AOSIS

Invasive amphibians in southern Africa: A review of invasion pathways

CrossMark

Authors:
John Measey[1]
Sarah J. Davies[1]
Giovanni Vimercati[1]
Alex Rebelo[1]
Warren Schmidt[2]
Andrew Turner[3]

Affiliations:
[1]Centre for Invasion Biology, Department of Botany & Zoology, Stellenbosch University, South Africa

[2]School of Life Sciences, University of KwaZulu-Natal, South Africa

[3]Scientific Services, CapeNature, South Africa

Corresponding author:
John Measey,
jmeasey@sun.ac.za

Background: Globally, invasive amphibians are known for their environmental and social impacts that range from poisoning of local fauna and human populations to direct predation on other amphibians. Although several countries on most continents have had multiple introductions of many species, southern Africa appears to have escaped allochthonous introductions. Instead, it has a small number of domestic exotic species that have rapidly expanded their ranges and established invasive populations within South Africa.

Objectives & methods: We used the literature to provide a historical overview of dispersal by some of the world's major invasive amphibians, give examples of species that are commonly moved as stowaways and discuss historical and current amphibian trade in the region. In addition, we give an overview of new South African legislation and how this is applied to amphibian invasions, as well as providing updates on the introduced populations of three domestic exotics: *Hyperolius marmoratus*, *Sclerophrys gutturalis* and *Xenopus laevis*.

Results: We show that frogs are mainly moved around southern Africa through 'jump' dispersal, although there are a number of records of 'cultivation', 'leading-edge' and 'extreme long-distance' dispersal types. Important pathways include trade in fruit and vegetables, horticultural products and shipping containers.

Conclusion: We suggest that southern Africa is becoming more vulnerable to amphibian invasions because of an increase in trade, agricultural and domestic impoundments as well as global climate change. Increasing propagule pressure suggests that preventing new introductions will become a key challenge for the future. Currently, trade in amphibians in the region is practically non-existent, suggesting potential for best practice to prevent importation of species with high invasion potential and to stop the spread of disease.

Introduction

Invasive species cause large economic impacts, have complex environmental impacts (Pimentel 2011) and are now considered to be among the four major threats to biodiversity. This has been recognised by their inclusion in the Strategic Plan for Biodiversity of the Convention on Biological Diversity (Aichi Target 9; UNEP 2011). Combating invasions clearly requires a prioritisation approach, taking account of invasive species' impacts as well as their pathways of dispersal (McGeoch et al. 2016). Impacts of introduced/invasive amphibians are significant (Kraus 2015; Measey et al. 2016) and include alterations to trophic networks (e.g. trophic cascades – Crossland & Shine 2010; Doody et al. 2009), novel and altered predator–prey dynamics (consumption of invertebrates – Beard 2007; Beard et al. 2003; vertebrates – Boland 2004), impacts on other amphibians' breeding systems (acoustic competition – Both & Grant 2012), alteration of ecosystem processes (Beard, Vogt & Kulmatiski 2002; Sin, Beard & Pitt 2008) and changes in socio-economic indicators such as property prices (Kaiser & Burnett 2006). The distribution of amphibian introductions is not even, with the majority occurring in Europe, North America and Australasia (Kraus 2008).

The African continent is remarkably free of many introduced and invasive amphibians that are prevalent elsewhere. Kraus (2008) lists 24 amphibian introductions in African countries, with only 14 successful. Almost all of these occur on islands (Canary Islands, Madagascar, Madeira, Maldives, Mauritius, Reunion and Seychelles) with the only continental introductions listed as successful being in Egypt (*Sclerophrys regularis*) and South Africa (Kraus 2008; Van Rensburg et al. 2011). Although this makes Africa the second least invaded continent for amphibians after Antarctica, this does not mean that there is no risk of new invasions. For example, not included in Kraus's (2008) review is the recent invasion of south-eastern Madagascar by the Asian toad, *Duttaphrynus melanostictus*, which is believed to have arrived in container shipments and has

now colonised a growing area around the port of introduction in Toamasina (Kolby et al. 2014a). The immediate call for eradication (Kolby et al. 2014a) was tempered by calls to assess the impacts and extent of the invasion (Mecke 2014). The global importance of biological invasions (UNEP 2011) and the need to prevent and respond to novel introductions led us to examine in detail the pathways that lead to introductions and range expansions in southern Africa.

There is no doubt that there is an increase in both the numbers of pathways as well as the frequency of individuals transported, that this is a general phenomenon (Wilson et al. 2009) and this is also true of amphibians (Kraus 2008; Van Wilgen, Richardson & Baard 2008). Kraus (2008) lists 103 species of amphibians that have successfully established populations outside of their native range. Most of these introductions and species have their pathways in the pet trade, with accidental introductions in cargo and horticulture being the next most important (Kraus 2008). These unintentional introductions are likely to increase as the quantities of cargo transported as well as the number of trading ports and connections increase. Currently, the most widespread invasions relate to intentional introductions of three species: *Rhinella marina* for intended use as biological control agent against a boring beetle in sugar cane, *Lithobates catesbeianus* for aquaculture associated with the consumption of frogs legs, and *Xenopus laevis* initially for use as a pregnancy diagnostic, and later in the scientific and pet trade. Although the high impacts of these species are generally recognised, the latter two species still form a large part of a growing trade in live amphibians (Herrel & van der Meijden 2014; Measey in press).

Here, we review the past, present and future potential for amphibian invasions in southern Africa. To do this, we use the scientific and popular literature to review the history of introductions for three invasive amphibians with the most significant impacts worldwide (*R. marina*, *X. laevis* and *L. catesbeianus*), asking why southern Africa has escaped these invasions and whether it is vulnerable to future invasions. We assess the current status of domestic exotics (*Sclerophrys gutturalis*, *Hyperolius marmoratus* and *X. laevis*) and determine whether there are pathways for more of these invasions. In addition, we review the current trade in amphibians in southern Africa to assess potential pathways for invasions. Lastly, we discuss the role of legislation and the currently published lists (Table 1) aimed at preventing and managing biological invasions in South Africa.

TABLE 1: Legal status of amphibians in South Africa.

No.	Species	Authority	Common names	Category/areas	Comment	Introduction stage	Impact category
(a)	**Invasive species**						
1	*Amietophrynus gutturalis*[a]	(Power 1927)	Guttural (African common) toad;	a. 1 b in Western Cape. b. Not listed elsewhere.	Appropriate	D2	MO
2	*Dendrobatidae species*		Poison arrow (or dart) frogs	2	Animals are present in exhibitions. But there may be privately traded animals within the region	B1/B2	MN
3	*Hyperolius marmoratus*	(Rapp 1842)	Painted reed frog	a. 3 in Western Cape. b. Not listed elsewhere.	Appropriate	E	DD
4	*Pelophylax* species		Marsh frog; Edible frog; Pool frog	1b	There is no indication that these species are currently or historically present	A (see text for explanation)	MV
5	*Triturus carnifex*	(Laurenti 1768)	Italian crested newt	1b	There is no indication that this species is currently or historically present	A (see text for explanation)	MR
6	*Xenopus laevis* hybridised with *Xenopus gilli*	(Daudin 1802) (Rose & Hewitt 1927)	Hybrids of African clawed frog × Cape (Gill's) platanna	1b	The hybrids of these species pose no intrinsic invasive threat, but *X. laevis* is invasive in many parts of the world and genetic evidence reported here suggests that its movement has formed extralimital colonies	NA (see text for explanation)	NA (see text for explanation)
7	Unless otherwise listed, all hybrids between indigenous and introduced species of amphibians			1b	Appropriate	NA	NA
(b)	**Prohibited amphibian species**						
1	*Ambystoma tigrinum*	(Green 1825)	Tiger salamander	Prohibited	-	A	MV
2	*Bufo bufo*	(Linnaeus 1758)	European toad	Prohibited	-	A	DD
3	*Eleutherodactylus coqui*	(Thomas 1966)	Puerto Rican coqui	Prohibited	-	A	MO
4	*Eleutherodactylus planirostris*	(Cope 1862)	Greenhouse frog	Prohibited	-	A	MC
5	*Lithobates catesbeianus*	(Shaw 1802)	American bullfrog	Prohibited	-	A	MR
6	*Litoria caerulea*	(White 1790)	Great green tree frog	Prohibited	-	B1	DD[b]
7	*Notophthalmus viridescens*	(Rafinesque 1820)	Red-spotted newt	Prohibited	-	A	DD
8	*Osteopilus septentrionalis*	(Dumeril and Bibron 1841)	Cuban tree frog	Prohibited	-	A	MO
9	*Rhinella marina*	(Linnaeus 1758)	Cane/marine toad	Prohibited	-	A	MR

