Supplementary Information 2

Invasive spread (sites colonized) of the Indian bullfrog *Hoplobatrachus tigerinus* at the end of model run (time-step 50), based on variation in model parameters: tadpole survival (0.1-0.3), juvenile survival (0.08, 0.13), adult threshold (2-18), human-mediated translocation (HMT) threshold (0.01 – 0.09), fecundity (500-1500 corresponding to a clutch size of 2000-6000) and initial propagule for each sex during introduction (5-15).

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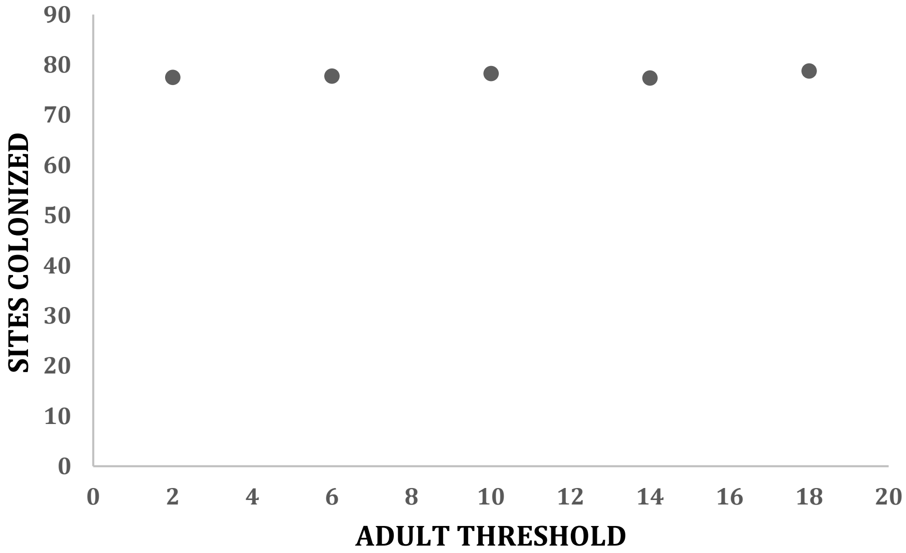
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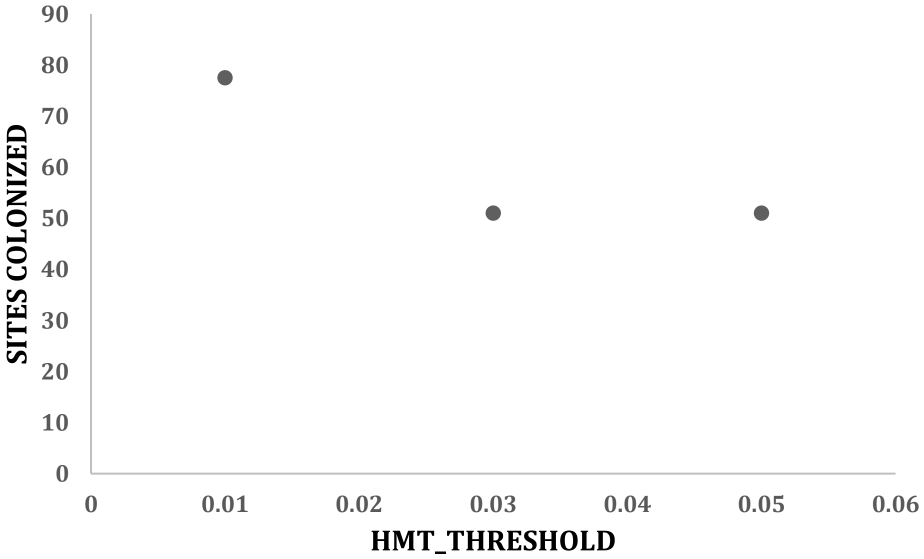
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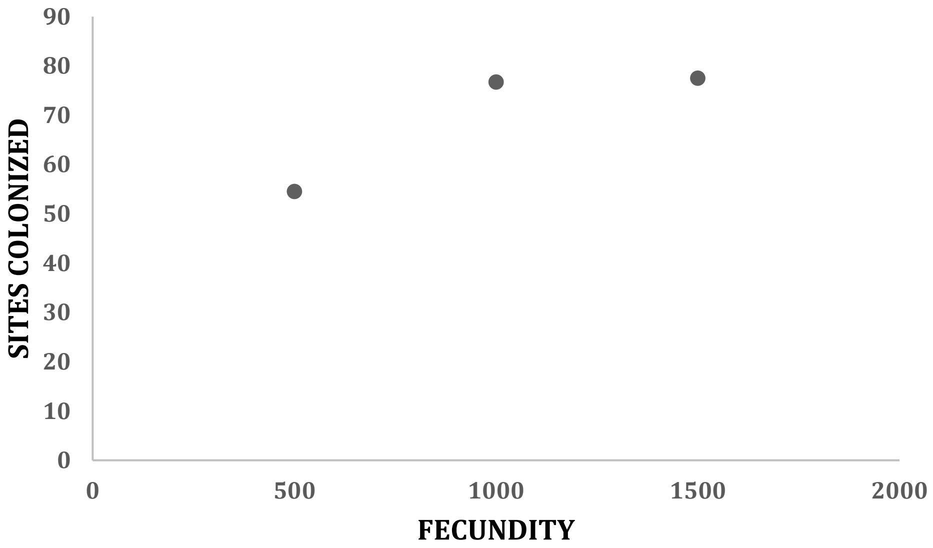
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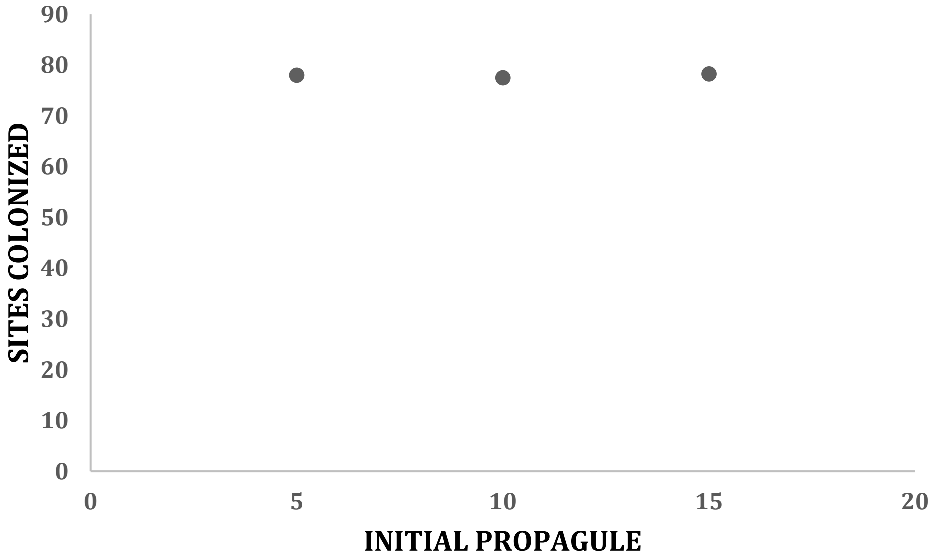
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INITIAL PROPAGULE

6 The Indian bullfrog *Hoplobatrachus tigerinus*: Extra-limital populations and global invasion potential of a large dicroglossid frog with carnivorous tadpoles

Chapter to be submitted to *Neobiota*

Co-authors: John Measey, Angelica Crottini

AUTHOR CONTRIBUTIONS

NPM and JM conceived the idea of the study; NPM and AC collected the data; NPM and JM analysed the data; NPM wrote the manuscript, AC and JM contributed to the writing.

