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BIODIVERSITY RESEARCH

A global assessment of alien amphibian impacts in a formal framework

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ABSTRACT

Aims The environmental and socio-economic impacts of alien species need to be quantified in a way that makes impacts comparable. This allows managers to prioritize their control or removal based on impact scores that can be easily interpreted. Here we aim to score impacts of all known alien amphibians, compare them to other taxonomic groups and determine the magnitude of their ecological and socio-economic impacts and how these scores relate to key traits.

Location Global.

Methods We used the generic impact scoring system (GISS) to assess impacts. These impacts were compared to other previously assessed taxonomic groups (mammals, birds, freshwater fish, invertebrates and plants). For each species scored, we investigated the relationship of impacts with key variables (taxonomy, size, clutch size, habitat and native range) using general linear mixed models.

Results Our data show that alien amphibians have similar impacts to other taxonomic groups, but comparatively fewer (41%) could be scored using available literature: < 7% of species had 71% of literature used for scoring. Concerning the environment, amphibians scored similar to birds and fish, but lower than mammals. Regarding socio-economy, only seven species scored impacts, but these were surprisingly serious. Bufonids and pipids consistently scored higher than other amphibian taxa. Species with larger body size and more offspring had higher environmental impacts.

Main conclusions Alien amphibians appear to be comparable to other taxa such as birds and freshwater fish in their environmental and socio-economic impact magnitude. However, there is insufficient literature to score impacts of the majority of alien amphibians, with socio-economic impacts particularly poorly represented.

Keywords

Anura, Caudata, economic impact, environmental impact, generic scoring system, Gymnophiona, invasive species, translocation.

INTRODUCTION

Human-mediated introductions of taxa to areas outside those to which they dispersed naturally is more diversified, rapid and dynamic and taking place at a larger spatial extent than any previous natural phenomena of dispersal (Ricciardi, 2007). Some alien species are generating massive and multi-faceted arrays of impacts across the globe that require investigation due to their consequences on native populations, communities and ecosystems (Vitousek, 1996), as well as on human health and economy (Pyšek & Richardson, 2010). From a management perspective, it is pivotal to quantify and compare impacts across alien taxa in order to minimize introductions of potentially detrimental species and to prioritize control and/or removal of established populations.

Proposed scoring systems assess and compare impacts of alien species (Pyšek & Richardson, 2008; Nentwig *et al.*, 2010). It is generally accepted that any reliable system must

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be evidence based, preferably with its origin in the literature, with peer-reviewed scientific publications being the gold standard (Blackburn *et al.*, 2014; Kumschick *et al.*, 2015a; Nentwig *et al.* 2016). Two such systems have been recently considered particularly promising to encompass the huge diversity of impacts generated by biological invasions. Blackburn *et al.* (2014) proposed a classification process that mirrors the IUCN red list. This proposes the rating of species from minimal to massive based on a number of environmental impacts. Conversely, the generic impact scoring system (GISS; Kumschick *et al.*, 2015a) considers both environmental and socio-economic impacts separately, but can combine both sets of scores to rank all species against each other. To date, this latter scoring system has assessed species alien to Europe for mammals, birds, freshwater fish (some) invertebrates and plants (Kumschick & Nentwig, 2010; Nentwig *et al.*, 2010; Kumschick *et al.*, 2015a), and birds alien to Australia (Evans *et al.*, 2014). Using the GISS, Kumschick *et al.* (2015a) found that alien mammals in Europe have the highest impact and alien freshwater fish, the lowest.

Although over 300 alien species have been assessed to date (Kumschick *et al.*, 2015a; Nentwig *et al.* 2016), the impacts of reptiles and amphibians have not been evaluated with the GISS. Kraus (2015) performed a general review of impacts of invasive reptiles and amphibians; however, he only took into account the species with considerable impacts as opposed to all alien species and focused on environmental impact. Some of these high impacting species, namely the American bullfrog *Lithobates catesbeianus* (Shaw), the cane toad *Rhinella marina* (Linnaeus) and the coqui *Eleutherodactylus coqui* (Thomas), were included among '100 of the world's worst' invasive species (Lowe *et al.*, 2000). Furthermore, the extent of the invaded range of some amphibians such as the American bullfrog, the cane toad or the African clawed frog *Xenopus laevis* (Daudin) has enabled researchers to test numerous hypotheses related to invasion biology and evolutionary ecology (Ficetola *et al.*, 2007; Measey *et al.*, 2012; Rollins *et al.*, 2015). Reviews suggest that an extensive literature addresses the environmental and/or socio-economic impact of at least some amphibian species (e.g. Shine, 2010; Snow & Witmer, 2010; Kraus, 2015), but an assessment of impact of all species using a standardized scoring approach has yet to be made.

Amphibian populations are currently declining across the globe (Wake & Vredenburg, 2008; Collins *et al.*, 2009; Pimm *et al.*, 2014) and alien amphibians are at least partially driving these declines through competition (Kupferberg, 1997), hybridization (Dufresnes *et al.*, 2015) and introduction of novel pathogens (Berger *et al.*, 1999; Daszak *et al.*, 2003; La Marca *et al.*, 2005; Martel *et al.*, 2013). Moreover, evidence of a direct relationship between the amphibian trade and the spread of disease is today largely accepted, at least for some pathogens such as chytrid fungi (Fisher & Garner, 2007), and this has led directly to the ban of imports and transportation of salamanders in the USA (US:FWS January 2016). Unlike trade in most mammals, which are often traded as meat, skins or body parts, amphibians are usually traded as live specimens (Rosen & Smith, 2010) thus increasing the chance that trade will result in propagules for invasive populations (Lockwood *et al.*, 2009), or seed a novel pool of pathogens (Schloegel *et al.*, 2012). Pathways leading to the largest introductions of populations have been via biological-control agents and aquaculture of animals for human consumption (Kraus, 2009). However, many more species have been introduced via accidental pathways, especially through movement of early life-history stages (e.g. as eggs or tadpoles) and/or through consignments of plants in the horticultural trade (Kraus & Campbell, 2002).

