A taxonomically and geographically constrained information base limits non-native reptile and amphibian risk assessment: a systematic review

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For many taxa, including reptiles, new records of non-native introductions globally occur at a near exponential rate. We undertook a systematic review of peer-reviewed publications on non-native herpetofauna, to assess the information base available for assessing risks of future invasions, resulting in 836 relevant papers. The taxonomic and geographic scope of the literature was also compared to a published database of all known invasions globally. We found 1116 species of herpetofauna, 95% of which were present in fewer than twelve studies. Nearly all literature on the invasion ecology of herpetofauna has appeared since 2000, with a strong focus on frogs (58%), particularly cane toads (Rhinella marina) and their impacts in Australia. While fewer papers have been published on turtles and snakes, proportionately more species from both these groups have been studied than for frogs. Within each herpetofaunal group, there are a handful of well-studied species: Rhinella marina, Lithobates catesbeianus, Xenopus laevis, Trachemys scripta, Boiga irregularis and Anolis sagrei. Most research (416 papers; 50%) has addressed impacts, with far fewer studies on aspects like trade (2%). Besides Australia (213 studies), most countries have little location-specific peer-reviewed literature on non-native herpetofauna (on average 1.1 papers per established species). Other exceptions were Guam, the United Kingdom, China, California and France, but even their publication coverage across established species was not even. New methods for assessing and prioritizing invasive species such as the Environmental Impact Classification for Alien Taxa provide useful frameworks for risk assessment, but require robust species-level studies. Global initiatives, similar to the Global Amphibian Assessment, using the species and taxonomic groups identified here, are needed to derive the level of information across broad geographic ranges required to apply these frameworks. Expansive studies on model species can be used to indicate productive research foci for understudied taxa.
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Short title: Non-native reptiles and amphibians
Abstract

For many taxa, including reptiles, new records of non-native introductions globally occur at a near exponential rate. We undertook a systematic review of peer-reviewed publications on non-native herpetofauna, to assess the information base available for assessing risks of future invasions, resulting in 836 relevant papers. The taxonomic and geographic scope of the literature was also compared to a published database of all known invasions globally. We found 1116 species of herpetofauna, 95% of which were present in fewer than twelve studies. Nearly all literature on the invasion ecology of herpetofauna has appeared since 2000, with a strong focus on frogs (58%), particularly cane toads (Rhinella marina) and their impacts in Australia. While fewer papers have been published on turtles and snakes, proportionately more species from both these groups have been studied than for frogs. Within each herpetofaunal group, there are a handful of well-studied species: Rhinella marina, Lithobates catesbeianus, Xenopus laevis, Trachemys scripta, Boiga irregularis and Anolis sagrei. Most research (416 papers; 50%) has addressed impacts, with far fewer studies on aspects like trade (2%). Besides Australia (213 studies), most countries have little location-specific peer-reviewed literature on non-native herpetofauna (on average 1.1 papers per established species). Other exceptions were Guam, the United Kingdom, China, California and France, but even their publication coverage across established species was not even. New methods for assessing and prioritizing invasive species such as the Environmental Impact Classification for Alien Taxa provide useful frameworks for risk assessment, but require robust species-level studies. Global initiatives, similar to the Global Amphibian Assessment, using the species and taxonomic groups identified here, are needed to derive the level of information across broad geographic ranges required to apply these frameworks. Expansive studies on model species can be used to indicate productive research foci for understudied taxa.

Key-words: Alien species, biological invasions, crocodiles, exotic, frogs, lizards, risk assessment, salamanders, snakes, turtles
Introduction

Alien or non-native species are taxa that have been transported beyond the limits of their natural range, and may become invasive in new areas if they are able to form established, self-sustaining populations in these new locations (Blackburn et al. 2011). For several taxa, new invasions continue to occur at a near exponential rate (Seebens et al. 2017). Evidence of the negative impacts of many invasive species (e.g. Pimentel 2011), including impacts from reptiles and amphibians (Shine 2014; Kraus 2015; Measey et al. 2016) is increasing. This has added urgency to the pursuit of achieving a thorough understanding of factors mediating success at different stages of the introduction-naturalization-continuum (Richardson et al. 2000; Blackburn et al. 2011) to inform policies to reduce the risk of further invasions. Effective and defensible policies are increasingly being introduced, or considered, to attempt to curb invasions at a national level (e.g. Genovesi, Carboneras, Vilà & Walton 2015), but require robust models to differentiate between innocuous and potentially problematic species (Springborn, Romagosa & Keller 2011).

The challenges posed to the assessment of invasion risk are unique to each taxonomic group (Kumschick & Richardson 2013). Such challenges include strategically prioritising research on the impacts of understudied species, in areas of the world where invasive species are less studied and different aspects of the invasion process less well covered. Although fairly robust models exist to explain the success of introduced plants (e.g. Pheloung, Williams & Halloy 1999), formal risk assessment still faces multiple challenges even for this group (Hulme 2013; Speek, Davies, Lotz & van der Putten 2013).