[a]*Amietophrynus gutturalis* has now been reassigned to *Sclerophrys gutturalis*; [b]denotes a species with a congener with a non-DD impact category, see Kumschick et al. (2017).
Impact categories are taken from Kumschick et al. (2017).
(a) Invasive amphibians and (b) prohibited amphibians in South Africa, adapted from the *National Environmental Management: Biodiversity Act* (Act No. 10 of 2004, NEM:BA) Alien and Invasive Species Regulations as at July 2016. The introduction stage and the impact category follow Blackburn et al. (2011, 2014), respectively.
ML, minimal; MI, minor; MO, moderate; MR, major; MA, massive; DD, data deficient; NA, not assessed.

Historical overview

The history of cane toad (*R. marina*) introductions has been well researched (e.g. Esteal 1981; Lever 2001). Although the earliest introductions were made prior to 1844, the major movements occurred during the 1930s and 1940s when these toads were introduced to at least 90 distinct places in the Caribbean and south-east Asia, including Australia (Esteal 1981). Deliberate introductions were as a biological control agent against cane beetles (*Dermolepida albohirtum*) stemming from the 1930s. But the scheme was a failure as the toads were not capable of reaching the cane beetle species, which feed on foliage. The South African sugar cane industry was established in the 1840s for domestic supply, but this rapidly grew to intercontinental supply (Richardson 1982). The plague of cane pests in the 1930s and 1940s which led to the introduction of cane toads throughout much of their introduced range did not appear to be a problem in South Africa. Reports from the 1940s suggest that South African cane was free of serious insect pests (Dick 1941); including remarks that this was unlike Louisiana and Puerto Rico where cane borers were having devastating effects and forcing the closure of factories, despite cane toads having been introduced to these locales in 1920 and 1934, respectively (Esteal 1981).

However, there may have been other reasons why cane toads were not regarded as useful biological control agents in southern Africa. Southern Africa has many species of indigenous toads, which may have been seen as adequate biological control agents for potential pests. Thus, it may be speculated that the region escaped the deliberate introduction of the most highly impacting amphibian species, *R. marina* (see Measey et al. 2016) because biological control was seen as unnecessary. The only reports of cane toad introductions in eastern and southern Africa were against sugar cane pests in Tanzania and Mauritius, but these failed to establish in either location (Greathead et al. 1971).

Initial introductions of American bullfrogs (*L. catesbeianus*) were made for aquaculture purposes, for which southern Africa has limited current or past markets. Indeed, there are local (and larger) species of the African family Pyxicephalidae (*Pyxicephalus adspersus* and *P. edulis*) which are eaten in the region, but not currently thought to be threatened by this custom (IUCN SSC Amphibian Specialist Group 2013). Most people in southern Africa would not eat frogs, and thus, a market has not developed. This is in contrast to parts of the USA where declines of local frogs brought on by harvesting for meat led to the introduction of American bullfrogs (Jennings & Hayes 1985), and Europe where the movement of frogs of the genus *Pelophylax* has led to major hybridisation impacts (see below).

The second set of American bullfrog introductions was through the pet trade. As discussed below, there is little or no trade of amphibians within southern Africa, and this appears to have prevented the introduction of bullfrogs through this pathway. There was a single suggestion of a population of *L. catesbeianus* in Namibia by Rueda-Almonacid (1999) and this was cited by Kraus (2008). No reference is given or context for why this author made specific reference to Namibia. We can find no other substantive account for *L. catesbeianus* in Namibia and suggest that the mention by Rueda-Almonacid (1999) was in error.

Although the African clawed frog, *Xenopus laevis*, has been the subject of historical trade around the globe, the movements of animals within southern Africa were an order of magnitude higher and demonstrate another purpose for the historical trade of frogs: for laboratory dissections (Van Sittert & Measey 2016). We discuss the implications of this trade below.

Stowaways

'Domestic exotics' are species that form invasive populations outside of their natural distribution, but within the borders of the same nation. Domestic exotics are a particular problem in megadiverse countries, which typically contain multiple regions of endemism, in part because they already exist in local guides and so are not immediately recognised as invasive (Guo & Ricklefs 2010). To date, South Africa's only amphibian invasions are domestic exotics, and all have been moved from summer to winter rainfall areas (Measey & Davies 2011). There is a risk that more domestic exotics could become invasive, so here we review the potential for their pathways to result in extra-regional introductions.

It is clear that most individuals are moved unintentionally (Table 2) and that tree frogs and reed frogs have a particular propensity for being moved. Historical records suggest that this has always been the case in southern Africa as there is an anecdotal record of introductions occurring, albeit at a low frequency, over a long period (Figure 1). However, most of these accidental introductions involve single individuals, and it is not until propagule pressure increases that an invasion may occur. The painted reed frog, *Hyperolius marmoratus*, is a good example of this. These frogs are capable of moving large distances on vehicles, and there is an anecdotal report of an individual *H. marmoratus* surviving a week long drive from Iringa (Tanzania) to Stellenbosch (South Africa: A. Channing pers. comm.). Painted reed frogs can survive long periods without access to water because of their skin's high resistance to water loss and their water-conserving posture (see discussion).