Scoring alien and invasive amphibians globally according to their impacts can provide numerous insights especially in the light of policy responses and management interventions at all stages of the invasion process (Blackburn *et al.*, 2011). By assessing both environmental and socio-economic impacts, we aim to assist and alert managers with prior knowledge on which amphibian species have the greatest impacts before they are introduced, as well as prioritizing resources for containment and/or eradication programs. In this study, therefore, we use the GISS to assess impacts of all species of amphibians known to have established populations outside of their native range. We then use these data to ask how amphibian impacts compare with impacts of other taxonomic groups (mammals, birds, freshwater fish, some terrestrial invertebrates and plants), and we explore how these impact scores relate to key traits: taxonomy, body size, clutch size, habitat and native range size. Among amphibians, we attempt to determine which species have the highest ecological and socio-economic impacts.

METHODS

To assess all global amphibian invasions, we used data on successful introductions of amphibians outside of their native range as listed in Kraus (2009), but excluding species introduced simply within their native ranges. Additionally, we searched for extralimital species on the IUCN red list (www.redlist.org) to supplement these records; five species were added: *Bombina orientalis* (Boulenger), *Ingerophrynus biporcatus* (Gravenhorst), *Ambystoma laterale* (Hallowell), *Rhinella jimi* (Stevaux) and *Pletodon jordani* (Blatchley). In some cases, we found that supposed successful introductions were actually novel taxa (e.g. *Bufotes viridis* (Laurenti)), and these were excluded from our list. This list represents all invasive amphibians (alien species that produce reproductive offspring which have colonized areas far from the initial introduction), as well as all alien species (see Richardson *et al.*, 2000). For ease of reading, we refer to the entire dataset as 'alien amphibians', which logically includes the entire subset of all 'invasive amphibians'. We used current taxonomic nomenclature and species numbers according to Frost (2015). The final list comprised 104 species on which we conducted literature searches to score impacts. We searched literature using the scientific name (current and previous taxonomic iterations) in Web of Science and on Google Scholar. In addition, we checked literature cited by Kraus (2009) and that listed by the IUCN. We filtered through the results by selecting publications according to the information provided in titles and abstracts and went through the selection in more depth. References cited within the selected publications were screened and included as appropriate, as was grey literature. This was supplemented by more specific searches for the species name and the name of each country (according to Kraus, 2009) in which it is known to be alien. Only the primary source of information or study was included on the score sheet (See Table S1 in Supporting Information).

Generic Impact Scoring System – GISS

The GISS consists of environmental and socio-economic impacts, with six subcategories each. Details on the scoring system are given in Kumschick & Nentwig (2010), Kumschick *et al.* (2015a) and Nentwig *et al.* (2016) as well as other applications of the GISS. Environmental impact is described as impact through competition, predation, disease transmission to wildlife, herbivory, hybridization and impacts on ecosystems as a whole not covered in the other subcategories. Socio-economic impacts contain agriculture, forestry, animal production, infrastructure, human health and impacts on human social life. Each impact subcategory has scores ranging from 0 (no impact detectable) to 5 (the highest possible impact at a given site), and each of those scores includes a verbal description of scenarios to ensure consistency among assessors. Where no score could be determined due to lack of literature, we entered a null value (999) into our score sheet to demonstrate that searches had been completed.

Species traits

Tingley *et al.* (2010) and Van Bocxlaer *et al.* (2010) identified various traits (including taxonomy, body size, native range size and clutch size) as potentially important correlates of amphibian invasiveness. From these, we selected clutch size, snout-vent length (SVL) and native range size as our explanatory variables as we could assess them for all species for which we had scored impact (i.e. Van Bocxlaer *et al.*, 2010 included more traits that were specific to bufonids). In addition, we added a hierarchical habitat variable that explained how many habitat types in which each species was known to occur. We also controlled for the effect of phylogeny by recording both the superfamily and family of each species.

The five species attributes we considered that may be associated with impact of alien amphibians were habitat specificity, taxonomy, extent of native range, body size (measured as SVL) and reproductive potential (measured as clutch size). For the 43 species in our dataset for which literature on impact was available, we assigned a habitat value based on that reported in the IUCN database. We followed Ficetola *et al.* (2015) in assigning species to one of three habitat categories: forest specialists, grassland and shrubland, and generalists. Species were scored as specialists (1) if their entry in the IUCN database mentioned that they could be found in only one habitat category, or generalists if found in more than one habitat category (2 or 3). To correct for the influence of taxonomy, we recorded family and grouped families into superfamilies because some families were represented only by a single species. We used a recent phylogeny of all Amphibia to group families at well-supported nodes (Pyron & Wiens, 2011; Pyron, 2014): Discoglossoidea, Hyloidea, Pelobatoidea, Pipoidea, Leiopelmatoidea and Ranoidea (see Measey *et al.*, 2015 for family contents). To estimate the extent of each amphibian species' native distribution, we used the total polygon area given to the anuran species in the IUCN Global Amphibian Assessment database (http://www.iucnedlist.org/amphibians; IUCN GAA 2008 version 3.1), excluding all areas of introductions. We also generated a typical snout-vent length (SVL; to the nearest mm) and clutch size for each species from a variety of sources (e.g. guidebooks, Amphibiaweb).

Analyses

We compared scores for alien amphibians with the scores produced by Kumschick *et al.* (2015a) for birds, mammals, fish, invertebrates and plants. To compare median scores of amphibians and those taxa previously assessed, we conducted Kruskal–Wallis tests in the statistical software R (version 3.2.1; R Core Team 2015), while boxplots were used to determine the relevant position of the median.

Similarly to the methods used for birds and mammals (Kumschick *et al.*, 2013; Evans *et al.*, 2014), we modelled the relationship between impact and our species traits (habitat specificity, extent of native range, SVL and clutch size) in a linear mixed-effects framework (function 'lme') fitted by restricted maximum likelihood with random effects (random = ~1) as implemented in the package NLME (version 3.1-122 Pinheiro & Bates, 2000), in the statistical software R (version 3.2.3; R Core Team 2015). SVL and clutch size were log-transformed to correct for non-normal distributions, and habitat was treated as a factor with three levels. We only used species for which we obtained literature to score impact; that is 43 species. We only report on correlates for total environmental impact (sum over the six environmental subcategories in GISS), as only seven species had data available for socio-economic impact. To control for phylogenetic effects, superfamily and family were retained as nested random effects in each model. Initial tests showed significant correlations between SVL and clutch size and extent of native range (Table S2; as expected and previously reported; Tingley *et al.*, 2010), and as these variables could not be used together in models, it was decided to compare models constructed with univariate terms. Comparisons between models were made using Akaike information criterion (AIC) and effect size using pseudo-R^2 (the conditional and marginal coefficient of determination for generalized mixed-effects models, R^2_{GLMM} in package 'MuMIn' version 1.15.1; Bartoń 2015).