Invasions of reptiles and amphibians (“herpetofauna”), although not nearly as well documented as plant invasions (Pyšek et al. 2008), have received significant attention in recent years,
especially in Florida (Krysko et al. 2011), with an emphasis on species in the pet trade and ‘hitchhiker’ species (Tingley et al. 2018). While there are currently relatively few invasive reptiles and amphibians, some species do have significant impacts (Kraus 2015; Measey et al. 2016) and records of first introduction for reptiles at least, have been increasing at an exponential rate since the 1950s (Seebens et al. 2017). Numerous studies have investigated the factors that influence the popularity in the pet trade, probability of introduction and release (e.g. Stringham & Lockwood 2018), and the likelihood of successful establishment of herpetofaunal species in new regions. Several strong and consistent patterns have emerged from these studies. For example, establishment success is enhanced for species introduced and released in high numbers (Garcia-Diaz, Ross, Ayres & Cassey 2015; Mahoney et al. 2015), into areas with high native species richness (Tingley, Phillips & Shine 2011; Ferreira et al. 2012; Poessel et al. 2013), for species that are less manageable (more expensive to keep, prone to escape, aggressive or venomous, Fujisaki et al. 2009), that have fast-paced life histories (Allen et al., 2017, van Wilgen & Richardson 2012), and that come from areas with similar environmental conditions to the area of release (Bomford, Kraus, Barry & Lawrence 2009; van Wilgen, Roura-Pascual & Richardson 2009; Tingley, Phillips & Shine 2011; Rago, While & Uller 2012). However, models using these predictors, can be relatively data hungry, making it difficult to regulate the import of species and prioritize management of those already present in an area in the absence of primary data. This is increasingly leading to disillusionment among traders who challenge restrictions placed on the importation of certain taxa and could spur illegal imports. Increasing objectivity and a better understanding of uncertainties are necessary to inform communication between legislators, managers, conservationists and pet traders.
Formal pre-border risk assessment, which is increasingly becoming mandatory in many countries to regulate the import of species that are not yet present, faces important challenges. Risk is defined by both the probability of an event taking place and the consequences of such an event (Kumschick & Richardson 2013). Most risk assessments for non-native reptiles and amphibians to date have focused on the potential for a species to establish (event probability). Another approach recently proposed is to assess the impacts of non-native species based on known impacts in other parts of its non-indigenous range (EICAT: Blackburn et al. 2014; Hawkins et al. 2015; SEICAT: Bacher et al. 2018). This approach, and others like it (e.g. Kumschick et al. 2015; Nentwig et al. 2016), attempt to provide an index to denote the likelihood of impact if a species is introduced into a new location, for example through trade. Managers could use these simple indices to inform decision-making. Unlike most risk-assessment protocols, EICAT and SEICAT rely exclusively on a systematic review of peer-reviewed publications of each species in their non-indigenous range. This ‘gold standard’ of data sources carries with it the need for a comprehensive set of literature on all non-native species, but assessments to date have highlighted problems with the assumption that sufficient published material exists. For example, an assessment of all non-native bird populations found published material detailing ecological impact for only 30% of 415 species (Evans, Kumschick & Blackburn 2016). A similar assessment for non-native amphibians found information on ecological impact for only 38% of 105 species (Kumschick et al. 2017), and socio-economic information for only 7% of these species (Measey et al. 2016; Bacher et al. 2018). It would be naive to assume that such biases result from an absence of impacts; it is well known that reporting biases exist between different taxa, and between continents/global regions (Dawson et al. 2017). However, until the extent of biases are better understood, it remains difficult to motivate studies on non-native species in poor
or underdeveloped localities, even though such data may be of great value to more developed nations who have legal and logistical infrastructure to prevent importation.

We aim to assess the information currently available to inform quantitative risk assessments of herpetofauna and the degree of taxonomic and geographic bias that exists in the literature. To do this, we performed a systematic review of research published to date on non-native reptile and amphibian species to assess the scope of peer-reviewed information currently available. In so doing, we highlight the species, subjects and geographic locations that received the most research, and enable identification of gaps.

Survey Methodology

For this analysis we split reptiles and amphibians into six taxonomically-based ‘morphological groups’ (hereafter herpetofaunal groups): lizards, snakes, turtles, crocodiles, frogs and salamanders, recognizing that snakes and lizards are not separate monophyletic groups. However, this distinction is reflective of the level at which these groups are often studied (e.g. Rodda, Sawai, Chiszar & Tanaka 1999) as a result of their distinct morphological characteristics and different selection pressures on these groups in the pet trade that result in divergent invasion patterns as well as other functional differences that are likely to affect their invasion probability.

To determine the knowledge base underpinning existing risk assessments for herpetofauna, we reviewed the literature available on the introduction, establishment and/or invasion and impact of
non-native reptiles and amphibians. Searches were conducted on the ISI Web of Science Core Collection (on 3 March 2016) using the following criteria: Topic = alien OR invasive OR non-native OR exotic OR non-indigenous OR feral AND Topic= reptil* OR amphibia* OR turtle* OR tortoise* OR lizard* OR herpetofauna OR crocod* OR anura OR caudata OR testudin* OR ophidia OR sauria OR squamata OR snake* OR frog* OR toad* OR salamand* OR newt*. The ISI subscription used literature dating back to 1970. We recognise that ISI is biased in many respects, including against non-English literature (e.g. Adam 2002). However, we justify the use of this database alone as it is a source likely to be used by those conducting risk assessments, and for whom non-English language content may also be inaccessible. This search yielded 3194 papers. Many of these papers were not relevant to the current study as a result of a number of homonyms (e.g. invasive and non-invasive medical techniques) that resulted from including the wide range of search terms (Westgate & Lindenmayer 2017). As a preliminary measure to reduce the papers from extraneous study fields (Westgate & Lindenmayer 2017), the results were refined by excluding irrelevant research areas (e.g. paediatrics and ophthalmology, see the full list in supplementary material), leaving us with 2383 papers (Fig. 1). The relevance of these papers was assessed by reading the abstract and, where necessary, the full paper. All studies that pertained to non-native herpetofaunal species were included in the review. These included those that addressed any aspect of the invasion process (e.g. establishment or potential establishment correlates, or bioclimatic models); impacts or potential impacts (including ecological impacts, human socio-economic impacts, spread of disease and envenomation); potential or actual spread dynamics; genetics of introduced populations; detectability; ecology in non-native range (diet, reproduction, interactions with other species); biology in non-native range; and factors relating to import or pathways of invasion, including trade in non-natives and translocation of non-natives;
or first records of populations. Studies focussing on the impacts of non-herpetofaunal non-native species (e.g. mammals or fish) on native reptiles and amphibians were excluded, as were purely veterinary studies, studies on parasites of non-native species where the parasite and not the non-native species was the focus, and any papers that had no clear link to the topics of interest (e.g. despite the filter on the research areas, the search identified a large number of papers from other disciplines, such as invasive versus non-invasive medical techniques). This final list included 836 papers that were used in the quantitative analysis.