The foam-nest tree frog, *Chiromantis xerampelina*, is another example of a species increasingly being reported outside its native range within the north-east of South Africa (Figure 1a; Table 2). However, unlike the painted reed frog, we know of no incidents where breeding has occurred at these introduced sites. These animals are capable of surviving long trips, but would not be likely to start invasive populations unless propagule pressure to a suitable breeding site was increased. It is also worth noting that these animals are relatively large (snout to vent length of 65 mm compared with *H. marmoratus* 29 mm) and are more likely to be noticed and removed before transportation. However, it seems probable that introductions of these, as well as other species of tree frogs and reed frogs,
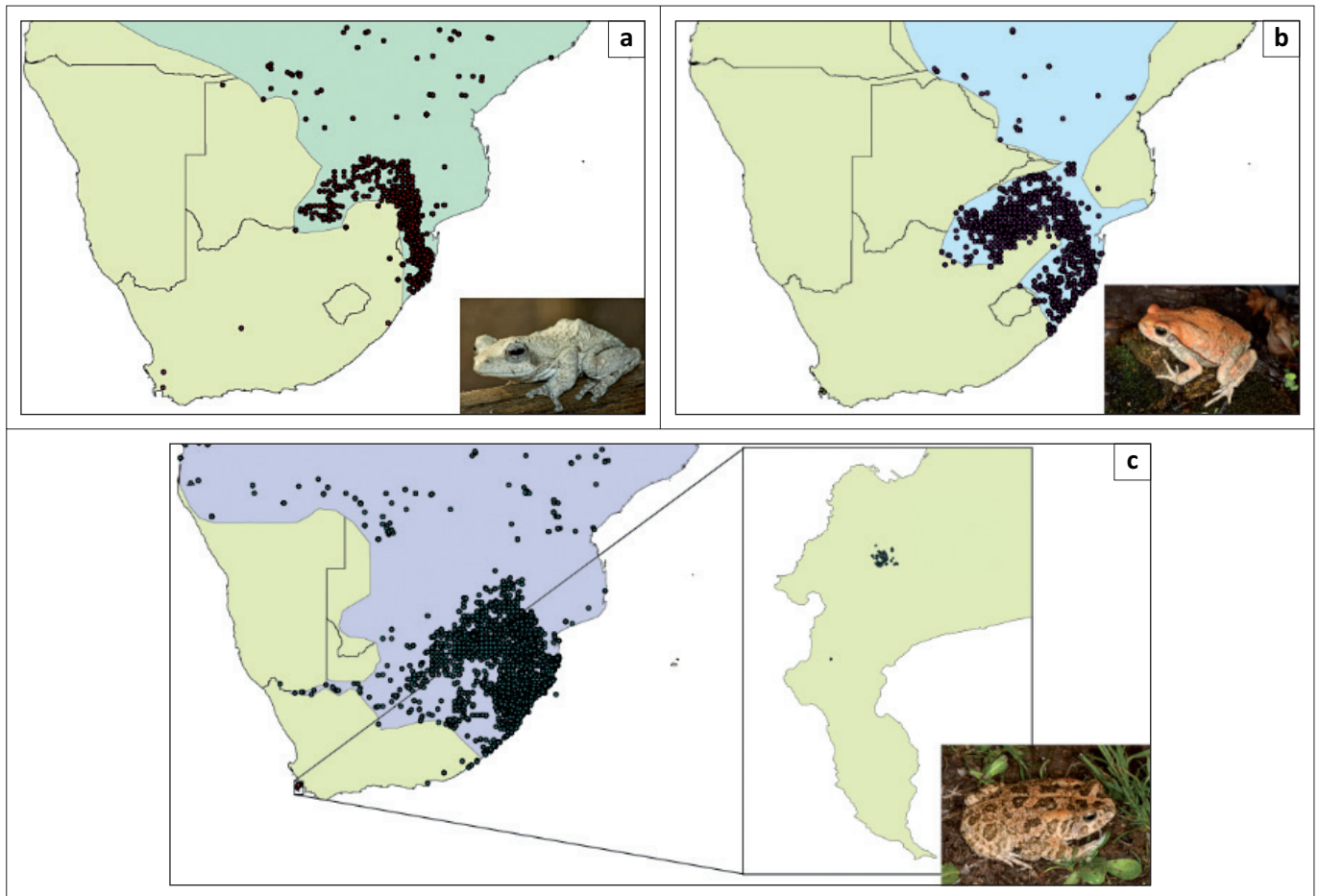
TABLE 2: Amphibians species found in southern Africa that have been translocated with their dispersive life history traits.

Species name	Origin	Place recorded	Anecdote	Current status of introduction	Dispersal pathway	Introduction stage	Impact category	References
Ambystoma mexicanum	Mexico city	Bloemfontein	Axolotls were very popular aquarium exhibits in the late 1980s and early 1990s. One population is known to have established in Bloemfontein for 3–4 years, but is now presumed extinct	Extinct	Cultivation	C2	DD[a]	Van Rensburg et al. (2011)
Sclerophrys gutturalis	Southern Africa	Cape Town (Constantia, Bishopscourt, Noordhoek)	Introduced to Cape Town and then relocated around the region	Invading	Mass dispersal or jump dispersal, leading-edge dispersal	D2	MO	This study
Duttaphrynus melanostictus	Singapore	Tokai, Bellville	Arrived in a consignment of furniture	Singletons	Extreme long-distance dispersal	C1	MR	A. Turner (pers. obs., Dec 2012)
Hyperolius marmoratus	Southern Africa	Many sites along southern coast and Stellenbosch	In addition to invasive population expansions (covered by Davies et al. 2013), there are a number of singletons being moved continuously: e.g. Bananas bought in Bellville, Lutzville June 2007	Invading and singletons	Leading-edge dispersal, jump dispersal	E	DD	Davies et al. (2013); A. Turner (pers. obs.); M. McGeoch (pers. comm.); E. Baard (pers. comm.); A. Channing (pers. comm.); L. du Preez (pers. comm.)
Phrynomantis bifasciatus	Southern Africa		Moved (around 100 km) in firewood and never found again	Singletons	Jump dispersal	B3	DD	Siegfried (1962); L. duPreez (pers. comm.)
Pyxicephalus adspersus	Southern Africa		Released in Muizenberg mountains	Extinct	Jump dispersal	C0	DD	de Moor and Bruton (1988)
Xenopus laevis	Southern Africa		Shipped *en masse* to tertiary institutes throughout southern Africa. Also moved for fishing bait.	Invading	Leading-edge dispersal, cultivation, jump dispersal	C3	MR	This study; Weldon et al. (2007); L. du Preez (pers. comm.)
Hyperolius tuberilinguis	Southern Africa	South Africa (Cape Town, Bloemfontein)	Found by greengrocers	Singletons	Jump dispersal	B3	DD	J. Harvey (pers. comm., Aug 2009); S. Davies (pers. obs., July 2014); A. Turner (pers. obs., Dec 2015)
Schismaderma carens	Southern Africa	Cape Town	Found in two different gardens in Rondebosch and Constantia; found in Bloemfontein moved in wood from Limpopo	Singletons	Jump dispersal	B3	DD	S. Richardson (pers. comm., Dec 2013); L. du Preez (pers. comm.)
Chiromantis xerampelina	Southern Africa	Stellenbosch, Porterville, Victoria West	Found in boxes of bananas in Porterville supermarket	Singletons	Jump dispersal	B3	DD	A. Turner (pers. obs., Dec 2012); J. Tarrant (pers. comm., Dec 2014)
Ceratophrys ornata	Argentina		Around 2008/2009 a shipment of these frogs came into South Africa and numerous individuals were available at one of the reptile trade shows	Pets	Cultivation	B2	DD	W. Schmidt (pers. obs.)
Dendrobates leucomelas	Northern South America	Montecasino Bird Gardens	Present in zoological collections	Exhibits	Cultivation	B1	DD[a]	W. Schmidt (pers. obs.)
Notophthalmus viridescens	North America	Western Cape	Pet trade	Pets	Cultivation	B2	DD	A. Turner (pers. comm., May 2016)
Dendrobates auratus	Central America	Montecasino Bird Gardens; uShaka; TwoOceans; pet trade	Present in zoological collections. May also be in undisclosed pet trade	Exhibits	Cultivation	B2	MN	W. Schmidt (pers. obs.)
Dendrobates tinctorius	Northern South America	Montecasino Bird Gardens	Present in zoological collections	Exhibits	Cultivation	B1	DD[a]	W. Schmidt (pers. obs.)
Litoria albolabris	Australia		Have been kept as pets in South Africa	Pets	Cultivation	B2	DD[a]	W. Schmidt (pers. obs.)
Litoria caerulea	Australia		Have been kept as pets in South Africa	Pets	Cultivation	B2	DD[a]	W. Schmidt (pers. obs.)
Dyscophus antongilii	Madagascar	Transvaal snake park	exhibits in 1990s	Exhibits	Cultivation	B1	DD	W. Schmidt (pers. obs.)
Cynops pyrrhogaster	Japan	National Zoological Gardens	Present in zoological collections. Present in the pet trade in KwaZulu-Natal. Confiscated from pet shop in Cape Town	Exhibits; pets	Cultivation	B2	DD	W. Schmidt (pers. obs.); A. de Villiers (pers. comm., May 2016)
Triturus cristatus	Europe	National Zoological Gardens	Present in zoological collections	Exhibits	Cultivation	B1	DD[a]	W. Schmidt (pers. obs.)

The introduction stage and the impact score follows Blackburn et al. (2011, 2014), respectively. Impact scores are taken from Kumschick et al. (2017).