ABSTRACT

Amphibians are an emerging group of invaders, with increasing global frequency of invasive populations. Invasive amphibians have considerable ecological impact on the recipient system, yet, taxonomic biases in assessments of amphibian invasions limit risk assessments. 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 species-traits and human-interaction, status of its extra-limital populations and global invasion potential have not been assessed. In this paper, our goal is to provide a profile of *H. tigerinus* as an invasive species to aid in risk assessment and management exercises. We reviewed the available knowledge on extra-limital populations of *H. tigerinus*, modelled its potential distribution in the introduced range and global invasion potential, and assigned species-level scores for ecological and socio-economic impact. Apart from the Andaman archipelago, we could only confirm another successful invasion on Madagascar. Reported populations on Maldives and Laccadive Islands do not have recent substantive records for validation; Thailand and Cuba have captive individuals and do not have confirmed populations in the wild. Of the three species distribution models built to predict globally suitable regions for *H. tigerinus*, the generalized boosting model

(‘GBM’) performed relatively better than other models (AUC = 0.86, TSS = 0.57). Mean precipitation of wettest quarter had relatively high importance (46.3%), followed by HII (27.2%), and isothermality (26.4%). We identified Nicobar Islands, Mascarene Islands, Malaysia and Indonesia, and East Africa to be likely recipients of bridgehead invasions. We assigned a score of ‘Moderate’ for ‘Socio-Economic Impact’, on account of reduction human activities of poultry keeping and threat to aquaculture. Similarly, ‘environmental impact’ was assigned a score of ‘Moderate’, based on documented population extirpations of native anurans.

INTRODUCTION

Invasive amphibians have environmental impact proportional to that of invasive birds and fish (Measey et al., 2016), along with a considerably high socio-economic impact (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), although ca. 100 non-native amphibians could possibly be considered with a level of uncertainty (Kraus, 2009; Measey et al., 2016). A recent review of extra-limital occurrence of amphibians recorded 263 species, including those in trade and captivity (van Wilgen et al., 2018). Further, the increase in extra-limital populations of amphibians has accelerated in recent decades (Seebens et al., 2017). However, studies on amphibian invasions are heavily taxon-biased. For example, only three species (*Rhinella marina*, *Lithobates catesbeianus*, and *Xenopus laevis*) account for 87% of all publications (427 out of 487) studying non-native amphibians (van Wilgen et al., 2018). A focus on emerging or unassessed amphibian invaders is therefore necessary to aid in risk assessments.

The Indian bullfrog, *Hoplobatrachus tigerinus*, a large dicroglossid frog (snout to vent length: up to 160 mm), is native to the Indian sub-continent (Dutta, 1997). The species was harvested and exported as part of the international ‘frog leg trade’, from India to Europe until the 1980s (Abdulali, 1985). Following apparent population decline, trade was banned, and the species accorded protection under Schedule IV of the Indian Wildlife Protection Act (Oza, 1990). Its 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). Further, the species is highly fecund (ca. 6000 eggs; Oliveira et al., 2017) and can breed successfully in ephemeral pools of human-modified habitats.

Hoplobatrachus tigerinus is likely to be successful across the stages of introduction, establishment, based on species-traits and human-interaction. ‘Intentional’ mode of introduction for cultivation boosts introduction and establishment success for anurans (Tingley et al., 2010; Rago et al., 2012). Further, high fecundity due to its large clutch size is advantageous for establishment (Allen et al., 2017). As *H. tigerinus* is likely to be moved within the non-native range, by intentional or unintentional translocations, its spread would be boosted (Liu et al., 2014). Further, large bodied amphibians with high reproductive potential have higher environmental impacts (Measey et al., 2016). The carnivorous tadpoles of *H. tigerinus* prey upon larvae of other anurans and even display cannibalism (Khan, 1996; Grosjean et al., 2004), whereas, post-metamorphic individuals consume a broad range of invertebrates and small vertebrates (Padhye et al., 2008). Despite the high likelihood of invasion success and impact for *H. tigerinus*, its extra-limital populations and global invasion potential have not been assessed.

Systematic literature reviews and species distribution modelling have been used to generate global species profiles for risk assessments of several amphibian invaders (*Lithobates catesbeianus*, Ficetola et al., 2007 a, b; *Xenopus laevis*, Measey et al., 2012; *Eleutherodactylus coqui*, Bisrat et al., 2012; *Duttaphrynus melanostictus*, Tingley et al., 2017). Such assessments can be particularly useful in understanding consistent patterns of invasion dynamics (e.g. dispersal pathways). Further, risk assessments rely on information about previous invasions of the species, invasion potential based on environmental niche, dispersal pathways, spread rates, impact and management action (Wilson et al., 2018). Although species distribution models used in risk assessments have typically incorporated only bioclimatic information, ignoring human influence on invasion potential can lead to underestimates (Rödder, 2010; Gallardo et al., 2015). For example, the modelled invasion potential for species can increase up to six-fold when indices of socio-economic factors are incorporated (Gallardo & Aldridge, 2013).

Similarly, Tingley et al. (2017) have proposed joint modelling of incursion probability (using biosecurity data) and habitat suitability to better inform invasion potential.

In this paper, our goal is to provide a profile of the Indian bullfrog, *Hoplobatrachus tigerinus*, as an invasive species, to aid in risk assessment and management exercises. To this end, we aim to, i) evaluate the global invasion potential using species distribution models, ii) synthesize existing knowledge on invasion status, dispersal pathways and spread, impact, and management action, and iii) assign standardized metrics of impact based on environmental and socio-economic effects.

METHODS

Extra-limital populations

We searched for literature on extra-limital populations of *Hoplobatrachus tigerinus* on Google Scholar (September 2018) by employing a combination of key words covering taxonomic variation (including the previous taxonomic assignments '*Rana tigerina*' and '*Rana tigrina*') and invasion status ('alien', 'introduced', 'non-native' and 'invasive'). We also considered local researchers and herpetologists as a source of information where published literature was lacking (Ficetola et al., 2007a). Excluding captive populations, extra-limital populations were evaluated for invasion status (residence time and evidence of establishment and spread), dispersal pathways, spread, impact type, and management actions.