RESULTS

Comparisons between amphibian taxa

Seven amphibian species scored over 10 for environmental and socio-economic impacts combined, comprising six frogs and one salamander (Table 1). These included all three amphibian species listed by Lowe *et al.* (2000) among '100 of the worst invaders'. There are no known alien populations of 206 known species of caecilians (Gymnophiona). Of the 692 described species of salamanders (Caudata), 19 were recorded on our list of aliens, and we were able to obtain scores for only four species (21.1%): *Ambystoma tigrinum* (Green), *Ichthyosaura alpestris* (Laurenti), *Plethodon jordani* Blatchley and *Triturus carnifex* (Laurenti). Of 6509 described species of frogs, 85 are alien and we obtained scores for 39 (45.9%). No salamanders were scored on socio-economic impacts, whereas we obtained socio-economic impact scores for seven frogs (8%), six of which also had environmental impacts. None of the species had literature which indicated a total of zero impact on the environment or socio-economy (i.e. zero entered in the dataset over not having any recorded impact); we found literature (33 papers) for four species which reported no impacts in at least one subcategory, but these were always replaced by higher impacts caused (in accordance with GISS procedure) through the same mechanism (i.e. within the respective subcategory).

To compare interfamilial differences in the Anura, we contrasted mean impact scores for selected families: Bufonidae (14), Eleutherodactylidae (5), Hylidae (15), Ranidae (15) and Pipidae (3) (see Fig. 1). This comparison shows that bufonids and pipids contribute substantially to environmental scores, while only bufonids contribute highly to socio-economic scores. While eleutherodactylids, hylids and ranids do show impacts, these are on average not higher than the average score of all anurans.

Correlates with traits

Our trait variables were strongly and significantly correlated (excluding the categorical variable 'habitat'; see Table S2),

Table 1 The top scoring amphibians for impact using the GISS. Sums for environmental and economic scores are made from six subcategories defined in Kumschick *et al.* (2015a). Note that the total score required to get into the top amphibians (> 10) is currently relatively low. Detailed information on scores and the literature used is available in Supplementary Material (Table S1 and Appendix S1).

Order	Family	Species	Sum environmental	Sum economic	Total
Anura	Bufonidae	**Rhinella marina*	15	4	19
Anura	Pipidae	*Xenopus laevis*	12	3	15
Anura	Bufonidae	*Duttaphrynus melanostictus*	7	6	13
Caudata	Ambystomatidae	*Ambystoma tigrinum*	12	0	12
Anura	Ranidae	**Lithobates catesbeianus*	12	0	12
Anura	Eleutherodactylidae	**Eleutherodactylus coqui*	7	4	11
Anura	Hylidae	*Osteopilus septentrionalis*	8	3	11

*Species listed in top 100 invaders by Lowe *et al.* (2000).

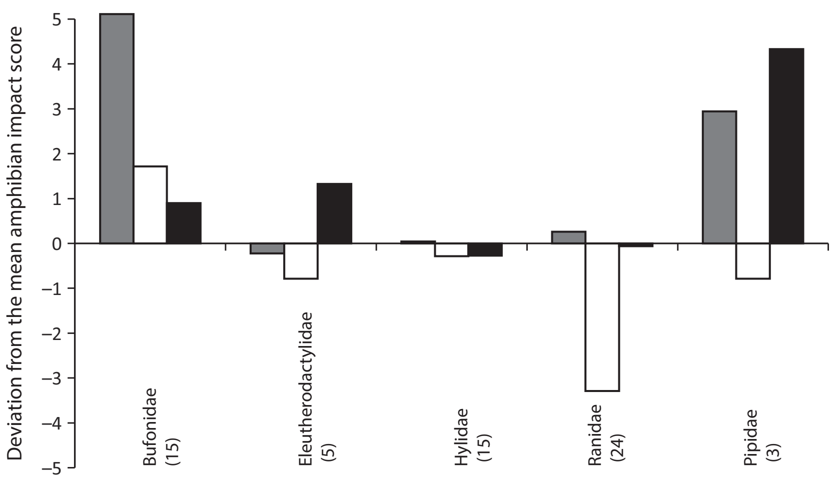

Figure 1 Anuran families and their relationship with the average anuran GISS impact score. Grey bars show total environmental impact scores, white bars are total economic impact scores, and black bars are total impact scores.

such that we did not construct any additive models. The four models showed that amphibians with bigger clutch size, snout-vent length and native distribution all have higher environmental impacts (Fig. 2). When the models were compared, we found that both body size (SVL) and clutch size were the best models, falling within 1 δAIC of each other (Table 2). The full model (including random effects of taxonomy) for clutch size was found to explain nearly 40% of the variance in the environmental scores (Table 2). On the other hand, the number of habitats does not seem to relate to impact magnitude (data not shown). Data for socio-economic impact was too scarce to be analysed, with only seven species having documented impact.

Comparison of amphibians with other taxa

Of the 104 species with successful amphibian introductions, we could score impacts with GISS for 43 species (41.3%). Compared to other taxa, a lower proportion of amphibian species has impact data available (even less than the previously lowest taxon, arthropods) (Fig. 3). Unlike other taxa where the proportion of species that could be scored was regularly as high as 50%, amphibians peaked at 20% with ecological scores on predation. This subcategory produced an average impact of 2 (± 1.23), with a maximum of 5 (*R. marina* in Oakwood & Foster, 2008). Literature available for scoring amphibian impacts was highly skewed, with most taxa (61.5%) having none, 21 species (20.2%) with one or two papers (8.5%), and seven (6.7%) species which had 76.6% of the literature (Fig. 4). In total, we found 259 relevant publications for all assessed amphibians. So even though information was available for less species than in other taxa, the average number of papers per species is just below the average of other taxa (around 3 papers per species, Kumschick *et al.*, 2015a) with a total of 252 papers and almost 2.5 papers per species (which includes all the species for which no literature was found).