[a]Denotes a species with a congener with a non-DD impact category, see Kumschick et al. (2017).

ML, Minimal; ML, minor; MO, moderate; MR, major; MA, massive; DD, data deficient.

Source: In all frames, the lines represent country borders in southern Africa while the coloured area represents the natural distribution. Points outside this natural distribution represent translocated individuals.

FIGURE 1: Examples of some southern African frogs that have been moved out of their range. (a) The foam-nest tree frog *Chiromantis xerampelina* has been found associated with bananas and other fruit; (b) The red toad *Schismaderma carens* is regularly transported in luggage, although records are scarce; (c) The guttural toad *Sclerophrys gutturalis* was moved to Constantia in the late 1990s and has now become invasive in the area and spread to other suburbs.

will likely increase as trade increases and that these species may survive transport out of South Africa and form invasive populations overseas. Indeed, Pyron (2014) suggests that the presence of the genus *Chiromantis* in southern Africa may be the result of a natural extreme long-distance dispersal event from the Asian stronghold of this family.

The red toad, *Schismaderma carens*, is occasionally found outside of its native range in southern Africa. Anecdotal observations suggest that within their range, adults are common in peri-urban areas and have a propensity to climb inside shoes and suitcases and are subsequently carried to new areas (Figure 1b; Table 2). Toads (and presumably other anurans tolerant of desiccation or high salinity) are capable of surviving ocean crossings inside containers, and we show that one species, *D. melanostictus*, arrived in South Africa in this manner, as it has in other countries (Church 1960; Kolby et al. 2014a; Mecke 2014). A successful invasion would require a container with many propagules or many containers with single propagules all of which are landed/unloaded at the same site within a reasonably short period.

Generally, people often feel that it is desirable to release animals back into the 'wild' regardless of their native/exotic status (see Measey et al. 2012); they have the concept that the animal is innocent and they are being ethically sound by releasing it. If a person in a key position, who repeatedly receives stowaways that arrive, always places them in the same (and appropriate) breeding site, it would be possible for multiple iterations of single stowaways to build up into levels that would support a self-perpetuating population and could become established or invasive. One such key position would be a manager in a cargo (e.g. food, building materials or nursery plants) distribution centre where goods are unpacked from containers from overseas, or even a site to where local goods are shipped within South Africa. This 'how possibly' scenario provides us with a potential pathway where individuals in key positions might be encouraged to report stowaways to the appropriate authorities. In addition, implementing a reporting procedure would be a useful way of keeping better track of the diversity and propagule pressure from stowaway species.

Trade

With the exception of trade in the African clawed frog, both locally for fishing and export overseas (see below), there appears to be little or no trade of amphibians in southern Africa either currently or in the recent past. From the 1930s,

before the start of the modern pet trade, herpetological hobbyists made connections with like-minded individuals on other continents and exchanged material via the postal service. Although many of the exchanged amphibians died, successful colonies of some exotic species were established and maintained by hobbyists. For example, the hobbyist Sidney Rose (son of prominent southern African amphibian taxonomist, Walter Rose) kept several species of exotic frogs, which were sent to him by similar enthusiasts overseas in the 1950s (B. Rose pers. comm.).

Since the 1980s, shipments of amphibians have been sent to southern Africa sporadically for the pet trade. These arrivals were quickly disseminated throughout the country, in both the pet and scientific trade, resulting in occasional introductions into the wild. One such example is the axolotl, *Ambystoma mexicanum*, which arrived in South Africa in the 1980s (Table 2) and was bred successfully in some laboratories as well as being sold in the pet trade. One set of animals released from a laboratory in Bloemfontein successfully reproduced for several years before the population could no longer be found (Van Rensburg et al. 2011). Axolotls have been regarded as 'colonial curiosities' and kept as pets and in laboratories throughout the world for over 150 years (Reiß, Olsson & Hoßfeld 2015). We classify this pathway as cultivation dispersal because, rather surprisingly, almost all the pet and laboratory trade originated from six animals imported to Paris in 1864 (Reiß et al. 2015). Subsequent introductions to Australia, Germany, Italy, New Zealand and Maryland in the USA are also recorded, although none are still thought to be extant (Kraus 2008).

Consignments of salamanders arrive infrequently in the region and are currently traded legally in KwaZulu-Natal (KZN Provincial Nature Conservation Ordinance No. 15 of 1974), while trade in the rest of the country is prohibited. Once they are out of the pet shops, individuals are occasionally traded at a low level as evidenced by private advertisements on Gumtree (2 June 2016: one 2.5-year-old *Cynops* sp. for sale, originally purchased from a pet shop in Hillcrest, KZN). However, animals can also be moved within the trade to areas where local ordinance allows. For example, in 2003 two fire-bellied newts (*Cynops* sp.) were confiscated from a Cape Town pet shop. These provincial differences have been recently reduced by the introduction of national legislation on invasive species (see below). It is also worth noting that South African nature conservation agencies do not know how many or which amphibian species are being kept within their provinces (Van Wilgen et al. 2008), such that the instances recorded here are likely only part of a larger trade.

One of us (W.S.) has made visits to at least 60 pet stores in Gauteng, KwaZulu-Natal, Eastern Cape and Western Cape since 2013 and did not encounter any amphibians for sale. However, we have observed limited interest in exotic amphibians in online reptile forums, often pointing to availability of amphibians for sale in pet shops in KwaZulu-Natal. According to several exotic reptile breeders, amphibians were viewed as being generally difficult to breed

and maintain in captivity; therefore, the demand was low and not commercially viable. However, from time to time, individuals have enquired about the availability of exotic amphibians, mainly poison dart frogs (Dendrobatidae). In addition, commercial breeders refrained from pursuing the acquisition of exotic amphibians for the pet trade when listed as 'prohibited' under the *National Environmental Management: Biodiversity Act* (Act No. 10 of 2004, NEM:BA) Alien and Invasive Species Regulations.

Legislation in South Africa

In 2014, South Africa promulgated a law (Act No. 10 of 2004, NEM:BA) which listed seven amphibian taxa that are covered by legislation controlling or prohibiting their trade (Table 1). While the consultative process which led to the production of this list was extensive (and included three of us: J.M., S.J.D. and A.A.T.), we did not encounter mention of some of the species in our review (*Pelophylax* species and *Triturus carnifex*) even though their categorisation as 1b in the NEM:BA A&IS regulations (a category that requires containment of the species) appears to suggest that they are already invasive in South Africa.

Species of the family Dendrobatidae (poison dart frogs) are currently present in the country in zoological exhibitions (Table 1a) and are popular pets elsewhere in the world with known invasive populations on a single island in Hawaii (Kraus 2008), with low levels of recorded impact (Measey et al. 2016). NEM:BA restricts trade in these species (category 2), which may be seen as a precaution against spread of diseases that they may carry (see Pessier et al. 1999). Survival of the species of this family released anywhere in southern Africa appears unlikely because their native climatic niche is in the tropical forests of South America.

Marsh frogs of the genus *Pelophylax* are a particular problem in Europe where they are endemic and include some threatened species with small ranges as well as wide-ranging species (Borkin 1999). Their traditional use in European cuisine emerged first as the Catholic church banned the consumption of meat on certain days, but 'meat' did not include frogs. Later, frogs' legs progressed to a delicacy and led to many movements of live animals for aquaculture (Kraus 2008). As these species readily hybridise, local *Pelophylax* species are sometimes severely threatened through these movements and subsequent hybridisation events with massive (MV) impacts (Kumschick et al. 2017). However, there are no records of any *Pelophylax* species ever having been traded or introduced into South Africa and their listing under NEM:BA (category 1b) is unwarranted. It seems unlikely that there would be any desire to import these frogs as there is a very limited local market for frogs as food (see above). But there has been a problem with trade in these species to stock garden ponds in central Europe (Holsbeek et al. 2008), and their presence in peri-urban ponds in South Africa is undesirable. Thus, it would make more sense if they were added to the prohibited list. Similarly, the salamander *Triturus carnifex* is also present on the controlled list although

there is no record of trade in South Africa, and the invasive impact in Europe is attributed to hybridisation with other species in the same genus. No salamanders occur naturally in southern Africa, so this listing appears inappropriate.