Species distribution modelling

Environmental niche modelling was carried out to determine the global invasion potential of *H. tigerinus*. Following recommendations to incorporate human effects into traditional climate envelope models (Gallardo et al., 2013, 2015), we evaluated the potential species distribution based on WorldClim bioclimatic factors and human influence index (WCS 2005). The package of 19 bioclimatic variables, based on monthly temperature and precipitation data (1960 – 1990), was downloaded at a resolution of 2.5 arc minutes (www.worldclim.org). The Human Influence Index (HII), representing a combination of population density, land use, and human accessibility parameters, was available at a finer resolution of 30 arc seconds. To ensure compatibility between these predictor layers, we resampled HII to 2.5 arc minutes by bilinear interpolation, using ArcMap version 10.6.2. We collated occurrence data for *H. tigerinus* from three sources: i) online databases – the Global Biodiversity Information Facility (www.gbif.org), India biodiversity portal, iNaturalist, and Herpnet, ii) literature records with precise locations and iii) field observations. We only considered presence-records with accurate geographic co-ordinates. After removing duplicates, a total of 153 'presence-only' points were gathered from the native range (Supplementary Information 1). We did not use occurrence records from the non-native range (n = 54) to train the model as they did not add 'novel environmental space' in terms of the chosen predictors (Supplementary Information 1).

Species distribution modelling was carried out in the R environment (version 3.4.4) using the package 'biomod2', designed to perform a range of modelling algorithms (Thuiller et al., 2016). Given our aim of predicting suitable regions for *H. tigerinus* occurrence globally, we chose to build simple models to maximize transferability and avoid overfitting. Therefore, we selected an initial set of biologically meaningful predictors for the species: isothermality (bio3), maximum temperature of the warmest quarter (bio5), minimum temperature of the coldest quarter (bio6), mean precipitation of the wettest quarter (bio16), and HII. After performing pair-wise correlation tests to account for collinearity in predictors (discarded if $r > 0.7$), we retained isothermality, mean precipitation of wettest quarter, and HII. As the occurrence records were sourced from a range of data types, (museum records, field surveys, and citizen science) we did not expect the sampling strategy to be inherently biased towards higher HII (e. g. human settlements).

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). Tingley et al. (2017) 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 dispersal of amphibians. Similarly, we limited the training range of our models in the Indian sub-continent to south of the Himalayas (Supplementary Information 1). Sampling bias in occurrence data is an important consideration that may affect model performance and predictions (Merrow et al., 2013). We visualized the environmental data in the training extent using bivariate plots and overlaid presence points (sampling points). As we did not find any patterns suggesting sampling bias, we proceeded to run models based on presence-pseudoabsence samples. Pseudo-absence points (n = 1000, iterations = 2) were selected randomly within the training extent; the entire training data was randomly split to set aside 20% of points for model evaluation.

We executed algorithms from model families, regression (Generalized Boosting Model, 'GBM'), classification (Classification Tree Analysis, 'CTA'), and machine learning (Maxent, 'MAXENT.Phillips'). Evaluation of the models were based on the Area Under the receiver operating characteristic Curve (AUC) and True Skill Statistic (TSS; Allouche et al., 2006). Both these metrics are based on sensitivity (probability of correctly identifying random presence point) and specificity (probability of correctly identifying a random absence point). To avoid extrapolation during global projection, we evaluated the 'clamping masks' to identify grid cells with environmental values falling outside the extent of values used for training.

Impact Scoring

We followed the Environmental Impact Classification of Alien Taxa (EICAT) scheme proposed by Blackburn et al. (2014), supplemented with guidelines by Hawkins et al. (2015). Socio-Economic Impact Classification of Alien Taxa (SEICAT) scheme was used as described by Bacher et al. (2018). We scored invasive *Hoplobatrachus tigerinus* for impact using published literature generated for extra-limital populations (see above). In both scoring systems, one or more impact mechanisms are identified based on literature (e.g. predation; Table 6.1). SEICAT evaluates constituents of human well-being to categorize impacts, including safety, material and immaterial assets, health and social, spiritual and cultural relations (Bacher et al., 2018). The intensity of each impact mechanism is then assessed. The lowest category in both schemes ('minimal concern') corresponds to no change in fitness of individuals of other 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' with currently available literature is ascribed to the species (Hawkins et al., 2015).

RESULTS & DISCUSSION

Extra-limital populations

Andaman Islands

Hoplobatrachus tigerinus was first reported from two localities (Mayabunder, Middle Andaman and Wandoor, South Andaman) on the Andaman archipelago in 2013, with the view that it was intentionally introduced in 2009-10 from the Indian mainland (Harikrishnan & Vasudevan, 2013). Subsequently, Rangaswamy et al. (2014) reported occurrence on Neil and Havelock Islands. Using public surveys to retrospectively assess invasion history, Mohanty and Measey (*in press*) reported first establishment in 2001, followed by a lag phase of eight to ten years. Two museum records of *H. tigerinus* from 1991, have subsequently been noted as a case of misidentification, although a record from 1978 needs confirmation (Harikrishnan & 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 (see Mohanty & Measey, *in press*). 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 & Measey, *in press*). Tadpoles of *H. tigerinus* were likely to be transported accidentally with fish fingerlings which are used for aquaculture; adults were released on at least 17 occasion, transporting individuals within and between islands (47.48 ± 11.81 km, range 6.2–188 km).

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 & Measey, 2018). Significant dietary overlap occurs with *Limnonectes* sp. indicating a potential for competition (Mohanty &

Measey, 2018). Economic loss to household level poultry and aquaculture has also been reported (Mohanty & Measey, *in press*). Predation by larval *H. tigerinus* has been documented to cause zero survival of the endemic *Microhyla chakrapaniii* and *Kaloula ghosi* under mesocosm conditions (Mohanty & Measey, *submitted*). No management action is in effect for the population, which is protected under the Schedule IV of the Indian Wildlife Protection Act (1972).

Madagascar

The first published record of *Hoplobatrachus tigerinus* in Madagascar comes from Guibé (1953), where the author reported a specimen that was collected by R. Paulian in the "Majungo" region, which probably refers to Mahajanga, in the northwest of the island. Guibé identified the specimen as *Rana t. tigrina* and suggested a 'recent' introduction of the species in Madagascar, probably as an intentional introduction (Guibé, 1953). The taxonomic identity of this specimen was supported by Blommers-Schlösser & Blanc (1991) and was later confirmed using molecular methods (Kosuch et al., 2001). Guibé (1953) also noted that this species is common in its native range and is consumed by humans, suggesting that the species might have been introduced to support the protein intake of local Malagasy communities. However, precise information on the introduction event(s) were, and continue to be unclear (Guibé, 1953; Kosuch et al., 2001; Vences et al., 2003). Two proposed reasons for introduction include, as a source of proteins for human populations and/or to be used as biocontrol of rodents and mosquitos.

Populations are widely distributed at low altitude sites in the north and northwest of Madagascar, with confirmed records from Ambanja, Ambilobe, Ampijoroa, Ampitsopitsoka, Anabohazo Forest, Ankarafa, Ankarana, Ankorikakely, Antafiabe, Antanambao, Antsirasira, Manondro (close to Antsiranana), near Manongarivo, Mitsinjo, Montagne des Français, Nosy Be and Sambava (Supplementary Information 2; Andreone et al., 2003, 2009; Vences et al., 2003; D'Cruze et al., 2006, 2007; Glaw & Vences, 2007; Rakotoarison et al., 2015; Penny et al., 2017). Recently, *H. tigerinus* has also been reported from Ivoloina and Tamatave (in the eastern coast of Madagascar; AC unpublished data). Overall, the species is expanding its range at low altitudes both in the northwest, in the eastern coast and on the island of Nosy Be (Padhye et al., 2008; AC unpublished data). Additionally, since the species is consumed by people it is highly likely that its current distribution is much larger than is currently known. Given the synanthropic nature of the species, it will be useful to conduct public surveys to gain more information on the invasion history in the eastern coast of Madagascar, where the species has established in recent years.