For each paper, the identity of all non-native reptiles and/or amphibians included in each study was recorded, as was the country or US state (locality) in/across which the study took place. Species recorded from papers included those that were the direct focus of study (e.g. for which field data were collected or species that were included in an experimental setup) and any species documented in a particular place outside of their native range. We recognize that detailed studies of single species are probably more useful to risk assessors. However, papers that provide general overviews of many species are also valuable (with specified confidence limitations) for risk assessment when specific information about focal species is not available, and also to provide evidence of pathways and introduction records, where introduction represents an important phase of invasion (Blackburn et al. 2011). Each paper was also classed into one or more of the following subject categories: Climate, Ecological Impacts, Pathways, Control, Invasion Correlates, Distribution, Translocation, or Trade. Once all data were captured, the taxonomy of species was cross-checked using Frost (2017) for amphibians and Uetz, Freed and Hošek (2017) for reptiles, and relevant entries in the database were consolidated. The family to which each species belongs, and the total size of these families, and herpetofaunal groups, were
taken from the same sources. Many papers that covered more than one taxon included species that were non-native, but had not necessarily been released into the wild, or did not have established populations. We did not attempt to remove these species from our list, which leads to discrepancies in numbers between our dataset and those of Kraus (2009). We did however compare results for papers that dealt only with one species with those that dealt with multiple species as well as the full set of papers, but found no difference in the focus of these subsets of publications. The full dataset is available as supplementary material (S2). Summary statistics were calculated by paper, subject and species.

We assessed taxonomic biases in the literature at family level by comparing the number of species per reptile or amphibian family present in the reviewed literature with a random expectation generated using the hypergeometric distribution (van Wilgen et al. 2010) in R v. 3.4.0 (R Development Core Team 2017). The hypergeometric distribution is similar to a binomial distribution and describes the probability of a given number of successes given a specified number of draws, without replacement. In this instance, a set number of species are sampled from a pool of families of known size. Families outside the 95% confidence intervals were deemed to be either over- or under-represented in the literature, compared to expectations based on the size of the family and the total number of species that appear in the literature. Results were visualised by plotting the number of species that have been described globally within each family against the proportion of species in the literature under review. We also performed the same analysis at the level of herpetofaunal groups.
Taxonomic bias was further assessed at herpetofaunal-group level by comparing information on known invasions published in Kraus (2009), to information available from peer-reviewed literature (this review). To provide a baseline of taxonomic and geographic scope of known reptile and amphibian invasions, we used data from Kraus (2009), a database that details all known introductions of non-native herpetofauna from the published and grey literature at the time (2006/7). While these data are somewhat out of date, they represented the latest comprehensive dataset of introduced and established species across taxa at the time and for the purposes of our analysis we assume that derived ratios and trends will have remained similar.

Populations in the Kraus (2009) database are recorded at country, island or US-state level (hereafter location). Any (or multiple) successful population(s) within a country or state is counted as a successful introduction for that location (and the total number of introductions or populations within a particular country or US state is not considered). We refer to “introduction” as the arrival, outside of captivity, of a species in an area where it is not native (i.e. having overcome a natural barrier to movement, Blackburn et al. 2011). Successful introductions (established species) were classified according to Kraus (2009) as introductions “reported to be established (within the country, island or US state) at the time of the most recent literature citation for the population in question”. “Established” is interpreted to mean a population that has shown the ability to reproduce regularly, without human intervention (or in spite of human interventions) to form populations of sufficient size to be resilient to stochastic events. From Kraus (2009), we extracted the total number of species introduced anywhere outside of their native range and the total number of known independent introductions per species per location (some species may have been introduced to more than one country or US state) for each herpetofaunal group. We then calculated the proportion of successfully established populations
and species as a fraction of those introduced and as a fraction of all described species within the
group.

Potential geographic bias in the literature on non-native herpetofauna identified in this review
was assessed at a crude level by comparing the number of studies for each country or US state
with the number of successfully established species in that country (Kraus 2009). For multi-
location studies, we scored only papers that truly collected/provided data for all localities defined
within a region, and excluded studies which did not have a defined geographic scope or had clear
geographical bias through selection of species (e.g. Kats & Ferrer 2003; Pilliod, Griffiths &
Kuzmin 2012, where geographic scope was restricted by the example species selected) or areas
(e.g. regional studies on reptile trade, such as Rataj et al. 2011 or Herrel & van der Meijden
2014, where information was clearly not sourced from all countries or locales). A total of 800
papers for which exact country locations could be identified were included in this analysis. This
included 22 papers deemed to be global in scope, for which all countries and US states were
scored.

We also conducted a more detailed assessment of geographic coverage, extracting the species
lists and locations from each paper and tallying the total number of species covered by each
paper per location (country or state). The number of species studied was compared to the number
of species established per location (Kraus 2009). Multi-location or global papers that dealt with
more than one species were only included in this analysis in instances where it was possible to
assign all the species in the paper to particular locations. Papers such as Bomford, Kraus, Barry
& Lawrence 2009 were therefore excluded as the paper did not specify whether the species used in the models had been introduced to Britain, Florida or California. A total of 767 papers were included in this analysis. All analyses were conducted in R v. 3.4.0 (R Development Core Team 2017), and maps produced in ARCMAP 10.3.1 (ESRI 2015).