In addition to the national list of invasive amphibian species, the same document contains a list of nine prohibited species (Table 1b). Several species with high impact status are included such as *R. marina* and *L. catesbeianus* (see above and Measey et al. 2016). The former is unlikely to be deliberately introduced but the latter is still in the international pet and aquaculture trade, so its presence on the list is important. Other species on the list include those popular in the pet trade (e.g. *Ambystoma tigrinum, Litoria caerulea* and *Notophthalmus viridescens*), although the impact of these species is either unknown or (in the case of *A. tigrinum*) rests on their ability to hybridise with other *Ambystoma* species, which are not present in South Africa. The two species of *Eleutherodactylus* (*E. coqui* and *E. planirostris*) are unlikely to be deliberately introduced, and it is not known whether they constitute a threat to southern Africa. However, missing are species including *D. melanostictus* which have been shown to have a high impact (Measey et al. 2016) and are known to arrive through existing trade routes (see above).

We suggest that South Africa's list of invasive species should exclude those classified by Blackburn et al. (2011) as category 'A', those species never recorded in South Africa (see Table 1a). Additionally, prohibited species should include all amphibian species with high impact (Kumschick et al. 2017), according to the Blackburn et al. (2014) criteria (Table 1), and which have climate-matched ranges. This list could also include species that have other invasive traits, such as resistance to desiccation and fat storage (see below), although this would require additional screening of physiological literature. Such a list would require considerable research to formulate and would require updates on an annual basis in line with changes in the pet trade. All other exotic species should be subject to risk assessment for import and controlled by permits if the risk assessment yields an acceptable risk.

Domestic exotics

Guttural toad – *Sclerophrys gutturalis*

The only southern African invasive population of guttural toad *S. gutturalis* is known from a peri-urban area in Cape Town (Constantia and Bishopscourt: Figure 1c). The species was heard calling for the first time in 2000 from a large artificial pond in the Constantia Valley (34°00′16.6″S, 18°25′45.5″E; De Villiers 2006). Although the exact pathway of dispersal to Cape Town is unknown, it has been speculated that the first toads may have arrived as eggs or tadpoles with a consignment of aquatic plants from Durban (De Villiers 2006; Measey & Davies 2011). In the following years, adults, eggs and tadpoles were constantly observed in an area of about 2 km² around the first observation locality. Because this area is within the range of the IUCN Endangered Western Leopard Toad (*Sclerophrys pantherina*), the alien population raised concern about its potential impacts on the native congeneric species. Some tens of guttural toads were opportunistically removed between 2003 and 2006, but the steady spread of the species across Cape Town (about 5 km² in 2009) led the CAPE Invasive Alien Animal Working Group (Measey et al. 2014) to contract a private company in order to perform a systematic extirpation campaign by hand that continues to the present. Currently, the spread of toads is thought to be mainly through leading-edge dispersal, but two confirmed instances of jump dispersal are known (see below).

From 2010 to 2015, the extirpation process removed more than 5000 post-metamorphic toads plus thousands of eggs and tadpoles. However, this invasive population is still known to be actively spreading across Constantia and, since 2013, into the neighbouring suburb of Bishopscourt (about 8 km² in 2015). The extirpation process is arduous because the species is invading a low-density, high-income peri-urban area, and most of the breeding sites are garden ponds located on private properties. The owners are not always willing to allow property access, especially in the evening when the animals are active. Some owners are opposed to removal because they enjoy having these toads in their gardens. However, other property owners are in support of the control programme because guttural toad males emit a loud call during the night that can be heard over hundreds of metres.

In January 2016, some guttural toads were reported calling for the first time in a different peri-urban area (Noordhoek) approximately 10 km from the invaded area in Constantia. Although toads (family Bufonidae) are known to have exceptional vagility (Smith & Green 2005) and laboratory trials on guttural toads have showed that some individuals have the physiological potential to disperse more than 1 km per night (G.V., unpublished data), this recent introduction is much more likely to be human mediated. Constantia and Noordhoek are physically separated by the central section of Table Mountain National Park (Vlakkenberg and Constantiaberg), which may be an important geographic barrier to guttural toad dispersal. Guttural toads have never been reported in the area between these two suburbs. Conversely, tadpoles, juveniles and adults of guttural toads are already known to have been actively moved by some owners from one property to another within Constantia and Bishopscourt (GV, personal observation) and there is a concern that similar mechanisms led to jump dispersal to Noordhoek, a practice known to be common in western Europe and Australia (Holsbeek et al. 2008; Low 2002). Another possible human mediated pathway involves accidental translocation of pre- and post-metamorphic individuals with consignments of ornamental plants. The presence of a few plant nurseries in Constantia and surrounding areas raises concern about future jump dispersal of individuals across the city and/or the country.

Painted reed frog – *Hyperolius marmoratus*

Around 1997, it became apparent that the painted reed frog, a widely distributed member of the genus *Hyperolius* (the largest genus of African frogs), was expanding its range

from the south-eastern Cape towards the south-west. Populations of *H. marmoratus* were detected in the central part of the Western Cape (Villiersdorp) in 1997 and in Cape Town, the extreme west of the province, in 2004 (Davies et al. 2013). Data collected during the South African Frog Atlas project (Minter et al. 2004) confirmed this range expansion. Subsequent surveys and analyses showed extremely uneven dispersal rates, as in many other invasive species such as birds, and pointed to varied mechanisms of dispersal during the invasion (Berthouly-Salazar et al. 2013). Jump dispersal into new localities in the invaded range seems to be largely because of accidental translocation in nursery plants and aquatic plants (several populations are in or close to nurseries and golf courses). However, the species is also able to travel long distances over land (Bishop 2004), and this may contribute to the leading-edge dispersal between water bodies. Together with genetic data on populations in the historical and invaded ranges (Tolley, Davies & Chown 2008), this suggests that both human-mediated jump dispersal and diffusion-based leading-edge dispersal are playing a role in the range expansion of this species, at least in areas where artificial water bodies are common. Long-term changes in rainfall seasonality in the southern Cape may also influence the distribution of amphibian taxa (Mokhatla, Rödder & Measey 2015; Tolley et al. 2008), but this possibility has not been systematically investigated. Thus, work on painted reed frogs so far suggests that landscape-level changes (e.g. construction of farm dams and garden ponds) will interact with long-term climate shifts and increases in trade and translocation of animals to ensure that populations continue to expand their ranges.

Apart from the natural history of range expansions, it is also important to understand the detailed mechanisms of extra-range dispersal, so that the pathways can be accurately identified and managed. For example, the high desiccation resistance and plasticity of thermal tolerance in painted reed frogs may facilitate their dispersal and survival in marginal habitats. If multiple animals can survive hostile conditions during transport, they can potentially establish populations in the receiving area. Genetic surveys of painted reed frogs in the invaded range point to multiple introductions occurring through time and space, so that the frogs in the invaded range are a mixture of genotypes from across the historical range (Tolley et al. 2008). This may pose particular challenges for management because there may be a wider set of environmental tolerances represented by the mixed genotypes in the population and because certain genotypes may warrant greater conservation efforts.