Comparison of amphibians with other taxa over the 12 impact subcategories showed amphibian impact, on average,

Table 2 Linear mixed-effects models run on environmental GISS scores of alien amphibian species in relation to response variables: the size of the native area ('native area'), the 'habitat', the clutch size of the species ('clutch'), the size of the species ('SVL').

Model	log likelihood	K	δAIC	wi	R^2_m	R^2_c
SVL	−111.072	5	0.00000	0.4816	0.1478	0.2876
Clutch	−111.169	5	0.19295	0.4373	0.1978	0.3896
Habitat	−112.347	6	4.55032	0.0495	0.0163	0.0580
Null	−115.434	4	6.72332	0.0167	0.0000	0.0109
Area	−114.546	5	6.94728	0.0149	0.0669	0.1856

Each model was run with 'family' nested with 'superfamily' as a random effect. ΔAIC is the difference in Akaike information criterion values (AIC) between the current model and the best, and wi is the relative support a model has from the data compared to the other models in the set: Akaike weight. K is the number of parameters in the model. Marginal (R^2_m) and conditional (R^2_c) R^2_{GLMM} are reported for each model and provide an estimate of the explained variance.

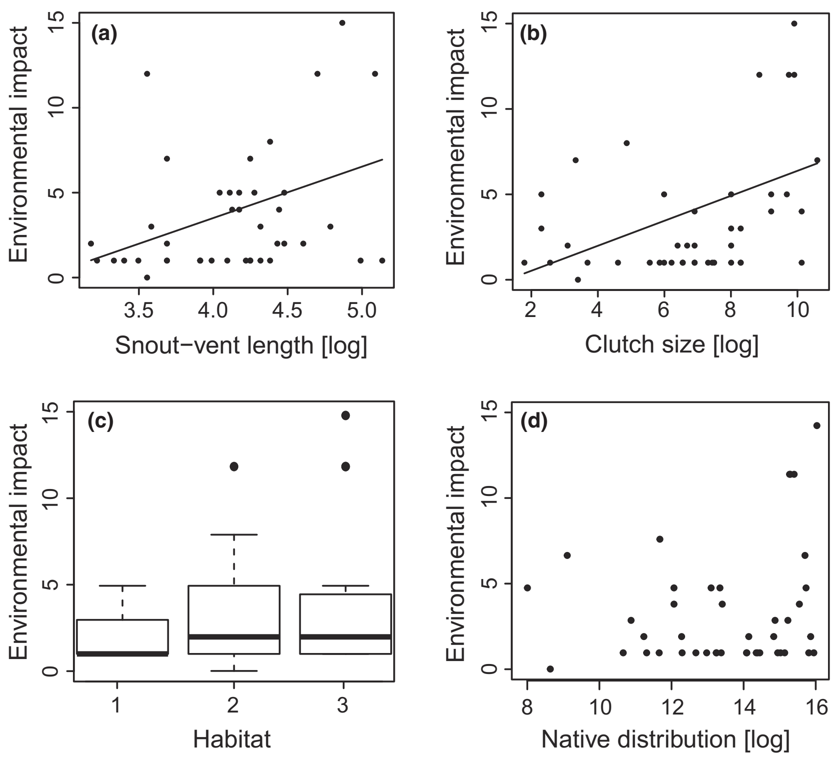

Figure 2 Correlates of environmental impacts of alien amphibians with traits: (a) snout-vent length, (b) clutch size, (c) habitat and (d) native distribution range. Only the 43 species which had reported impacts were included in the analyses and are shown here.