Results

**Representation of herpetofaunal groups in the literature**

Only 1116 species (6% of c. 18 145 described herpetofaunal species; Frost 2017; Uetz, Freed & Hošek 2017) are included in the 836 studies relating to herpetofaunal invasions in this review. Five-hundred-and-fifty-two (49%) of these species appear in only one study, and 909 species (81%) appear in fewer than 5 studies. Ninety-five percent of species were included in fewer than twelve studies. Hardly any studies were conducted on non-native herpetofauna before 1990, and most studies were published after 2000 (Supplementary Figure S1). A large proportion of papers (653/836, 78%) focused on a single species, and only a minority (54 or 6%) reported on more than 10 species.

Of the papers included in this review, most focus on or include frogs (58%, Table 1), while lizards appear in almost a quarter of studies. The remaining herpetofaunal groups are represented in 18% or fewer of papers relating to non-native herpetofauna. However, frogs and lizards are the largest herpetofaunal groups and as such, the number of species from these groups present in the literature actually under-represents these groups as a whole (Fig. 2a). Turtles and crocodiles are comparatively small herpetofaunal groups (25 crocodile species and 347 testudine species
have been described to date) and have the most representative sample of species covered by the
literature. Both groups are overrepresented in the papers that were reviewed (Fig. 2a, 47% and
56% of species from these respective groups occur in at least one of the papers included in this
review, Table 2), as are snakes.

Some families have received more attention than others. For reptiles, nearly all the testudine and
crocodilian families (e.g. Cheloniidae, Testudinidae, Emydidae, Alligatoridae, Crocodylidae) are
overrepresented in the literature, i.e. they have more species written about than expected by
chance given the size of the family, compared to reptiles as a whole (Fig. 2b). Snake families that
stand out include boids (Boidae and Pythonidae), Viperidae and Elapidae, while the lizard
families most overrepresented across studies are iguanids (Iguanidae and Corytophanidae),
varanids and chameleons. Over-represented amphibian families include three of the nine
salamander families (Ambystomatidae, Cryptobranchidae and Salamandridae), and nine out of
56 frog families, including Ranidae, Pipidae, Dendrobatidae, Ceratophryidae and
Bombinatoridae (see Fig. 2c for these and others). Families might be under-represented in the
literature if (1) species in these families are being translocated without being reported, or if (2)
species in these families are genuinely not moved around, typically resulting in no or very few
non-native representatives for the group. The fleshbelly frogs (Craugastoridae, approximately
800 species) were the largest amphibian family with no species present in the invasion ecology
literature. The largest reptile family with no representatives was the Uropeltidae (shielddtail
snakes, 54 species).
There are a handful of well-studied species within each herpetofaunal group (Fig. 3). These include the cane toad (*Rhinella marina*; 243 papers, or 29% of all papers focus on or include this species), the American bullfrog (*Lithobates catesbeianus*; 130 papers), the red-eared slider (*Trachemys scripta*; 95 papers), the brown tree-snake (*Boiga irregularis*; 57 papers), the African clawed frog (*Xenopus laevis*; 51 papers) and the brown anole (*Anolis sagrei*; 41 papers, Fig. 3 & 4). The best-studied salamander is the tiger salamander (*Ambystoma tigrinum*, 15 papers), and the best-studied crocodilian is the spectacled caiman (*Caiman crocodilus*, 14 papers, Fig. 3 & 4). The literature on crocodiles, frogs and turtles is particularly skewed towards individual species. Over half (59%) of papers that include crocodiles focus on or include *C. crocodilus*, and half (50%) of the literature on frogs is focussed on or includes the cane toad *R. marina* (while *L. catesbeianus* appears in 27% of frog papers). The red-eared slider features in nearly three-quarters (73%) of literature on non-native turtles (Fig. 4). The literature on lizards is least dominated by a single taxon, with the most well-represented species, *A. sagrei*, appearing in 21% of papers that cover non-native lizards (Fig. 4).

**Subject focus of research**

Most research (416 papers; 50%) has been conducted on impacts (Fig. 4). A large portion of this impact literature (42%), however, covers impacts of only two species, *R. marina* and *T. scripta* (Fig. 4). Similarly, the literature on control of non-native herpetofauna is heavily biased in favour of cane toads (included in 33% of papers on control) and brown tree-snakes (24% of papers on control, Fig. 4), while cane toads appear in over a third of studies (39%) on invasion correlates. There was no significant difference in the distribution of literature across subjects.
between papers that focussed on one species and papers that covered multiple species or which made no specific mention of species (V = 21, p = 0.7422).

Geographic distribution of work

Excluding the 22 global studies, which largely made use of the same information base as the well-studied areas, the bulk of research on non-native herpetofauna covered in our review has been conducted in Australia (217 studies), the United States (195 studies, mostly focussed on or including Florida, 86 studies and California, 41 studies), Brazil (40 studies) and Spain (40 studies), as well as several islands or island groups such as Guam (47 studies), Hawaii (46 studies) and the greater Caribbean (47 studies), with very limited information from other localities (Fig. 5). For example, the seven studies that were identified specifically from continental Africa, were all conducted in South Africa.

We further compared the geographical distribution and frequency of literature on herpetofauna to the distribution of documented introductions from Kraus (2009). One third (33%) of the ~600 species (nomenclature updated to match our list) included in the Kraus (2009) database have been studied in fewer localities than they have been introduced (Table 3). Excluding non-location-specific studies, only 8 countries, 5 oceanic islands/island states and 6 US states have two or more location-specific studies per successful invasive amphibian or reptile introduction. The majority of localities (79%) where established populations have been recorded (n =191: 145 countries and 46 US states) have fewer than two location-specific studies (aside from global or continental reviews) for every successful species (mean = 1.1), providing a poor basis on which
to base their risk analyses. Only six of the 23 localities that have more than 10 established non-native species, have more than two location-specific studies per successful species: Australia, Guam, the United Kingdom, China (inclusive of studies in Taiwan), California and France.