African clawed frog – *Xenopus laevis*

The African clawed frog (*X. laevis*) has greatly expanded its natural distribution in southern Africa through colonisation of farm dams, irrigation channels and other artificial water bodies (e.g. Measey 2004). Poynton specifically suggested that most populations of *X. laevis* in the Cape Province are derived from translocations (De Moor & Bruton 1988), but subsequently it has been suggested that this was a

misunderstanding and that Poynton was referring to leading-edge dispersal into artificial water bodies (J.C. Poynton pers. comm.). The uncertainty suggested by de Moor and Bruton (1988) about the native range of *X. laevis* appears to be unwarranted and has been superseded by genetic information demonstrating four genetic lineages within southern Africa (e.g. Furman et al. 2015). Despite this assertion, it is certain that large numbers of *X. laevis* have been moved around within southern Africa.

Van Sittert and Measey (2016) reviewed amphibian movements recorded by the Cape Provincial Authority (CPA: based in Jonkershoek near Stellenbosch) finding that during the major phase of their activity, the majority of *X. laevis* had not been exported but sent to universities within southern and eastern Africa for dissection. Interestingly, this included areas where *X. laevis* occurs naturally suggesting that either the prices offered by the CPA were so low that it was easier to order animals for dissection than to collect them or that their natural abundance was limited (Hey 1946; Van Wyk 1953; Weldon, de Villiers & du Preez 2007). Sales of *X. leavis* to institutions continued after this period and are reported until the mid-2000s (Weldon et al. 2007), and permits are still issued to harvest individuals for this reason (D. Hignett pers. comm., April 2015). Van Sittert and Measey (2016) identify two sources for *X. laevis*, which correspond to two of four genetic clades within the species (see Furman et al. 2015), and they mention the possibility that movement of large numbers could result in genetic introgression of native local *X. laevis* populations.

The conservation status of the Endangered Cape platanna, *Xenopus gilli* rests, in part, on the threats produced by sympatric populations of *X. laevis* which competes, predates and hybridises with *X. gilli* (De Villiers, de Kock & Measey 2016; Fogell, Tolley & Measey 2013; Picker & de Villiers 1989). It is unclear whether *X. laevis* was always present in the range of *X. gilli*, but density of *X. laevis* is thought to have been increased through the building of nearby dams (De Villiers et al. 2016; Picker & de Villiers 1989). Hybrids resulting from the interbreeding of these species have been reported to be both common (Fogell et al. 2013; Picker & de Villiers 1989) and almost absent (Evans et al. 1998). Similarly, evidence of genetic introgression varies from common (Picker 1985) to absent (Evans et al. 1998). Without confirmation on whether genetic introgression occurs between these species, it is not possible to assess the threat from hybrids. However, their inclusion on NEM:BA A&IS's list of invasive amphibians appears unwarranted (see Table 1).

Weldon et al. (2007) investigated the use of *X. laevis* by the fishing community, in which juveniles are frequently used as bait for invasive and native fish throughout the country despite this practice being illegal. As these animals appear to be commercially available, it is likely that small numbers are moved by fishermen. Additionally, fishermen are known to seed dams with *X. laevis* in order to produce a local supply of live bait (J.M. pers. obs.), and there are reports that fishermen even utilise laboratory stocks (L. du Preez pers. comm.).
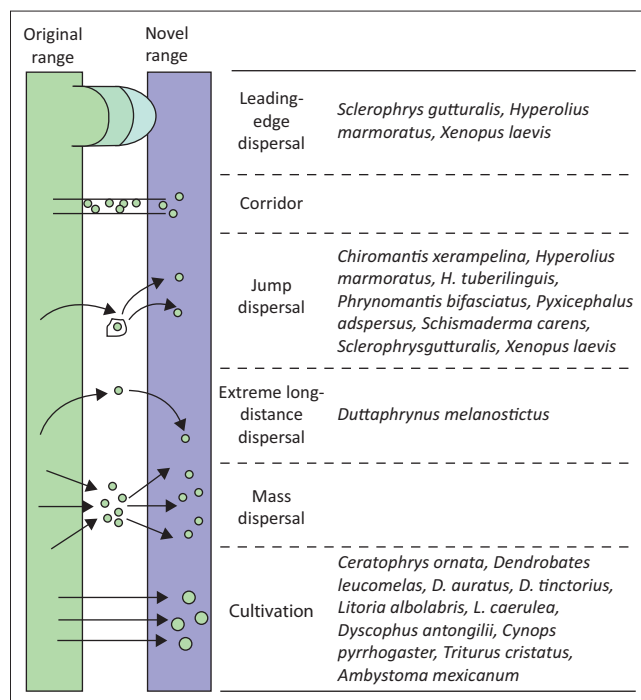
Each of these practices is likely to propel propagules of *X. laevis* into new water bodies through jump dispersal. This is not to say that these animals cannot reach isolated water bodies through their own diffusion-based dispersal (see Measey 2016).

Discussion

In this paper, we show that while southern Africa has relatively few amphibian invasions, there are a number of endemic species, which have been moved within the region. In two cases (*S. gutturalis*, *H. marmoratus*), these have formed invasive populations with tangible impacts. In each case, their status as domestic exotics contributed to a delayed response (Guo & Ricklefs 2010). However, there is hope that this will change as a recently promulgated law in South Africa recognises the potential of indigenous species to form invasive populations within the country. For example, this law includes *S. gutturalis* and *H. marmoratus*, as category 1b in Western Cape Province, but they are not listed in their native areas of KwaZulu-Natal, Limpopo and Mpumalanga. This shows how national legislation can be used to protect against domestic exotics, as well as invasive species from outside national boundaries.

Our examination of pathways illustrates the diversity of ways in which amphibians are moved into and throughout southern Africa. Davies et al. (2013) demonstrate how *H. marmoratus* are moving via a network of artificial impoundments in a combination of leading-edge and jump dispersal. These agricultural dams harbour a number of species which may facilitate their colonisation by frogs, including marginal vegetation (Davies et al. 2013). Vimercati et al. (in press) demonstrate a very similar process of leading-edge dispersal of *S. gutturalis* through ponds in an urban setting, with the additional issue that access to breeding sites on private property can hamper or even prevent the eradication of an invasive species. The increase in both rural and urban artificial water bodies suitable for amphibian breeding is one aspect of global change that has increased southern Africa's vulnerability to amphibian invasions. It is of particular interest that both examples of local invasive species are summer breeding and yet have invaded South Africa's winter rainfall region. The presence of numerous artificial water bodies in agricultural and residential landscapes has supplemented the available suitable habitat for these species, allowing them to continue to breed during the dry summer period. Similar findings have been made for *X. laevis* moved to northern France (Fouquet & Measey 2006). Our results indicate that, for pond-breeding invasive amphibians, anthropogenic landscape change will likely have more impact than climate change in facilitating the invasion processes. Despite this, climate change may also play a part in shifting regions where climatically suitable niches are available (e.g. Ihlow et al. 2016; Mokhatla et al. 2015). Thus, it appears likely that the region's vulnerability to amphibian invasions will increase.

It is perhaps unsurprising that we find jump dispersal to be a prominent invasion pathway for invasive frogs in southern Africa. Figure 2 shows that most of the dispersal types

Source: Modified after Wilson et al. 2009.
Note that some species have several dispersal modes. None, to our knowledge, have used corridor or mass dispersal.

FIGURE 2: Dispersal mechanisms of invasive southern African frogs using the classification scheme of Wilson et al. (2009).

identified by Wilson et al. (2009) are present in introductions of southern African frogs. However, it is noteworthy that corridor and mass dispersal are not present, and both seem unlikely for the time being.

Although, southern Africa currently has no exotic invasive amphibians, a number of southern African species are invasive elsewhere. This includes the domestic exotic, *S. gutturalis*, which also has invasive populations on Mauritius and Reunion (Cheke 2010), the clicking stream frog, *Strongylopus grayii*, on St. Helena, and *X. laevis*, currently invasive on four continents (Measey et al. 2012). We highlight the potential for more southern African species to become invasive in other countries and regions: *H. marmoratus* has demonstrated abilities to survive extreme long-distance dispersal (Table 2) and is regularly found in consignments of fruit and vegetables within southern Africa. Within the region, it unselectively exploits agricultural impoundments that are common the world over (Davies et al. 2013; Davies, McGeoch & Clusella-Trullas 2015).