Within Madagascar, the trade of *H. tigerinus* for human consumption is likely to be involved in the expansion and establishment of new pocket populations. *Hoplobatrachus tigerinus* in Madagascar is among the most common species of amphibians sold as food both in street markets and restaurants of urban centres, such as Antananarivo and Toliara (Glaw & Vences, 2007; Jenkins et al., 2008; Gardner & Jasper, 2009). 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 (with the production of the popular "cuisses de nymphe"), with a large number of people 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 relatively long time on Madagascar, it has proved difficult to disentangle its dispersal pathways. But, it is worth noting that there has been very little research conducted on the spread and impacts of this population. In addition to potential predation and competition with native amphibians, *H. tigerinus* may be involved in the introduction and spread of multiple pathogens and parasites. Traded frogs sold in street markets and restaurants can also act as reservoirs for zoonotic agents (Spitzen-van der Sluijs et al., 2011).

No management against the spread and proliferation of this frog in 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 the rice paddies of the Marovoay area (northwestern Madagascar), followed by a strong proliferation of rodents. This incident apparently convinced the regional authorities (Département de la Production végétale within the Ministère de l'Agriculture) that the species has to be considered beneficial rather than a threat (Vences, Raselimana, & Glaw, 2003). Following this situation, a community-based conservation strategy was developed, where regional authorities forbid the use of this species as food supplies in the area and the harvesting of this species was reduced. However, we lack information if this program is still active.

Maldives & Lakshadweep (Laccadives)

Dutta (1997) recorded introduced *H. tigerinus* on Maldives, however, recent records confirming establishment and spread are missing. *Hoplobatrachus 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 obtain any positive response of observation; the only amphibian reported from both Maldives and Lakshadweep by researchers were of bufonids, possibly *Duttaphrynus melanostictus*.

Captive extra-limital populations

Hoplobatrachus tigerinus populations are present in captivity in Cuba (Borroto-Páez et al., 2015) and Thailand (Timsina, 2013), with no records of populations occurring in the wild.

Species distribution modelling

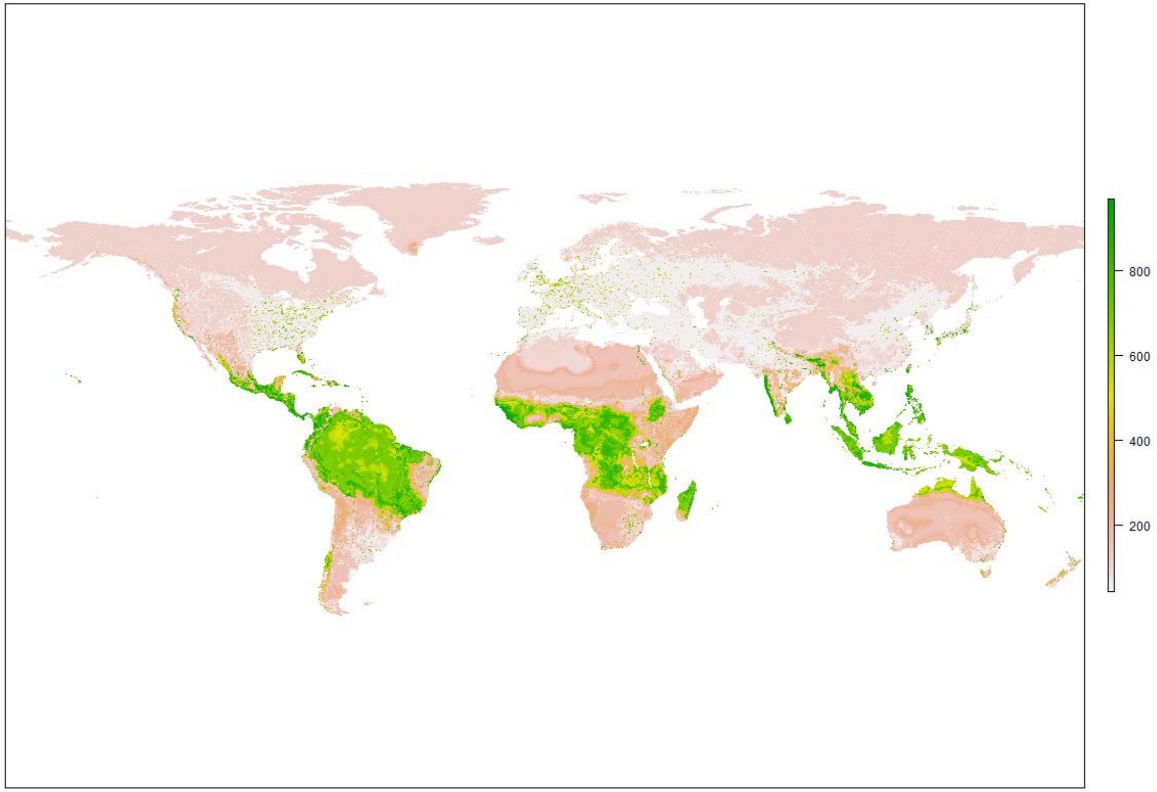
Of the three species distribution models built to predict globally suitable regions for *H. tigerinus*, the generalized boosting model ('GBM') performed relatively better than other models. The three predictors had non-zero influences where the mean precipitation of wettest quarter had relatively high importance (46.3%), followed by HII (27.2%), and isothermality (26.4%). The model performance was characterized with AUC = 0.86 and TSS = 0.57. While sensitivity was 83.3% specificity was low (73.4%), leading to a level of false positives associated with the predictions. For understanding invasion potential of a species, a relatively high sensitivity is desirable (Webber et al., 2011), allowing for high true positive detection and limited false positive detections. The predicted range for *H. tigerinus* (Fig. 6.1) should thus be considered as a hypothesis to base further range assessments, specifically in the introduced range (Jarnevich et al., 2015).

Most regions on the Andaman Islands were suitable for *H. tigerinus* occurrence, whereas, coastal Madagascar was particularly conducive. The population on the Andaman archipelago is likely to continue spreading, at least to two more human inhabited islands hitherto uncolonized (Long and Baratang). As the predicted model indicates, the population on Madagascar may move further south along the east coast. Pearson (2015) identified similar landscape suitability on Madagascar for the introduced *Duttaphrynus melanostictus*, another anuran native to the Indian subcontinent. Clamping masks suggested that most predicted regions in the confirmed introduced range (Andaman and Madagascar) had very limited regions with extrapolations.