Additional anomalies are apparent when considering the number of species covered in the literature per location (n = 767 studies, Fig. 5b). In South Africa, where only seven established species have been recorded (Kraus 2009), 285 species are covered by the local literature (seven studies, although the bulk of the species appear in a list of traded species), equating to 41 species documented per successfully established non-native. For localities with more than 10 established non-natives (n = 23), rates of study range from <0.08 species studied per successful species for La Reunion, to >3.5 species studied per successful species in Texas, the United Kingdom, Indonesia, Florida, China, Japan and the United States as a whole. The United States has the highest recorded number of successfully established non-natives (108 species), covered at a rate of four species studied per invasive species (451 species appear in the 192 papers that have a US focus). In the case of China (25 studies, including Taiwan, that document 47 species, at 4.3 species studied per established species), the number of successfully established species (11) is likely an underestimate (Liu, McGarrity & Li 2012).

At a location level, there is clearly also selection towards studying certain species in particular places. For example, in Australia, where 28 established non-natives have been recorded (Kraus 2009), 91% of studies focus on or include the cane toad. Similarly, 92% of the papers that include Guam and the Mariana Islands dealt with or include the brown tree snake, and 44% of
papers that include China focus on or include the American bullfrog. Of the five most widely
introduced species (Kraus 2009: *T. scripta*, 84 localities [countries/US states], the Brahminy
blind snake *Indotyphlops braminus*, 65 localities, *L. catesbeianus*, 58 localities, *R. marina*, 48
localities and the common house gecko *Hemidactylus frenatus*, 45 localities), only the American
bullfrog - studied in 27 countries and 18 US states - has been studied in at least three quarters of
the number of localities to which it has been introduced. The common house gecko (33%) and
Brahminy blind snake (28%) have been studied in a third or less of the number of introduction
locales.

Success of different herpetofaunal groups

According to the data contained in Kraus (2009), lizards and frogs have had the highest rates of
successful establishment per species introduced (over 55% of frogs and lizards introduced
outside their native range have established in at least one location), while crocodiles (at 14%)
have the lowest (Table 2). However, crocodiles and turtles (~27% of known species in both
groups) have had the most representative sample of species introduced from their respective
herpetofaunal groups (Fig. 2). It is therefore not surprising that turtles have the most
representative sample of established or invasive species: 11.5% of all described turtles have
successfully established somewhere outside their native range (Table 2). The proportion of
successful non-native species is much lower for other groups (typically 1-2% and as low as 0.8%
for snakes, Table 2).
Despite the high rates of establishment for those lizards and frogs that have been introduced, the low representation of species that have been introduced outside of their native ranges (according to the literature on which Kraus 2009 is based) means that we know nothing about the invasive potential of the ~6200 lizards and ~6600 frogs that have never been given the opportunity to demonstrate their potential to establish or invade (Table 2).

**Discussion**

Our review of the herpetofaunal invasion literature identified 836 studies, covering 1116 species. A number of distinct taxonomic, geographic and subject patterns are highlighted. Most of the literature has been produced post-2000, with a strong focus on frogs (Table 1), particularly cane toads and their impacts in Australia. While comparatively less work has been conducted on turtles and snakes, proportionately more species from both these groups have been included in studies than is the case for frogs (Fig. 2). Most countries have very little peer-reviewed literature on non-native herpetofauna (fewer than two papers per established species). Africa and Asia, in particular have had very few studies, though for southern Africa at least, this is probably a realistic reflection of the small number of introductions and invasions (Measey et al. 2017).

Interestingly, the role of trade in the introduction of non-native species has received little attention in the period under review, despite the obvious link between trade and invasion pathways for these groups (but see Garner, Stephen, Wombwell & Fisher 2009). Although rates of establishment success are likely inflated by higher reporting of successful introductions, the remarkably high rates of establishment success [33% for reptiles and amphibians introduced to Florida (Krysko et al. 2016), 25% reported for vertebrates globally (Wilson 2016), and >50% for lizards and frogs (Table 2; Kraus 2009)], make trade regulation and pre-border risk assessment
very important management components for these species. As of 2017, research on trade of non-native herpetofauna appears to be expanding (e.g. García-Díaz, Ross, Woolnough & Cassey 2017; Measey 2017).

Geographic and taxonomic biases in the literature are well known for most groups of invasive species (Dawson et al. 2017), and we expect research effort to be concentrated in areas and on species that have the biggest impacts. However, while research effort has been largely appropriate, understanding the extent of existing biases is crucial for predicting and preventing future invasions and their likely impacts, especially if for most places and most species, the number of studies is insufficient. For example, half of the work on frogs has been conducted on the cane toad and nearly all the work on the cane toad (86%) has been conducted in Australia, meaning that despite a massive literature, this species’ potential impacts on mammals, aside from marsupials, remains largely unstudied. At the same time, less well-studied species like the Asian toad (*Duttaphrynus melanostictus*) are scored as having high potential impact as a result of area-specific cultural traits, such as eating toads that has resulted in poisoning of people (see Measey et al. 2016), although not necessarily applicable in areas where frogs are not routinely eaten.