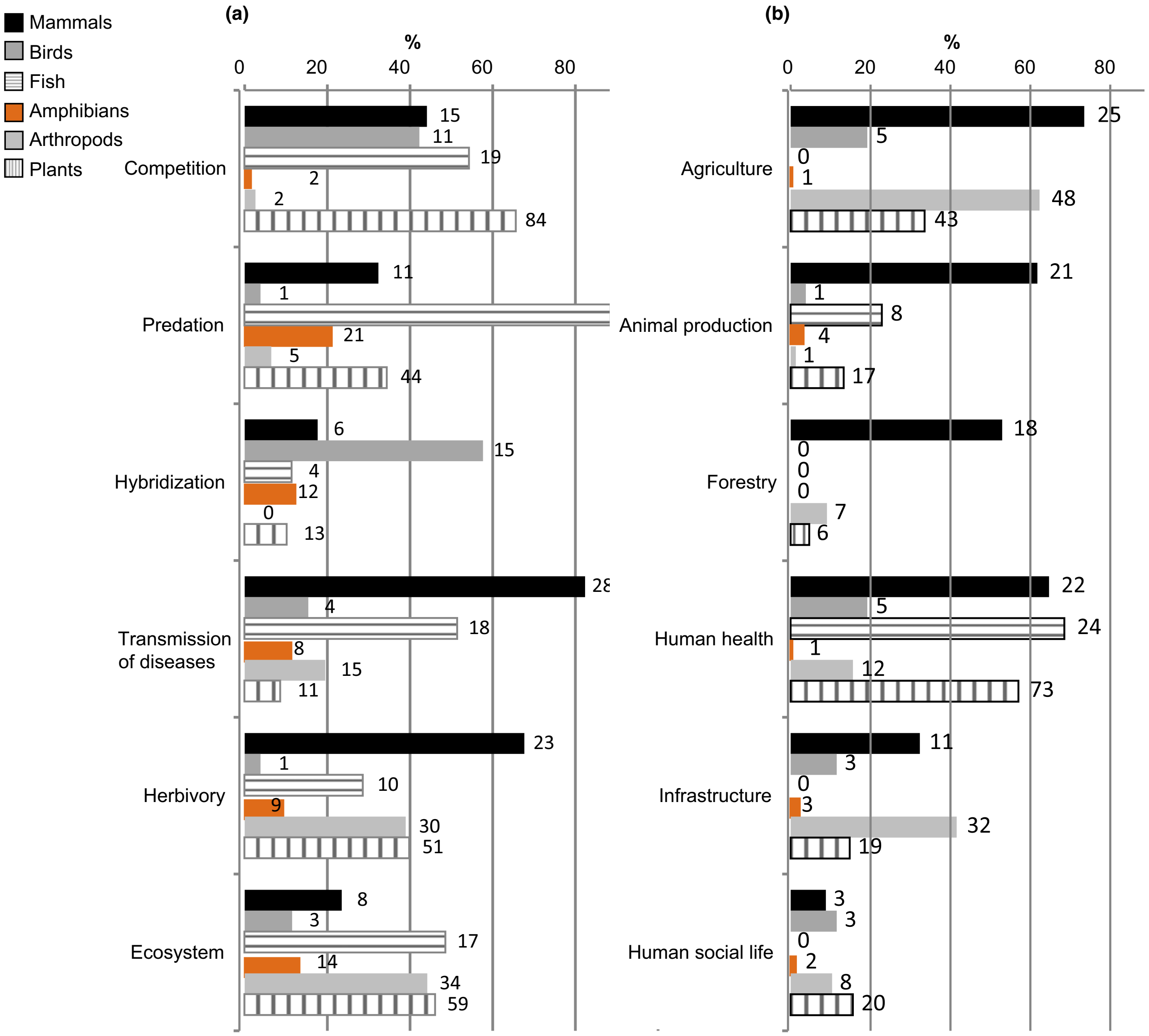

Figure 3 Percentage (and number) of species of alien amphibians where impacts could be scored in each respective subcategory compared to other taxa already assessed (Kumschick *et al.*, 2015a). The number at the end of each bar represents the number of species for which impact was found in the respective subcategories. (a) Environmental impact and (b) socio-economic impact.

to be lower than that of mammals, but higher than that of birds and fish (Fig. 5). Regarding environmental impacts, amphibians had a mean score of 2.3, but scored lower than mammals (the taxon with the highest impact) in competition (2 vs. 2.5) and herbivory (1.5 vs. 3.5). Surprisingly, amphibians scored higher than mammals, and all other taxa, in herbivory (3.5 vs. 3). So for most of the individual environmental impact subcategories, amphibians were within the mean scores of all other taxa, except ecosystem impact where they scored higher.

For socio-economic impacts, amphibians scored in all subcategories apart from forestry, as Kumschick *et al.* (2015b) found for birds and fish. They had surprisingly high impacts on human health, infrastructure and human social life, comparable with impacts previously found for birds, arthropods and plants, although only seven species were scored as having socio-economic impacts. The average score in the socio-economic impact category was higher than that published for fish (Veer & Nentwig, 2014; Kumschick *et al.*, 2015b), with the exception of the animal production subcategory.

DISCUSSION

This study represents the first use of the GISS for amphibians and therefore closes an important taxonomic gap regarding impact assessment for alien species. Our study takes the scoring of impact further by including all amphibians for which impact scores could be assessed, while another recent study only considered high impact species with limited taxonomic coverage (Kraus, 2015). Comparing impacts

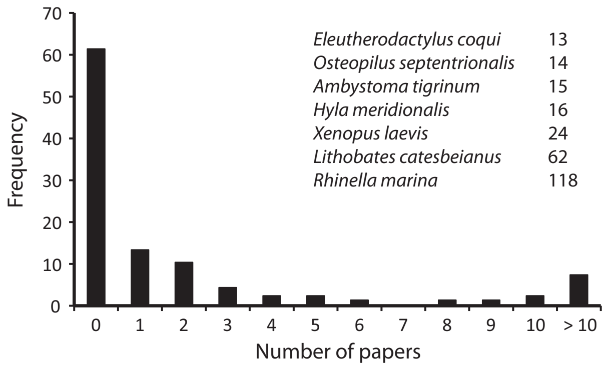

Figure 4 Literature available for scoring impacts of global amphibian invasions. Most of the species have no literature available, while seven species (listed inset) have the majority of papers (76.6%). Papers reporting on more than one species were counted separately for each species.

between species and among families is not only important to show gaps in the available literature, which we have certainly done here, but also to aid management decisions and inform policy.

Our study shows that some amphibians can have devastating impacts to the environment in their introduced ranges. Furthermore, some have shown to affect socio-economic systems (not covered by Kraus, 2015), even though studies are still rare. Generally, socio-economic impacts by alien amphibians are surprisingly varied. For example, in Australia, some aboriginal people have changed their traditional habits due to invasion of the cane toad (Seton & Bradley, 2004). In Hawaii, there has been a significant fall in property prices in areas invaded by the coqui frog due to noise disturbance (Kaiser & Burnett, 2006). Interestingly, the only species we scored which has a recorded economic and no recorded environmental impact is *Eleutherodactylus johnstonei* Barbour, as a possible vector of leptospirosis (see Everard *et al.*, 1990). In East Timor, frogs are widely eaten by villagers and at least one child has been killed and many others have become sick after eating the invasive toad, *Duttaphrynus melanostictus* (Schneider) (see Trainor, 2009). In Florida, USA, there have been localized power outages attributed to Cuban tree frogs taking refuge in transformers (Johnson, 2007). Lastly, invasion by African clawed frogs in Japan was found to impact on aquaculture by preying on juvenile carp (Kokuryo, 2009),