The importance of climatic variables, isothermality and high precipitation, underlie the thermal tolerance limits of the species and dependence on formation of lentic water bodies. The positive effect of HII may indicate the use of artificial ponds, paddy fields, and plantations by *H. tigerinus* in rural and peri-urban settings (Daniels, 2005). Globally, these variables predict high suitability in the tropical parts of Central and South America, Africa, South-East Asia and Australia (Fig. 6.1). However, this prediction does not necessarily translate to invasion risk. The only regions at risk are those with a potential for introduction through translocation for food or biocontrol and contamination of fish culture (Mohanty and Measey, *in press*). Intentional release is highly likely in the Nicobar archipelago, which is also suitable environmentally. Screening of ports is therefore strongly recommended for live transport of animals. Further bridgehead introductions are also possible to Malaysia, Indonesia, Mascarene Islands and Eastern Africa.

Figure 6.1

Predicted environmental suitability of *Hoplobatrachus tigerinus* globally, based on boosted regression tree modelling. Higher values (in green) indicate greater suitability for *H. tigerinus* occurrence. Predictor variables include isothermality, mean rainfall of the wettest quarter, and human influence index (HII). Modelling based on occurrence records from the native range in the Indian sub-continent.



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Impact Scoring

Based on dietary assessments of adult *H. tigerinus* on the Andaman Islands, the EICAT score of ‘minor’ impact was assigned to the species by Mohanty and Measey (2018). Previously, a global evaluation by Kumschick et al. (2017a) had resulted in the same score. Predation on endemic vertebrates and competition with the native anuran genus *Limnonectes*, were noted as the primary impact categories (Mohanty & Measey, 2018). However, this assignment was explicitly stated to be constrained due to the study design, which did not assess population level effects. Impact of larval *H. tigerinus* on tadpoles of the endemic *Microhyla chakrapaniii* and *Kaloula ghosi* on the Andaman archipelago were documented, where predation by carnivorous *H. tigerinus* resulted in zero survival in a mesocosm experiment (Mohanty & Measey, *submitted*). Based on the results of this study, we assign a score of ‘moderate’ impact to the species with a ‘medium’ confidence score due to the scale of the experiment (Table 6.1). Interview data from key informants (farmers, plantation workers, and pond owners; see Mohanty & Measey, *in press*) record population declines in native anurans, which we score as ‘moderate’ with a ‘low’ confidence score due to the inferred nature of the information.

Socio-economic impact was also scored as ‘moderate’ based on the same set of key informant interviews, which recorded ceasing of poultry keeping by many households (Table 6.1). We assign a confidence score of ‘medium’ due to possible ambiguity given the data resulted from semi-structured questionnaire surveys, lacking a directed question at abandonment of activity (Mohanty & Measey, *in press*). Based on evaluation of extra-limital populations, we provide a species summary of *H. tigerinus* describing key aspects of its invasion process, including dispersal pathways, environmental suitability, and impact (Table 6.2). Apart from known impact mechanisms for *H. tigerinus*, competition for acoustic niche (Both & Grant, 2012), indirect excarberation of predation on native species by predator supplementation (Woolbright et al., 2006), hybridization (Dufresnes et al., 2015), disease transmission (Mutnale et al., 2018) and faciliative interaction with non-native species (Adams et al., 2003) are probable mechanisms that require future evaluation (Table 6.1).

Generalities with other taxa

The invasion process and life-history traits of *Hoplobatrachus tigerinus* share many commonalities with the well-studied *Lithobates catesbeianus* (130 publications on its extra-limital populations; Ficetola et al., 2007a; van Wilgen et al., 2018). Both *H. tigerinus* and *L. catesbeianus* are large bodied (ca. 140-170 mm), semi-aquatic anurans with high fecundity and indirect development through a carnivorous tadpole stage (Oliveira et al., 2017). Post-metamorphic stages are clustered around lentic water bodies, though *L. catesbeianus* also occurs along rivers. Although, permanent water bodies are preferred for breeding by *L. catesbeianus* (with tadpole stage lasting > 1 yr), ephemeral pools are generally used by *H. tigerinus* for oviposition (tadpole stage < 70 days; Dutta & Mohanty-Hejmadi, 1976; Mohanty & Measey, *submitted*). Both species have a history of human consumption and trade, which has resulted in many introduced populations, into and within the non-native range (Rago et al., 2012). The pet trade pathway is recorded in some introduction of *L. catesbeianus*, but not yet for *H. tigerinus*. Impact mechanisms are similar, with significant predation of vertebrates in the adult stage along with competition; however, *L. catesbeianus* has a higher EICAT score of ‘major’ with studies documenting local extirpations (Kumschick et al., 2017a). Transmission of diseases (e.g. chytridiomycosis) by *L. catesbeianus* is considered likely (Kraus, 2015), although this aspect is yet to be assessed for extra-limital *H. tigerinus* (Table 6.1). Similarities of such emerging invasive species to well-studied model species should be leveraged to frame hypothesis and inform management.

Table 6.1 Impact scores (and associated confidence) 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	*H. tigerinus*	Confidence	Remarks
Competition	MN	High	Mohanty & Measey, 2018; competition for acoustic niche is probable
Predation	MO	Medium	Mohanty & Measey, 2018; Mohanty & Measey, *submitted*; indirect predation of native species by predator supplementation
Hybridisation	DD		Probable if introduced to regions with congeneric species (e.g. *H. occipitalis*)
Transmission of diseases to native species	DD		Probable
Parasitism	DD		Unlikely
Poisoning/ Toxicity	DD		Unlikely
Bio-fouling	DD		Unlikely
Grazing/ herbivory/ browsing	DD		Unlikely
Chemical, physical, or structural impact on ecosystems	DD		Unlikely
Interaction with other alien species	DD		May facilitate survival of larval *Duttaphrynus melanostictus* in Madagascar
Material & immaterial assets	MO	Medium	Mohanty & Measey, *in press*