Taxonomic biases

While few non-native herpetofaunal taxa have been studied in comparison to species from other groups (Dawson et al. 2017), the bias in studies on non-native herpetofauna is similar to the bias in information on native species. Less than half (40%) of reptile species have had their conservation status assessed (Bland & Böhm 2016; Meiri & Chapple 2016). Those families with
the fewest conservation assessments included either families with no species identified in this review, or families that were under-represented (e.g. Amphisbaenidae). With the exception of Opluridae (Madagascan iguanas), from which no species were identified in our review, those families with the most conservation assessments (Meiri & Chapple 2016) were identified to be either over-represented (Iguanidae) or proportionately represented (neither over nor underrepresented, e.g. Crotaphytidae, Phrynosomatidae) in the invasion literature. Amphibians, on the other hand, have all been assessed through The Global Amphibian Assessment (Stuart et al. 2004). All families identified through the global assessment to be threatened by over-exploitation (for at least one species in the family, Stuart et al. 2004) were also found to be well- or over-represented in the invasion literature (e.g. Leptodactylidae, Ranidae, Dendrobatidae, Microhylidae, Ambystomatidae, Salamandridae, Cryptobranchidae, Fig. 2), highlighting that families or species that are used by people are more likely to become invasive.

For plants, grasses are an example of a huge family with many known invasive species. Yet only a tiny portion have been assessed to determine the extent of introduction to new localities and the level of establishment and invasion (Visser et al. 2016). Focussing on functional (e.g. Canavan et al. 2018) or taxonomic groups (e.g. Canavan et al. 2017) has allowed scientists to distinguish syndromes of traits that enhance invasiveness. For herpetofauna, we suggest that a useful approach is to classify relevant functional groups of invaders and identify traits within these groups that correlate with invasive success (Allen, Street & Capellini, 2017; Tingley et al. 2010). For example, there is likely a difference in invasion correlates for species that are intentionally introduced (e.g. via the pet trade) and those that tend to move around as ‘hitch-hiker’ species (Kraus 2007). Some groups, despite their large size, are absent from the invasion literature.
because no species have been introduced to localities outside their native range. For example, families that do not make good pets (e.g. snakes from the family Uropeltidae, Fig. 2) and/or are unlikely to be transported accidentally (e.g. groups that have small, remote distributions and very specialised habitat). Other families appear to be over-represented in the invasion literature. For example, nearly all testudine families are overrepresented. This makes sense because tortoises and turtles are popular pets and are therefore widely traded and documented outside of their native ranges. The dominance of the red-eared slider in the literature, however, suggests that although testudines in general are exceptionally widely traded, proportionately fewer species actually become invasive or have notable impacts. Red-eared sliders are traded in vast numbers (common estimates are upward of 3 million hatchlings traded globally on an annual basis, Ramsay, Ng, O’Riordan & Chou 2007). Reducing the volume of this trade could be achieved by enforcing stricter controls on animal husbandry and trade, and encouraging the public to be more responsible pet keepers (Williams 1999).

Geographic biases

For the large majority of countries, especially in Africa, where little information is available, there are few known established non-native species and few studies. There are, however, also countries where despite several (e.g. Egypt, Greece) or many (e.g. Japan, Indonesia) established species, very few studies have been conducted (Fig. 5c). For Japan and Indonesia, at least, the studies that have been conducted have covered a broader range of species than are known to be established (Fig. 5b). Peer-reviewed studies from these two countries, along with others like the United Kingdom, New Zealand and South Africa have covered many more species than are currently established (Fig 5b). The reason for this is not always clear, but could be due to a keen
interest in herpetology in these areas or proactive research into trade and/or risk assessment (e.g.
Goka, Okabe & Takano 2013; Chapple, Knegtmans, Kikillus & van Winkel 2016).

In other locations, such as Australia and Guam, the peer-reviewed literature generation has been
prolific (Fig. 5a), but focussed on single species. This means that although Australia has the most
peer-reviewed literature (Fig. 5a) and the most papers produced per invasive species (Fig. 5c),
most of the species that are established in Australia are still understudied (Fig. 5b). With the
exception of a few places such as Florida where there is significant interest in the high numbers
of invasions that appear to be driven by a large number of ports, a well-developed trade in exotic
pets, and high levels of environmental disturbance (Krysko et al. 2016); the United Kingdom,
which has a large number of English-language academic hubs; and Brazil, the bias is worse for
the rest of the globe. This likely reflects a lack of research capacity where there are invasions that
are not reported or studied. For example, there are almost no studies or invasions recorded for
Africa. This could be the result of fewer introductions and/or a capacity gap in herpetologists to
report invasions. In other instances (e.g. China and Russia), it is possible that both invasions and
literature on them have gone undetected because documentation regarding these events are not
available in English, and therefore not searchable using the Web of Science (Adam 2002).

Records of first introductions for reptiles show exponential growth since about the 1950s, with
no end in sight to this trend (Seebens et al. 2017). While there are likely already many
undetected invasions, new areas remain vulnerable and increased awareness is important for
preventing future invasions.

487
Setting priorities

Countries like New Zealand that have focussed on allowing importation and trade in only a short list of permitted species appear to have achieved the highest success in reducing introductions (Genovesi, Carboneras, Vilà & Walton 2015; Seebens et al. 2017). The current trend for assessing which species should be permitted on such lists is to quantify the impacts of the species based on published information. This begs the question: How many publications are needed to provide adequate information to allow for the accurate assessment of risk of invasiveness and impact? This is not an easily quantifiable number, but we can gain some insights using recent EICAT assessments and their confidence levels to suggest numbers. Without directed research, only 265 of 365 papers on 39 invasive amphibians had impacts that could be scored using the EICAT scheme (Kumschick et al. 2017). Of these, only 8 species could be rated with high confidence for at least one impact mechanism and no species was rated with high confidence on more than one impact mechanism (EICAT scores 12 impacts, of which 8 are applicable to reptiles and amphibians: Predation, Poisoning/Toxicity, Competition, Hybridization, Disease Transmission, Interaction with other species, Parasitism, and Grazing/Herbivory/Browsing). Given that these 8 species include the five most commonly studied frogs and salamanders (see Fig. 2b&d), we might conclude that even hundreds of studies are not sufficient to produce high-confidence scores on each impact mechanism for EICAT (ignoring SEICAT impacts). However, one study is capable of producing high confidence on one impact mechanism. Two such examples of species that were rated highly on confidence with just a single study: Dubey, Leuenberger & Perrin (2014) on hybridisation in Italian water frogs (*Pelophylax bergeri*) and Holsbeek et al. (2010) on hybridisation with Levant water frogs (*P. bedriagae*). This suggests that with more work focussed on such impact assessments, total impact for EICAT may be
assessed with a minimum of 8 papers, relating to each of the impact mechanisms in Hawkins et al. (2015, see above). To date, no EICAT assessment has found a comprehensive literature for any invasive species (Evans, Kumschick & Blackburn 2016). From our work, we know that a minority of invasive herpetofaunal species have been the focus of any research. Clearly, much more directed work is needed.