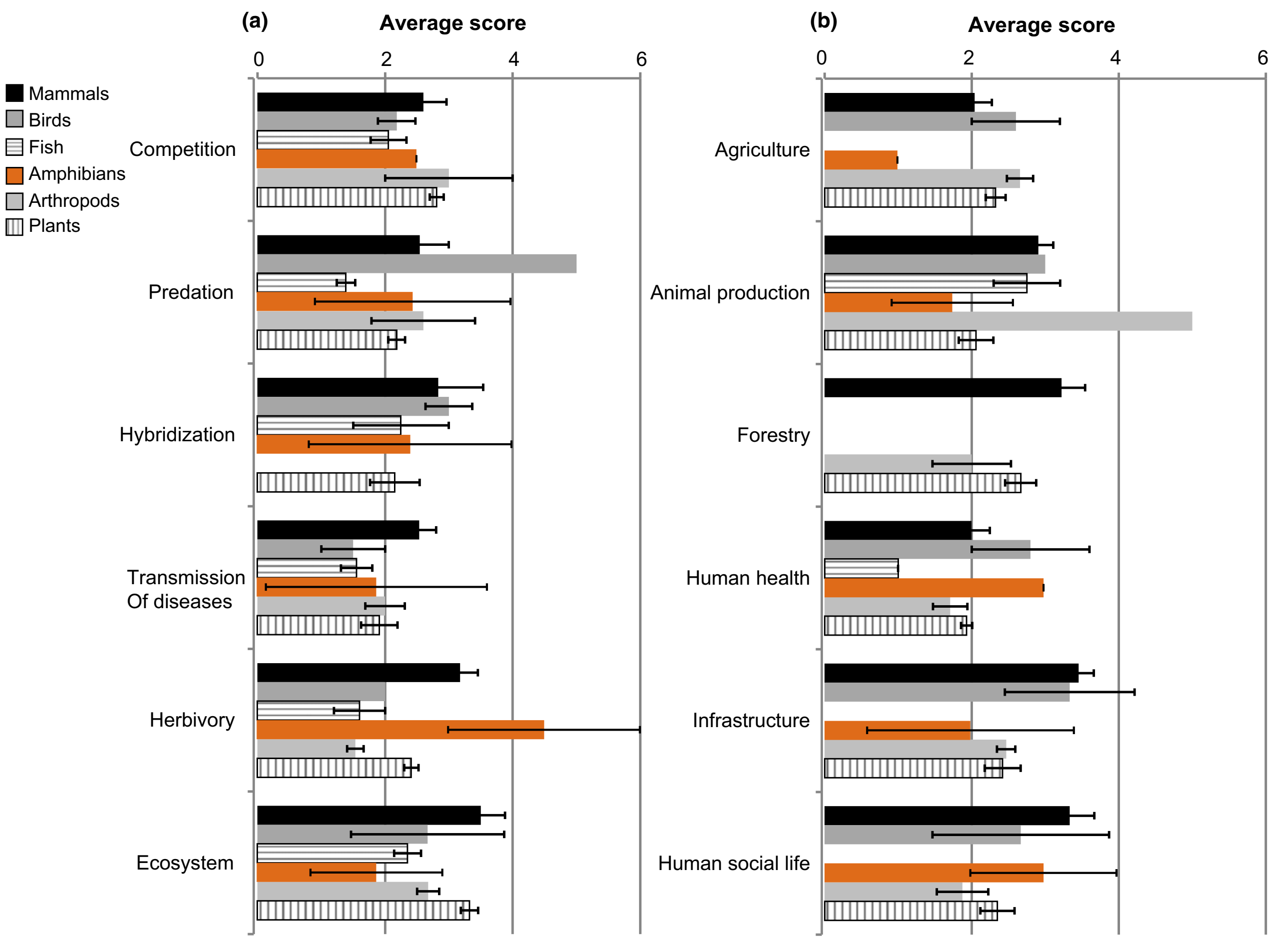

Figure 5 Average impact scores per subcategory for alien amphibians compared to other taxa already assessed (Kumschick *et al.*, 2015a). (a) Environmental impact and (b) socio-economic impact.

much as they do in their native range in South Africa (Schramm, 1987). These and other impacts were scored for a small minority of alien amphibian species (6.6%), and we consider that there are likely to be many more economic impacts that remain unrecorded in the scientific literature. This study represents the first attempt to classify and compare socio-economic impacts of amphibians. This is an important first step, as economic impacts of alien species are likely to be of key importance for managers making decisions with limited resources and we highlight the importance of studying and documenting known cases.

There is an inherent bias in GISS (or any impact scoring system) as it relies on published information that can be accessed in the scientific literature (see Kumschick & Nentwig, 2010; Kumschick *et al.*, 2015a). This means, for example, that species which are alien in economically impoverished areas of the globe (normally where fewer academic institutions occur) are less likely to be studied, and their impact scores will therefore not reflect their true impact. This is likely to apply to our study for a large number of alien amphibians have no score. Similarly, species which have been studied disproportionately may have inflated scores, although we do provide example of species with relatively few studies and a high GISS score (e.g. *Duttonophrynus melanosticus*). As in all impact assessments that rely on scientific publications, our amphibian impact scoring using GISS comes with serious caveats regarding the lack of score for the majority of species that can only be redressed by further studies on the impacts of alien amphibians, both ecological but especially regarding economic impacts.

While the number of papers documenting ecological impacts is proportionately higher than the socio-economic impacts, there are still fewer than for almost all other taxa of alien species considered to date, with an average of 2.5 papers per species. Amphibians scored particularly highly on hybridization, an average score of 3.55 from 15 studies. Alien populations of tiger salamander and Italian crested newt both threaten other species by hybridizing with indigenous salamanders (e.g. Arntzen & Thorpe, 1999; Fitzpatrick & Shaffer, 2007; Ryan *et al.*, 2013). This issue also exists with frogs, especially in the ranids where alien marsh frogs hybridize with local species (e.g. Holsbeek *et al.*, 2008). The most frequently recorded ecological impacts were with respect to the GISS category predation. These mostly relate to dietary studies which are relatively numerous for amphibians (Measey *et al.*, 2015). However, it is noteworthy that articles about the capacity of the cane toad to intoxicate predators were also scored in the predation subcategory.

Many amphibian species are facing extinction, making the translocation of threatened species for conservation increasingly attractive. Add to this the threat of global climate change, and there are increasing suggestions of moving populations of threatened species far from their centres of origin (Thomas, 2011; Schwartz & Martin, 2013; Dade *et al.*, 2014). Our study raises the issue that threatened species may have impacts on native species in their extralimital range. We found that 11 species on our list of alien amphibians (10.5%) are threatened in their native range and that two of these also have recorded impacts. The red necked salamander *Plethodon jordani* Blatchley (IUCN Near Threatened) is a domestic exotic in the USA with impacts on native salamanders (Rissler *et al.*, 2000). The growling grass frog *Litoria raniformis* (Keferstein) is native in Australia (IUCN Endangered), but introduced populations in New Zealand may be reservoirs for *Batrachochytrium dendrobatidis* (Hero & Morrison, 2004). Relocations of threatened species within their native ranges require careful thought and planning, but we join those questioning the wisdom of making long-distance translocations (Webber *et al.*, 2011), which may result in impacts on local species.