We also highlight the dispersal pathways of many other amphibian species within the region (Table 2; cf. Faulkner et al. 2017). It is worth considering whether any of these species has the potential to become either a domestic exotic or an extra-regional invasive species. Intriguingly, the species listed in Table 2 are characterised by physiological and behavioural traits that could facilitate their introduction by accidental extreme long-distance dispersal pathways. For example, tolerance of dehydration may allow multiple individuals to survive hostile conditions during transport, resulting in higher propagule pressure. Painted reed frogs

adopt a resting posture with their limbs tucked under their body and head lowered to be in contact with the substrate, and thereby greatly reduce water loss. This behaviour has been observed in several related members of the genus *Hyperolius* (Withers et al. 1984) and in other tree-dwelling frogs such as African *Chiromantis* (e.g. foam-nest tree frog, *C. xerampelina* – Shoemaker, Baker & Loveridge 1989) and Australian *Litoria* (e.g. tree frogs, *L. caerulea* and *Litoria chloris* – Buttemer & Thomas 2003). This allows them to survive transport when the environment is variable or dry and extends the period or length of the journey they can undertake. However, if frogs become active, the permeable skin on the belly and sides is exposed and results in much higher rates of evaporative water loss (Davies et al. 2015). Therefore, reliance on the water-conserving posture to limit water loss means that if frogs can remain undisturbed in a resting position, they are most likely to survive transport without access to water.

Similarly, toads exhibit low evaporative water loss because of their large adult size that minimises their surface to volume ratio (Bentley & Yorio 1979) and maximises relative bladder size (Bentley 1966). Moreover, their parotoid glands allow them to retain water during hydration stress through glycosaminoglycans secretion. Interestingly Van Bocxlaer et al. (2010) showed that these traits, among others such as presence of inguinal fat bodies, form part of an optimal range expansion phenotype in the bufonids, possibly also driving their recent success as invaders. We suggest that the extra source of energy guaranteed by fat bodies could help toads to cope with starvation and adverse environmental conditions during an extreme long-distance dispersal event, therefore promoting invasion potential.

The southern African species listed in Table 2 are also characterised by large native distributions and synanthropic behaviour. Native range has been shown to be an important predictor of invasion probability in Amphibia for two reasons. Firstly, because large ranges lead to an increased probability of encounter between humans and amphibians, which determines in turn a higher probability of translocation (Tingley et al. 2010). Secondly, because species with large geographic distributions should be able to live across a broader spectrum of habitats and environmental conditions than species characterised by small distributions, and they should also present higher physiological and behavioural flexibility. This flexibility may be important during both the introduction and the establishment of a taxon into a novel environment. Furthermore, their synanthropism could play a role, increasing the probability that some individuals are accidentally translocated during human activities such as trade or tourism (Tingley et al. 2010). For example, *S. gutturalis* and *S. carens* inhabit numerous South African peri-urban areas, where they have been frequently observed to feed on insects attracted by artificial illumination (du Preez et al. 2004) and breed in artificial ponds. Thus, it is not surprising that these toads which move close to human habitation are occasionally moved across southern Africa.

Some of the physiological and behavioural traits discussed above are not only able to promote high survival along introduction pathways but also to promote higher establishment success. The fact that domestic exotics have been able to establish in South Africa despite being moved from subtropical to mediterranean climates suggests that long-distance dispersal acts as a selective filter (Tingley et al. 2010) favouring only the species that are pre-adapted to cope with prolonged conditions of environmental stress. Once introduced, these same pre-adaptations (e.g. drought and heat tolerance) may facilitate their establishment. Pre-adaptation has been demonstrated to play a pivotal role in driving biological invasions (Schlaepfer et al. 2009), and there has been a call for more studies to investigate traits related to invasion success through each stage of the introduction process (Chapple, Simmonds & Wong 2012; Tingley et al. 2010).

Many pet shops are affiliated with the South African Pet Traders Association and adhere to current trading regulations with respect to amphibians. However, the 'informal' market, which takes place between individuals, online forums and digital advertising platforms, needs further monitoring. Despite legal regulations, it is practically impossible to prevent private individuals from illegally importing amphibians for their personal collection, and it is possible that these animals and/or their hybrids could find their way into the informal trade should they produce viable offspring. The current NEM:BA *Alien and Invasive Species Regulations* (August 2014) prohibit importation of only nine amphibian species, such that other unlisted species, favoured by the pet trade, could be introduced in the future.

The movement of disease with amphibians in the pet trade is well documented (Kolby et al. 2014b), and there have been calls that the trade is regulated so that best practice eliminates the movement of disease rather than banning trade *per se* (Garner et al. 2009). Nevertheless, a ban in trade of salamanders has taken place in North America (Yap et al. 2015). Given the current status of amphibian sales in southern Africa, if a trade in amphibians did emerge, there is the potential for it to be a global model for best trade practice including certified disease-free amphibians with a low risk of establishing invasive populations in the region. Although these laws may not be in place for all countries in the region, South Africa's status as the commercial hub could facilitate the extension of this best practice to the entire region (cf. Faulkner et al. 2017 in press).

Conclusion

In summary, southern Africa is fortunate to have escaped invasions by exotic amphibians and South Africa is using national legislation to control domestic exotic invasions and minimise risk of new invasions of exotic amphibians. This has the additional benefit of controlling disease risk, which can only be practically managed by minimising introduction risk as exemplified by the ban on trade of salamanders that has taken place in North America (Yap et al. 2015). Although modifications are necessary, the mode of operation in South Africa may constitute an example of best practice that

could be extended and adopted more broadly. Yet, for amphibian invasions, the numerous dispersal types and a landscape that has become more favourable to their invasion means that there are undoubtedly challenges ahead.

Acknowledgements

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

J.M., G.V. and S.D. conceived and designed the study, analysed the data, wrote the paper and prepared figures and/or tables. A.R., W.S. and A.T. contributed information on amphibian trade, legislation and distribution. All authors reviewed versions of the manuscript.

References

Beard, K.H., 2007, 'Diet of the invasive frog, *Eleutherodactylus coqui*, in Hawaii', *Copeia* 2007, 281–291. https://doi.org/10.1643/0045-8511(2007)7[281:DOTIFE]2.0.CO;2

Beard, K.H., Eschtruth, A.K., Vogt, K.A., Vogt, D.J. & Scatena, F.N., 2003, 'The effects of the frog *Eleutherodactylus coqui* on invertebrates and ecosystem processes at two scales in the Luquillo Experimental Forest, Puerto Rico', *Journal of Tropical Ecology* 19, 607–617. https://doi.org/10.1017/S0266467403006011

Beard, K.H., Vogt, K.A. & Kulmatiski, A., 2002, 'Top-down effects of a terrestrial frog on forest nutrient dynamics', *Oecologia* 133, 583–593. https://doi.org/10.1007/s00442-002-1071-9

Bentley, P., 1966, 'The physiology of the urinary bladder of Amphibia', *Biological Reviews* 41, 275–314. https://doi.org/10.1111/j.1469-185X.1966.tb01494.x

Bentley, A. & Yorio, T., 1979, 'Do frogs drink?', *Journal of Experimental Biology* 79, 41–46.

Berthouly-Salazar, C., Hui, C., Blackburn, T.M., Gaboriaud, C., Rensburg, B.J., Jansen van Vuuren, B. et al., 2013, 'Long-distance dispersal maximizes evolutionary potential during rapid geographic range expansion', *Molecular Ecology* 22, 5793–5804. https://doi.org/10.1111/mec.12538

Bishop, P.J., 2004, '*Hyperolius marmoratus*', in L.R. Minter, M. Burger, J.A. Harrison, H.H. Braack, P.J. Bishop & D. Knoepfer (eds.), *Atlas and red data book of the frogs of South Africa, Lesotho and Swaziland*, pp 141–143. SI/MAB Series No 9, Smithsonian Institution Press, Washington, DC.