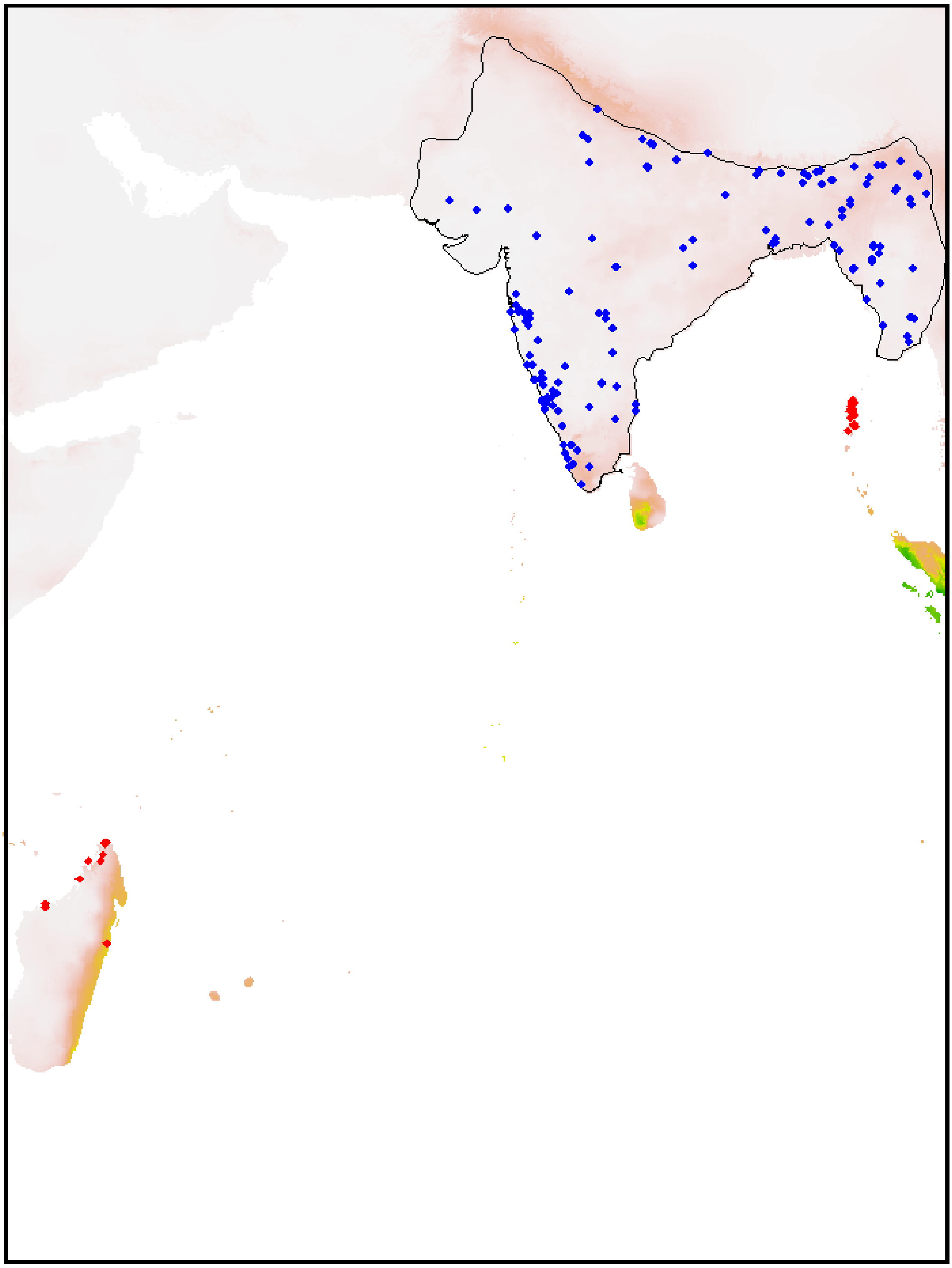
Table 6.2 Summary of invasion dynamics of the Indian bullfrog *Hoplobatrachus tigerinus* with supporting literature and remarks.

	Description	**Literature**	**Remarks**
Native Range	Indian sub-continent	Dutta, 1997	
Introduced Range	Andaman Islands, Madagascar	Mohanty & Measey, *in press*; Vences et al., 2003	Distribution on Madagascar updated in current study
Unaided Pathways	Contamination of freshwater fish culture by tadpoles	Mohanty & Measey, *in press*	Likely to benefit from farm dams (e.g. Govindarajulu et al., 2005; Davies et al., 2013)
Aided Pathways	Intentional release for consumption and biocontrol	Harikrishnan & Vasudevan, 2013; Mohanty & Measey, *in press*; Guibé, 1953	
Environmental Predictors	Isothermality, 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 & Measey, 2018; Mohanty & Measey, *submitted*	Population level declines of native anurans likely
Socio-economic Impact	Predation of poultry and fish stocks by adults	Mohanty & Measey, *in press*	May lead to reduction and ceasing of poultry keeping

Summary

Overall, extra-limital populations of *H. tigerinus* are likely to spread to climatically suitable regions with potential for live trade (consumption and future pet trade) and contamination of fish culture. Regions for probable incursions include Nicobar archipelago, Malaysia, Indonesia, Mauritian Islands and Eastern Africa. Screening of ports is strongly recommended for live transport of animals along with monitoring of pet trade for emergence of *H. tigerinus* 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. Future studies must evaluate impact mechanisms such as transmission of diseases and hybridization, and invasion facilitation (Table 6.1).

Supplementary Informantion 1 Occurrence points of the Indian bullfrog *Hoplobatrachus tigerinus* used for species distribution models. Native range points (n = 153, blue) used for model building with background points being selected within the bio-geographic extent available to the species (black boundary); introduced range points (n = 54, red) only used to measure potential of novel environment.



Supplementary Information 2

Updated distribution range of invasive Indian bullfrog *Hoplobatrachus tigerinus* on Madagascar.

7 General discussion

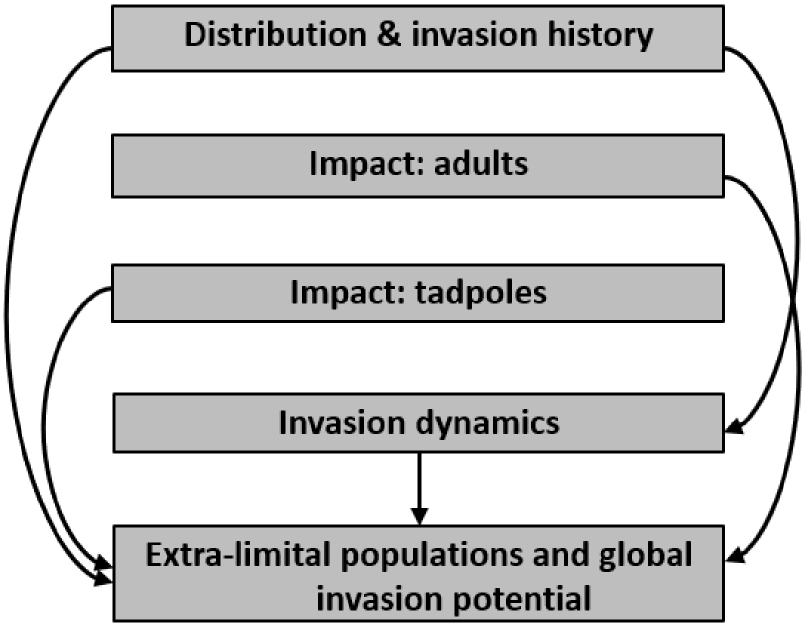
This thesis, consisting of five inter-dependent studies (Fig. 7.1), aimed to evaluate the invasion of the Indian bullfrog *Hoplobatrachus tigerinus* on the Andaman archipelago with the following key questions:

- How has the invasive spread on the Andaman Islands occurred spatio-temporally?
- What is the potential trophic impact of post-metamorphic *H. tigerinus* on native anurans?
- What is the potential impact of pre-metamorphic *H. tigerinus* on native anurans through predation and competition?
- Can different management strategies or lack thereof imapct the ongoing invasion?
- What is the global invasion potential of *H. tigerinus* and likelihood of spread in introduced populations?