Alien amphibians scored surprisingly low on transmission of diseases, given the high importance that *B. dendrobatidis* (and now *B. salamandrivorans*) is known to have in global amphibian declines (Fisher *et al.*, 2009; Martel *et al.*, 2013). Two hypotheses concerning the global transmission of *B. dendrobatidis* both involve transfer to wild populations from alien species (Fisher *et al.*, 2009). However, there have been few documented cases of transfers directly attributable to invasions. Most studies were scored on the ability of the alien populations to act as reservoirs for chytrid (see Fisher & Garner, 2007 for a summary). It is noteworthy that in salamanders, one of the best reported cases involves a virus and not a fungal pathogen like *B. dendrobatidis* or *B. salamandrivorans* (Jancovich *et al.*, 2001). Similarly, in Australia, myxosporean parasites have been facilitated by populations of invasive cane toads to indigenous tree frogs (Hartigan *et al.*, 2011, 2012).

Comparing impacts of amphibians with other taxonomic groups, we show that the impacts of alien amphibians are lower than those of mammals, being similar to those of birds and fish. However, it is important to note that our scores are likely to change with additional studies. In addition, species which are currently listed with low or no GISS impact scores could, on further study, turn out to have high scores. However, a lower proportion of amphibian species were found to have recorded impacts than for other taxa studied to date (Nentwig *et al.*, 2010; Evans *et al.*, 2014; Kumschick *et al.*, 2015a). This could be related to the selection of species: all amphibians successfully introduced anywhere in the world (i.e. established outside their native range) were included in this study, whereas only species established in Europe were included for the other taxonomic groups (~300 species; Kumschick *et al.*, 2015a). It is important to note that in all the species scored for GISS so far, impacts from their entire introduced ranges were considered (not just Europe), so there is no regional impact bias in the data used for the comparison. In addition, birds have been assessed for established aliens in Australia (27 species; Evans *et al.*, 2014) as well as the birds listed on selected '100 of the worst list' (Kumschick *et al.*, 2015b). So, for example, for over 400 species of birds introduced in the world (Blackburn & Dyer, unpubl.), only about 13% have been studied systematically to date; of the species studied, only 35 have been found to have impacts. Thus, globally, the impacts of alien amphibians have been poorly studied, but this may also be true for some other taxonomic groups.

Even though our top scoring species include all amphibians on the '100 of the worst list', we found that only one of three amphibian taxa listed by Lowe *et al.* (2000) were in our top three scoring species (see also Kumschick *et al.*, 2015b). This may have already led to the reduction of efforts to control species that were not listed (see Fouquet & Measey, 2006), as well as contributed to the bias in literature on impact for these species; two of the three species listed as '100 of the worst invaders' (*Rhinella marina* and *Lithobates catesbeianus*) account for 65% of all papers found on impacts of amphibians.

Few studies have compared traits of alien species with the magnitude of their impacts; however, such comparisons can contribute to a more predictive understanding of impacts. Generally, the number of habitats a species can occupy in its native range has shown to be strongly linked with the magnitude of impacts in the alien range for both, birds and mammals (Nentwig *et al.*, 2010; Kumschick *et al.*, 2013; Evans *et al.*, 2014). As we could only classify the amphibians' ability to occupy a very limited range of habitats, it is not surprising that we did not find any pattern related to habitat generalization. Clutch size is strongly correlated with impact for amphibians (according to AIC values), as with mammals (Kumschick *et al.*, 2013), although no strong pattern emerged for birds (Evans *et al.*, 2014). Amphibians and mammals with a higher number of offspring show higher impacts, whereas there is a trend towards birds with smaller clutches having higher impacts. More work is needed to see whether there are common predictors of impact for all vertebrates, or generally for all alien species.

A suite of traits of alien amphibians have been found to be associated with key invasion events including their establishment success and spread rates (Liu *et al.* 2014; Tingley *et al.*, 2010; Rago *et al.* 2012). Native geographic size range, larger body size and more fecund amphibians are more likely to be introduced (Tingley *et al.*, 2010), while establishment success is a factor of introduction pathway and climatic similarity over life-history traits such as body and clutch size (Rago *et al.* 2012). However, species traits were not found to be predictors of spread rates, which were better linked to congener diversity, topographic heterogeneity and human-assisted dispersal (Liu *et al.* 2014). Our finding that body size, clutch size and native geographic range size are related to environmental impact is not an exhaustive list of potential traits correlated with impact as well as parts of the invasion process, but adds to the growing body of literature that suggests that large, fecund species which are widely distributed have a range-expansive phenotype that aids natural colonization (Van Bocxlaer *et al.*, 2010) and the potential for impact. Similarly, body size, clutch size and native geographic range size are likely to be predictors of invaded range, which may produce a similar correlation with environmental impact.

The relationship between clutch size and environmental impact may come through the increased ecosystem impact that the larvae of highly fecund species have on naïve aquatic communities. In addition, larvae had the only scored impacts on vegetation: that is, herbivory. For example, the American bullfrog has one of the largest clutch sizes (around 20,000 eggs), and its tadpoles change the phytoplankton of pools in the introduced range resulting in competition with the larvae of native species (e.g. Kupferberg, 1997). This effect could be more widespread than has yet been reported for species with aquatic larvae (e.g. McClory & Gotthardt, 2008). Larger amphibians may be more likely to have a higher impact through predation, related to the larger range of prey items available to them (e.g. Caldwell & Vitt, 1999; Toledo *et al.*, 2007; Measey *et al.*, 2015). In addition, large (and vocally prominent) alien amphibians may drive an investigation bias that leads to publication bias resulting in higher GISS scores. Given that clutch and body size are highly correlated (see Table S2), it may not be possible to determine the causative factors.