Our study revealed that the majority of publications (78%) focus on single species, and that a large proportion of these, and other studies in this review (50%) concern impacts, which is good news for those hoping to score EICAT and SEICAT for these species. However, we caution that risk assessments require a fuller understanding of the invasive species, and that studies on pathways (11%) and trade (2%) are particularly poorly represented (Fig. 3). Given the importance of the first in risk assessment and the volume and key role of the latter in introductions (García-Díaz, Ross, Woolnough & Cassey 2017), we emphasise the need for more strategic publications analysing the trade in herpetofauna and other pathways related to their unintentional movement (Tingley et al. 2018).

The Global Amphibian Assessment is a good example of a world-wide initiative that drove substantial work to collate information for all species to provide a baseline and a fantastic resource for refining data. Given that only a small portion of herpetofauna currently appear to be moved around in high numbers, or show invasive tendencies, setting up more global initiatives to focus on groups of invaders across a broader geographic range is not an unrealistic task, particularly considering that distribution information is already available for amphibians.
Initiatives for invaded countries to work together on the impacts of common invasive taxa could provide an important platform for accumulating crucial information on impacts. One such initiative in Europe saw members from four EU countries funded to work jointly on the impacts of the invasive African clawed frog, *X. laevis*: INVAXEN (http://www.anthonyherrel.fr/INVAXEN/). This initiative has added 15 published articles on this species, nearly doubling the available data on their invasive populations (e.g. Courant et al. 2017; Louppe, Courant & Herrel 2017; Rödder et al. 2017). Funded by BIODIVERSA, this call did not include funding for studies on populations in non-participating EU countries (e.g. Italy), or in the native range of the species in southern Africa. There is scope for similar work on species like the red-eared slider, and other turtles that are currently studied in fewer locations than which they have been introduced (e.g. European pond turtles, *Emys orbicularis* and common snapping turtles *Chelydra serpentina*), several widespread gecko species, agamids like oriental garden lizards (*Calotes versicolor*), the Asian toad, and selected species from the families that are overrepresented in the literature and trade or even the cane toad outside of Australia.

Local and regional herpetological societies have a crucial role to play in this regard and should be encouraged to publish all new records of reptiles and amphibians in online databases and society websites. Many societies already do record such information in newsletters, but digitizing these data and making them available online could go a long way to improving the geographic coverage of literature and even reducing the taxonomic bias in published information. McGeoch et al. (2016) provide a protocol for prioritizing species, pathways and sites to assist countries in meeting Aichi Biodiversity Targets (Convention on Biological Diversity). Herpetological societies should contribute relevant information to the Global Register of Introduced and
Invasive Species (GRIIS) currently under development within the Global Invasive Alien Species Partnership (GIASIP) framework (McGeoch et al. 2016). In the absence of information, risk assessments will continue to rely on information from models based on well-studied species. Improving the geographic coverage of studies on model organisms and then the taxonomic coverage of model taxa will go a long way to improving predictions for invasive species and ultimately reducing their impacts.

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Supplementary information

Details of the research areas excluded from the ISI search during the systematic review, and an additional figure illustrating the accumulation of studies on non-native reptiles and amphibians over time are available in the Supplementary Material, S1. Details of the 823 papers included in the systematic review are provided in the Supplementary Material, S2. The raw data include the
names of each species covered by each paper as well as the geographic scope (at country level) of each paper.
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Figure 1 (on next page)

Prisma flowchart

Prisma flow diagram (from Moher D, Liberati A, Tetzlaff J, Altman DG, The PRISMA Group (2009) Preferred Reporting Items for Systematic Reviews and Meta-Analyses: The PRISMA Statement. PLoS Med 6(7): e1000097. https://doi.org/10.1371/journal.pmed.1000097) for systematic review of articles on invasive amphibians and reptiles from the Web of Science (formerly Science Citation Index) on 3 March 2016. Search criteria used: Topic = alien OR invasive OR non-native OR exotic OR non-indigenous OR feral AND Topic= reptil* OR amphibia* OR turtle* OR tortoise* OR lizard* OR herpetofauna OR crocod* OR anura OR caudata OR testudin* OR ophidia OR sauria OR squamata OR snake* OR frog* OR toad* OR salamand* OR newt*
Records identified through database searching (n = 3194)

Additional records identified through other sources (n = 0)

Records after duplicates removed

Records screened (n = 2383)

Records excluded (n = 811)

Full-text articles assessed for eligibility (n = 2383)

Full-text articles excluded, with reasons (n = 1547)

Studies included in qualitative synthesis (n = 836)
Patterns in taxonomic representation of (a) herpetofaunal groups and (b) reptile and (c) amphibian families present in the invasion ecology literature. The median (middle green line) and 95% confidence intervals (brown lines), adjusted for multiple comparisons, were estimated from the hypergeometric distribution. The points represent herpetofaunal groups or families; those that fall between the brown lines are not significantly over or under-represented (relative to amphibians or reptiles as a whole). Where multiple points overlap, lines indicate the number of points at each location.
**Figure 3** (on next page)

Number of articles per species of functionally-grouped amphibians and reptiles on the Web of Science.