In Chapter 2, I used a novel approach to reconstruct the *Hoplobatrachus tigerinus* invasion of the Andaman Islands, combining public surveys and field surveys in a formal analytical framework. Employing false-positive occupancy analyses, I was able to incorporate spatial information from public surveys (key informant interviews) and ensure data reliability. The *H. tigerinus* invasion has resulted in colonization of at least 62% of sites (out of 91), distributed on six of the eight human inhabited islands. Establishment of populations reportedly started in 2001, followed by a brief lag phase, culminating in rapid spread post 2009. Human mediated dispersal within and between islands is frequent, through intentional and unintentional pathways. Adults have been intentionally moved for consumption and novelty, whereas, tadpoles are likely to have been contaminants of the aquaculture trade (with freshwater fish fingerlings). I was able to identify an ‘introduction hub’ on the Indian mainland and ‘dispersal hubs’ on the Andaman Islands, which likely served as sources for multiple introductions to and within the archipelago, respectively. Occupancy modelling also revealed that sites closer to these dispersal hubs were more likely to be colonized than sites further away.

Figure 7.1

Contribution of each chapter, sequentially from Chapter 2 to Chapter 6, to the thesis and linkage among chapters



The information generated on spatio-temporal patterns in invasive spread, dispersal pathways, and the current distribution comprehensively describes the *H. tigerinus* invasion. Further, the novel approach employed in the study can be applied to other invasions (new to moderately old), to understand processes occurring in the early stages which lead to exponential expansion in many cases (Table 7.1). The use of public surveys in a systematic framework adds a complimentary tool to the existing methods for reconstructing invasions. This study also contributes to the relatively recent efforts to focus on human dimensions in invasion science (see Shackleton et al., 2018a). Mohanty et al. (2018) showed that public surveys can be used to estimate distributions of multiple invasive species reliably and rapidly. Such approaches can be useful in generating large scale baseline information (McGeoch et al., 2016; Latombe et al., 2017), especially in developing countries which still lack invasive species inventories (Early et al., 2016).

The efficacy of utilizing community knowledge depends on the strength of interaction between stakeholders and the species (Mohanty et al., 2018; Chapter 2). This interaction is manifest in human perception of the species. Therefore, species that humans view positively and/or negatively, can be better assessed using community knowledge and simultaneously inform management strategies (Shackleton et al., 2018b). Although synanthropic species are likely to have high level of interactions with humans, compared to other species, community knowledge can still be harnessed for species in uninhabited areas using targeted key informant surveys (e.g. large mammals; Pillay et al., 2014). As human modified areas serve as launching pads for invasions in many cases, using publicly sourced data can also act as an early warning system (e.g. horticulture trade and gardeners; Dehnen-Schmutz & Conroy, 2018).

In Chapter 3, I assessed the diet of the invasive *H. tigerinus* and two syntopic native frogs to assess the impact of post-metamorphic stages of bullfrogs through predation and competition. An intensive sampling effort in three sites of the Andaman archipelago, across the dry and wet seasons, resulted in diet samples of 798 individuals. Vertebrates made up the majority of the bullfrog's diet in terms of volume, whereas, invertebrates were numerically dominant. I only found a significant dietary overlap between *H. tigerinus* and individuals of the genus *Limnonectes*. Prey size electivity was governed by body size of the three species. Individuals of *Hoplobatrachus tigerinus* and *Fejervarya* chose evasive prey, suggesting that these two taxa are mostly ambush predators. Individuals of the genus *Limnonectes* elected a majority of sedentary prey along with a large portion of evasive prey; such electivity indicates a combination of 'active search' and 'ambush' foraging. Most prey consumed by the three species of anurans, were terrestrial.

In describing these patterns, I emphasize the necessity to evaluate prey availability and volume in future studies for meaningful insights into diet of amphibians. For species with shared evolutionary history, niche segregation is studied to explain community structure (e.g. Toft, 1981). Conversely, niche overlap can be an indicator for potential competition between recent invaders and native species, which are less likely to have shared evolutionary history. For the trophic niche, overlap must be investigated both along prey taxa and size. This assessment would only be reasonable in conjunction with prey availability data to inform prey electivity. Therefore, future studies on trophic competition by invasive species must assess electivity by taxa and size (volume) and ideally document scarcity of resources (Table 7.1). This intensive study on a hitherto unassessed genus of invasive amphibians contributes to the knowledge on impacts of amphibian invasions. Further, the study elucidates the feeding ecology of *H. tigerinus* and species of the genera *Limnonectes* and *Fejervarya* with a large sample size.

In Chapter 4, to assess the impact of the pre-metamorphic stage of *H. tigerinus* on endemic anurans of the Andaman archipelago, I carried out a mesocosm experiment with larval *H. tigerinus, Microhyla chakrapaniii,* and *Kaloula ghosi*. The invasive *H. tigerinus* breeds along with the two endemic species in ephemeral pools formed in paddy fields and plantation moats at the onset of the south-west monsoon. I replicated single-species treatments thrice, and two-species and three-species treatments four times to generate a total of 25 mesocosms. Keeping food resources (40g of sediment litter and 150 l water with zooplanktons) and density (30 tadpoles per mesocosm) constant, I evaluated effects of *H. tigerinus* predation on survival of endemic tadpoles. Inter- and intra-specific competition was also evaluated based on larval period, growth rate, and metamorph size. Predation by *H. tigerinus* resulted in no survival of endemic tadpoles, with all native individuals being consumed within a three-week period. In contrast, the single-species treatments of *M. chakrapaniii* and *K. ghosi* led to a survival of 90% and 62% respectively. Although *H. tigerinus* survival was higher in the presence of the other species, mean number of tadpoles surviving did not significantly differ between treatments suggesting density dependent survival.

The study is timely as the rapidly expanding invasion is likely to affect other native anurans including many anuran genera which are awaiting formal taxonomic re-assessments (Harikrishnan & Vasudevan, 2018). The findings augment the limited existing knowledge on the impact of amphibian invaders with carnivorous larvae (Table 7.1). Further, the severe level of predation has not been observed in previous studies on amphibian invaders (Smith et al., 2005). Although fractionally lowering the survival of pre-metamorphic stage may not translate into significant population declines (Govindarajulu et al. 2005), a severe reduction in successful clutches (as observed in the study) may hamper recruitment. As the clutch size of *H. tigerinus* is markedly higher than those of native genera, *Limnonectes*, *Fejervarya*, *Microhyla* and *Kaloula*, carnivory effects can be more pronounced than the observed levels at equal density.

In Chapter 5, I developed a model to evaluate the effect of human-mediated translocations, natural dispersal, and demography on the invasion dynamics of *H. tigerinus*. I combined an age-structured demographic model with a gravity model of human influence, in a spatially explicit modelling context. This approach allowed me to disentangle the differential influence of human-mediated translocations and natural dispersal on invasive spread. Human influence had a positive effect on spread rates, facilitating both between island and within island movement of *H. tigerinus*. Interestingly, the model predicted an overriding effect of human influence on origin of the invasion (one or two origins). The modelling framework also allowed for testing the efficacy of management interventions in limiting the invasive spread. Based on the modelled predictions, I recommend immediate deployment of screening mechanisms between islands (especially for the hitherto uncolonized Baratang and Long Island).