CONCLUSIONS

Alien amphibians appear to be comparable to other taxa such as birds and freshwater fish in their environmental and socio-economic impact magnitude. For a few species, many studies on impact have been conducted, but for most other species, literature is scarce. Socio-economic impacts are particularly poorly studied, but a few studies show remarkable impact (e.g. *Duttaphrynus melanostictus*). Generally, impacts that were scored were very varied and are likely to occur in more alien amphibians yet to be investigated. Despite the low proportion of species obtaining scores, we found that bufonids and pipids in particular scored highly, as well as species characterized by large body size and large clutch size. This makes these amphibians a priority for management interventions at all stages of the invasion process. A concerted effort is required to document instances of impact of alien amphibians, and we call for more studies on impacts of alien amphibians in general as these may be critical for making decisions relating to management of alien and threatened amphibians alike.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1 Trait variables and impact scores.

Table S2 Correlation coefficients between variables.

Appendix S1 Literature used to score global amphibian impacts.

BIOSKETCHES

John Measey and the Measey Lab works on invasive amphibians at the Centre for Invasion Biology (C·I·B) at Stellenbosch University. Laboratory members' interests range from evolutionary radiations through experimental biology, modelling and physiology. More information can be found at http://john.measey.com.

Sabrina Kumschick is a researcher at the C·I·B working closely with the South African National Biodiversity Institute and has been involved with the conception of several scoring systems. For this article, she collaborated with the Measey Lab.

Author contributions: G.J.M. and S.K. conceived the ideas; all authors collected the data; G.J.M. and S.K. analysed the data; and G.J.M. and S.K. led the writing.

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Table S1: Trait variables and impacts (sum over environmental and socioeconomic categories separately, and sum overall) for all 43 species for which impact data was available.

		Species' traits				Impact		
Species	Family	Clutch size	Polygon Area [km2]	Habitat	SVL [mm]	Environmental	Socioeconomic	Total
Rhinella marina	Bufonidae	20000	9751855.87	3	130	15	4	19
Xenopus laevis	Pipidae	17000	4623781.56	3	110	12	3	15
Duttaphrynus melanostictus	Bufonidae	40000	6980654.98	2	70	7	6	13
Ambystoma tigrinum	Ambystomatidae	7000	5146312.97	3	35	12	0	12
Lithobates catesbeianus	Ranidae	20000	4528410.68	2	162	12	0	12
Eleutherodactylus coqui	Eleutherodactylidae	28	8821.83	2	40	7	4	11
Osteopilus septentrionalis	Hylidae	130	118780.97	2	80	8	3	11
Pelophylax bergeri	Ranidae	3000	176443.40	2	57	5	0	5
Pelophylax perezi	Ranidae	10000	641244.01	3	61	5	0	5
Plethodon jordani	Salamandridae	10	2884.88	1	65	5	0	5
Triturus carnifex	Salamandridae	400	500699.14	2	72	5	0	5
Pelophylax ridibundus	Ranidae	16000	7188548.09	3	88	5	0	5
Pelophylax bedriagae	Ranidae	10000	176598.82	2	62	4	0	4
Hyla meridionalis	Hylidae	1000	684748.35	3	65	4	0	4
Amietophrynus gutturalis	Bufonidae	25000	5962507.32	3	85	4	0	4
Scinax quinquefasciatus	Hylidae	10	52938.04	2	36	3	0	3
Pipa parva	Pipidae	40	82000.88	2	40	1	2	3
Pelophylax nigromaculatus	Ranidae	3000	4318431.71	3	75	3	0	3
Hoplobatrachus rugulosus	Dicroglossidae	4000	3013136.03	3	120	3	0	3
Eleutherodactylus planirostris	Eleutherodactylidae	22	75806.36	2	24	2	0	2
Scinax ruber	Hylidae	600	8190338.90	3	40	2	0	2
Rana aurora	Ranidae	800	218710.40	2	84	2	0	2
Pelophylax esculentus	Ranidae	1000	2904533.67	2	88	2	0	2
Lithobates berlandieri	Ranidae	3000	1441721.95	3	100	2	0	2

Syrrhophus cystignathoides	Eleutherodactylidae	13	42452.29	2	25	1	0	1
Litoria fallax	Hylidae	500	577853.50	1	28	1	0	1
Microhyla pulchra	Microhylidae	100	1962717.74	3	30	1	0	1
Dendrobates auratus	Dendrobatidae	6	116551.79	1	33	1	0	1
Eleutherodactylus johnstonei	Eleutherodactylidae	30	5484.64	2	35	0	1	1
Strongylopus grayii	Pyxicephalidae	350	582999.67	3	40	1	0	1
Litoria ewingii	Hylidae	700	326574.85	2	50	1	0	1
Triturus alpestris	Salamandridae	260	1365239.51	3	50	1	0	1
Polypedates megacephalus	Rhacophoridae	400	1778244.65	3	50	1	0	1
Fejervarya limnocharis	Dicroglossidae	1000	8945614.25	2	54	1	0	1
Pelophylax lessonae	Ranidae	4000	3246722.92	2	60	1	0	1
Fejervarya cancrivora	Dicroglossidae	1000	1351726.18	2	68	1	0	1
Discoglossus pictus	Alytidae	1500	221852.39	3	70	1	0	1
Litoria raniformis	Hylidae	1700	441921.27	3	70	1	0	1
Rana temporaria	Ranidae	4000	7765814.34	3	70	1	0	1
Hylarana guentheri	Ranidae	3000	1845645.91	2	75	1	0	1
Polypedates leucomystax	Rhacophoridae	700	3948656.09	3	80	1	0	1
Rhinella jimi	Bufonidae	25000	665045.72	3	147	1	0	1
Hoplobatrachus tigerinus	Dicroglossidae	1800	3512356.72	2	170	1	0	1

Table S2: Pearson's product-moment correlation coefficients between variables for 43 alien amphibian species. Variables with significant correlations are shown with asterisks (P<0.001 = ***; P<0.01 = **; P<0.05 = *).

	SVL	Clutch size	Polygon area	Habitat
SVL	1	**	*	n.s.
Clutch size	0.479226184	1	***	n.s.
Polygon area	0.318828344	0.486889615	1	*
Habitat	0.223578032	0.214284288	0.365969027	1

Appendix S1: Literature used to score global amphibian impacts

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