Density plots show that the number of articles per species of functionally-grouped amphibians and reptiles on the Web of Science is always highly skewed toward one or two taxa, with the majority of species featuring only in one article. Taxa featuring in the highest number of articles have been highlighted for each group.
Subject of literature on non-native amphibians and reptiles for each herpetofaunal group and across all species.

Composition of subject of literature on non-native amphibians and reptiles for each herpetofaunal group and across all species. In each group, literature on the most frequently studied species (Crocodiles *Caiman crocodilus*; Frogs *Rhinella marina*; Lizards *Norops sagrei*; Salamanders *Ambystoma tigrinum*; Snakes *Boiga irregularis*; and Turtles *Trachemys scripta*) is shown in black, showing that the knowledge of most non-natives comes from single taxa. For example, almost all papers on non-native turtles include or focus on *Trachemys scripta*. (Note each of the studies listed may have been included in more than one subject category as appropriate).
Figure 5 (on next page)

The geographic distribution of studies on non-native reptile and amphibian species.

(a) The geographic distribution of 789 studies on non-native reptile and amphibian species (20 global studies have been scored for each country and state). (b) The difference between the number of species that have been included in studies pertaining to a particular country and the number of species known to be established in that country (Kraus 2009), normalized to the largest difference. (c) The difference between the number of studies conducted in a particular country and the number of species known to be established in that country (Kraus 2009), normalized to the largest difference.
**Table 1** (on next page)

Representation of herpetofaunal groups of reptiles and amphibians across papers from the systematic review
Table 1. Representation of herpetofaunal groups of reptiles and amphibians across papers from the systematic review

| Group      | Number of papers (out of 836) |
|------------|-------------------------------|
| Crocodiles | 22 (3%)                        |
| Frogs      | 487 (58%)                      |
| Lizards    | 198 (24%)                      |
| Salamanders | 33 (4%)                      |
| Snakes     | 149 (18%)                      |
| Turtles    | 131 (16%)                      |
Table 2 (on next page)

Success rates for introductions and species in each herpetofaunal group of reptiles and amphibians (lizards, crocodiles, snakes, turtles, frogs and salamanders) as per Kraus (2009).
Table 2. Success rates for introductions and species in each herpetofaunal group of reptiles and amphibians (lizards, crocodiles, snakes, turtles, frogs and salamanders) as per Kraus (2009).

| Order     | Total species (Frost 2017; Uetz, Freed & Hošek 2017) | Number of species included in our review (% of total species described per herpetofaunal group) | Introduction success | Species success | Proportion of taxonomic sampling |
|-----------|------------------------------------------------------|------------------------------------------------------------------------------------------------|--------------------|----------------|---------------------------------|
|           |                                                      |                                                                                 | Total introductions Kraus (2009) | Successful introductions Kraus (2009) | Success rate of introduction Kraus (2009) | Total species introduced Kraus (2009) (approximate) | Successful species Kraus (2009) | Success rate of species Kraus (2009) | Proportion of species introduced outside of native range | Proportion of species naturalised/invasive outside of native range |
| Lizards   | 6459                                                 | 347 (5.4%)                                                                      | 716                 | 445            | 62%               | 243                      | 139 | 57%             | 3.8%             | 2.2%             |
| Crocodiles | 25                                                  | 14 (56%)                                                                         | 29                  | 3              | 10%              | 7                        | 1 | 14%             | 28%             | 4.0%             |
| Snakes    | 3619                                                 | 320 (8.8%)                                                                       | 370                 | 115            | 31%              | 139                      | 30 | 22%             | 3.8%             | 0.8%             |
| Turtles   | 347                                                  | 162 (46.7%)                                                                      | 423                 | 147            | 35%              | 93                       | 40 | 43%             | 26.8%            | 11.5%            |
| Frogs     | 6776                                                 | 223 (3.3%)                                                                       | 508                 | 313            | 62%              | 147                      | 82 | 56%             | 2.2%             | 1.2%             |
| Salamanders | 713                                                  | 38 (5.3%)                                                                       | 81                  | 35             | 43%              | 37                       | 19 | 51%             | 5.2%             | 2.7%             |
| Caecilians| 206                                                  | 2 (1%)                                                                           |                     |                |                  |                          |    |                  |                  |                  |
Table 3(on next page)

Overlap between species included in papers in the review and species documented by Kraus (2009), the most comprehensive database of introduced reptiles and amphibians currently available
**Table 3:** Overlap between species included in papers in the review and species documented by Kraus (2009), the most comprehensive database of introduced reptiles and amphibians available at the time of the review

| Category                                                                 | Number of species in Kraus database | Percentage of taxa in Kraus | Percentage of species in Kraus |
|--------------------------------------------------------------------------|-------------------------------------|-----------------------------|--------------------------------|
| Species not identified to species level in Kraus                         | 65                                  | 10%                         | NA                             |
| Species not recorded in any of the papers in this review                 | 43                                  | 6%                          | 7%                             |
| Species in this review that only appear in global or multiregional studies | 177                                 | 27%                         | 29%                            |
| Species studied in more localities (states and countries) than recorded in Kraus | 107                                 | 16%                         | 18%                            |
| Species studied in the same number of localities as recorded in Kraus    | 121                                 | 18%                         | 20%                            |
| Species studied in fewer localities than recorded in Kraus               | 197                                 | 30%                         | 33%                            |
| Total species in Kraus (2009)                                           | 6021, plus 65 taxa not identified to species level | 667                         | 602                            |

1 Another 557 taxa were listed in papers in this review but do not appear in the Kraus (2009) database.