The modelling approach used in the chapter attempted to incorporate several complexities of invasive spread, especially of human-mediated translocations in the extra-limital region which is frequent in biological invasions across taxa (Table 7.1; Hui & Richardson, 2017). Predicting such facilitative movements is particularly important for amphibians as pet trade and subsequent releases account for a growing number of amphibian introductions (Kraus, 2009) and translocations (Stringham & Lockwood, 2018). Several attempts have been made recently to understand pet ownership and trade in amphibians (Carpenter et al., 2014; Herrel & van der Meijden, 2014; Measey et al., *submitted*). Research should quantify the effects of pet releases on invasive spread in the extra-limital region. Such efforts can benefit from the modelling approach developed in this study, that allows for utilization of surrogates of human influence (e.g. pet shops listed in a county).

Finally, in Chapter 6, I assessed the profile of *H. tigerinus* as a hitherto unstudied and potentially emerging invasive species (Table 7.1). To this end, I reviewed the available knowledge on extra-limital populations of *H. tigerinus*, modelled its potential distribution in the introduced range and global invasion potential, and assigned species-level scores for ecological and socio-economic impact. Apart from the focal study area of the Andaman archipelago, I could only confirm another successful invasion (Stage E, Blackburn et al., 2011) on Madagascar. Reported populations on Maldives and Laccadive Islands do not have recent substantive records for validation; Thailand and Cuba have captive individuals and do not have confirmed populations (Stage B1 or B2, Blackburn et al., 2011) in the wild. The overarching pattern across extra-limital range indicates human use of *H. tigerinus* for consumption, novelty, cultivation and biocontrol. Human use is known to drive introduction and invasion success in amphibians (Tingley et al., 2010; Liu et al., 2014) and other taxa (e.g. bamboo, Canavan et al., 2017). Therefore, frequent human use enhances the potential of *H. tigerinus* as a future invasive species in suitable regions of the world.

The environmental niche model identified isothermality, high precipitation, and human modification as factors conducive for *H. tigerinus* occurrence. The presence of such conditions in the confirmed invaded range (Andaman and Madagascar) indicates a high probability of further spread. Regions with potential for live trade in *H. tigerinus* and aquaculture are vulnerable to introduction. Considering environmental suitability and potential for introductions, I identified Nicobar Islands, Mascarene Islands, Malaysia and Indonesia, and East Africa to be likely recipients of bridgehead invasions. The overall potential for socio-economic impact was 'Moderate' for the species (Socio-Economic Impact Classification of Alien Taxa, SEICAT; Bacher et al., 2018), on account of reduction human activities of poultry keeping and threat to aquaculture (Chapter 2). Similarly, the ecological impact was assigned a score of 'Moderate' (Environmental Impact Classification of Alien Taxa, EICAT; Blackburn et al., 2014), based on documented population extirpations of native anurans in mesocosms (Chapter 3).

A previous assessment of the ecological impact of *H. tigerinus* had assigned an EICAT score of 'Minor' (Kumschick et al., 2017), signifying reduction of individual fitness in native species. The species was previously considered 'data deficient' for its socio-economic impact (see supporting information in Bacher et al., 2018). Chapter 1, Chapter 2, and Chapter 3 contributed to the reassessment of the species and led to a revision of the EICAT score to a higher category of 'Moderate' from 'Minor'. Therefore, a considerable amount of research (spanning 3 years, and costing approx. 10,000 USD) was required to assign EICAT and SEICAT scores with 'medium' confidence. A better assessment of population level and community level impact would require even further effort. This data intensive nature of the assessments can be a constraint on their rapid adoption and application in risk assessments globally.

Table 7.1

Chapter-wise breakdown of novel insights generated and scope of generalizations.

Chapter	Novel insights	Scope
Distribution & invasion history	Use of public survey data in a formal analytical approach	Invasions across taxa; new to moderately old invasions
Impact: adults	Trophic niche of anurans sampled; recommendations on trophic impact assessments	Invasions with trophic impact through predation and competition
Impact: tadpoles	Intensity of predation in *H. tigerinus* tadpoles	Invasions of amphibians with carnivorous tadpoles
Invasion dynamics	Combined use of age-structured and gravity models; effect of human-mediated translocations	Invasions with frequent translocations in extra-limital range
Extra-limital populations & global invasion potential	Influence of humans on invasion potential; similarity of invasion process with well-studied invasions	Species-specific

Overall, *Hoplobatrachus tigerinus* is likely to increase it extra-limital range by spreading to Nicobar Islands and in new locations of Madagascar and Andaman Islands. Currently, these regions do not have legislation enabling management actions for the species, with *H. tigerinus* being protected under Schedule IV of the Indian Wildlife Protection Act in the Andaman & Nicobar Islands (a union territory of India). Therefore, legal provisions must be modified to allow management interventions. Screening at points of entry is likely to be effective for small islands on both Andaman and Nicobar archipelagos due to the relatively low human traffic they experience. Further, awareness generation campaigns targeting aquaculturists can reduce unintentional spread of tadpoles. Failing to manage existing and likely extra-limital incursions of *H. tigerinus* place an increasing area and associated species under risk. Small vertebrates, a group with high endemicity on island systems, will be the most impacted through documented and hitherto unstudied but likely impact mechanisms of *H. tigerinus*. These mechanisms include predation (direct predation by adult and larval stages, and indirect effects through predator supplementation), competition (along trophic and acoustic niche), disease transmission, hybridization and facilitative interaction with non-native species.

As emphasized through the thesis, the number of amphibian invasions globally is increasing rapidly, whereas, knowledge on amphibian invasions is heavily taxa biased (Seebens et al., 2017; van Wilgen et al., 2018). Such a taxa bias hinders risk assessments as many emerging invasive species lack key information on invasion potential, pathways, and impacts (see van Wilgen et al., 2018 for a detailed account). Further, a high taxonomic bias limits our understanding of processes underlying amphibian introduction, establishment, spread, impact and effective management. In this context, research on amphibian invasions must be recalibrated to identify and address crucial knowledge gaps. Apart from identifying species and regions that require research attention, studies must explicitly evaluate gaps in literature focussing on invasion hypotheses on amphibian species traits, pathways, and context (Kueffer et al., 2013).

Research and management of new species may benefit from hypotheses and recommendations based on the ‘invasion syndromes’ framework (Kueffer et al., 2013). The framework attempts to find repeated patterns in combination of pathways, species traits, and context that lead to successful invasion. Functional groups of amphibians (e.g. arboreal anurans, bufonids) are prima facie moved through different dispersal pathways (Kraus, 2009) and applicable management strategies differ (Vimercati et al., 2017). In Chapter 6, I discussed the similarities between *H. tigerinus* and the American bullfrog *Lithobates catesbeianus* in the invasion process and life-history traits. Identifying such similarities for functional groups in amphibians may be useful in order to generate and test hypotheses and inform management in the absence of species-specific data.

Overall, the thesis used a suit of methodological approaches to understand the invasion dynamics of the Indian bullfrog *Hoplobatrachus tigerinus*. The study generated novel insights which are transferable to other taxonomic groups and contexts (Table 7.1) and contribute to existing knowledge gaps in invasion science. The chapters contributed a significant body of knowledge in combination with each other (Fig. 7.1), which has theoretical and applied implications for biological invasions and population ecology in general.

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