Blackburn, T.M., Essl, F., Evans, T., Hulme, P.E., Jeschke, J.M., Kühn, I. et al., 2014, 'A unified classification of alien species based on the magnitude of their environmental impacts', *PLoS Biology* 12, e1001850. https://doi.org/10.1371/journal.pbio.1001850

Blackburn, T.M., Pyšek, P., Bacher, S., Carlton, J.T., Duncan, R.P., Jarošík, V. et al., 2011, 'A proposed unified framework for biological invasions', *Trends in Ecology & Evolution* 26, 333–339. https://doi.org/10.1016/j.tree.2011.03.023

Boland, C., 2004, 'Introduced cane toads *Bufo marinus* are active nest predators and competitors of rainbow bee-eaters *Merops ornatus*: Observational and experimental evidence', *Biological Conservation* 120, 53–62. https://doi.org/10.1016/j.biocon.2004.01.025

Both, C. & Grant, T., 2012, 'Biological invasions and the acoustic niche: The effect of bullfrog calls on the acoustic signals of white-banded tree frogs', *Biology Letters* 8, 714–716. https://doi.org/10.1098/rsbl.2012.0412

Buttemer, W.A. & Thomas, C., 2003, 'Influence of temperature on evaporative water loss and cutaneous resistance to water vapour diffusion in the orange-thighed frog (*Litoria xanthomera*)', *Australian Journal of Zoology* 51, 111–118. https://doi.org/10.1071/ZO02057

Chapple, D.G., Simmonds, S.M. & Wong, B.B., 2012, 'Can behavioral and personality traits influence the success of unintentional species introductions?', *Trends in Ecology & Evolution* 27, 57–64. https://doi.org/10.1016/j.tree.2011.09.010

Cheke, A., 2010, 'The timing of arrival of humans and their commensal animals on Western Indian Ocean oceanic islands', *Phelsuma* 18, 38–69.

Church, G., 1960, 'The invasion of Bali by *Bufo melanostictus*', *Herpetologica* 16, 15–21.

Crossland, M.R. & Shine, R., 2010, 'Vulnerability of an Australian anuran tadpole assemblage to the toxic eggs of the invasive cane toad (*Bufo marinus*)', *Australian Ecology* 35, 197–203. https://doi.org/10.1111/j.1442-9993.2009.02027.x

Davies, S.J., Clusella-Trullas, S., Hui, C., & McGeoch, M.A., 2013, 'Farm dams facilitate amphibian invasion: Extra-limital range expansion of the painted reed frog in South Africa', *Austral Ecology* 38, 851–863. https://doi.org/10.1111/aec.12022

Davies, S.J., McGeoch, M.A. & Clusella-Trullas, S., 2015, 'Plasticity of thermal tolerance and metabolism but not water loss in an invasive reed frog', *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* 189, 11–20. https://doi.org/10.1016/j.cbpa.2015.06.033

De Moor, I.J. & Bruton, M.N., 1988, *Atlas of alien and translocated indigenous aquatic animals in southern Africa*, SANSP report 144, National Scientific Programmes Unit, CSIR, Pretoria, South Africa, pp. 317.

De Villiers, A.L., 2006, 'Amphibia: Anura: Bufonidae *Bufo gutturalis* Power, 1927 guttural toad introduced population', *African Herp News* 40, 28.

De Villiers, F.A., de Kock, M. & Measey, G.J., 2016, 'Controlling the African clawed frog *Xenopus laevis* to conserve the Cape platanna *Xenopus gilli* in South Africa', *Conservation Evidence* 13, 17.

Dick, J., 1941, 'Insects and sugarcane', *Proceedings of the South African Sugar Technologists' Association* 45, 107–111.

Doody, J., Green, B., Rhind, D., Castellano, C., Sims, R. & Robinson, T., 2009, 'Population-level declines in Australian predators caused by an invasive species', *Animal Conservation* 12, 46–53. https://doi.org/10.1111/j.1469-1795.2008.00219.x

du Preez, L., Weldon, C., Cunningham, M. & Turner, A., 2004, '*Bufo gutturalis*', in L.R. Minter, M. Burger, J.A. Harrison, H.H. Braack, P.J. Bishop & D. Knoepfer (eds.), *Atlas and red data book of the frogs of South Africa, Lesotho and Swaziland*, pp 67–69. SI/MAB Series No 9, Smithsonian Institution Press, Washington, DC.

Esteal, S., 1981, 'The history of introductions of *Bufo marinus* (Amphibia: Anura); a natural experiment in evolution', *Biological Journal of the Linnean Society* 16, 93–113. https://doi.org/10.1111/j.1095-8312.1981.tb01645.x

Evans, B.J., Morales, J.C., Picker, M.D., Melnick, D.J. & Kelley, D.B., 1998, 'Absence of extensive introgression between *Xenopus gilli* and *Xenopus laevis laevis* (Anura: Pipidae) in southwestern Cape Province, South Africa', *Copeia* 1998, 504–509. https://doi.org/10.2307/1447452

Faulkner, K.T., Hurley, B.P., Robertson, M.P., Rouget, M. & Wilson, J.R.U., 2017, 'The balance of trade in alien species between South Africa and the rest of Africa', *Bothalia* 47(2), a2157.

Fogell, D.J., Tolley, K.A. & Measey, G.J., 2013, 'Mind the gaps: Investigating the cause of the current range disjunction in the Cape Platanna, *Xenopus gilli* (Anura: Pipidae)', *PeerJ* 1, e166. https://doi.org/10.7717/peerj.166

Fouquet, A. & Measey, G.J., 2006, 'Plotting the course of an African clawed frog invasion in Western France', *Animal Biology* 56, 95–102. https://doi.org/10.1163/157075606775904722

Furman, B.L., Bewick, A.J., Harrison, T.L., Greenbaum, E., Gvoždík, V., Kusamba, C. et al., 2015, 'Pan-African phylogeography of a model organism, the African clawed frog *Xenopus laevis*', *Molecular Ecology* 24, 909–925. https://doi.org/10.1111/mec.13076

Garner, T.W., Stephen, I., Wombwell, E. & Fisher, M.C., 2009, 'The amphibian trade: Bans or best practice?', *EcoHealth* 6, 148–151. https://doi.org/10.1007/s10393-009-0233-1

Greathead, D.J., Lionnet, J.F.G., Lodos, N. & Whellan, J.A., 1971, *A review of biological control in the Ethiopian region*, Commonwealth Agricultural Bureaux, Farnham Royal, Slough, UK.

Guo, Q. & Ricklefs, R.E., 2010, 'Domestic exotics and the perception of invasibility', *Diversity and Distributions* 16, 1034–1039. https://doi.org/10.1111/j.1472-4642.2010.00708.x

Herrel, A. & van der Meijden, A., 2014, 'An analysis of the live reptile and amphibian trade in the USA compared to the global trade in endangered species', *The Herpetological Journal* 24, 103–110.

Hey, D., 1946, 'A report on the culture of the South African clawed frog *Xenopus laevis* (Daudin) at the Jonkershoek inland fish hatchery', *Transactions of the Royal Society of South Africa* 32, 45–54. https://doi.org/10.1080/00359194909519849

Holsbeek, G., Mergeay, J., Hotz, H., Plötner, J., Volckaert, F. & De Meester, L., 2008, 'A cryptic invasion within an invasion and widespread introgression in the European water frog complex: Consequences of uncontrolled commercial trade and weak international legislation', *Molecular Ecology* 17, 5023–5035. https://doi.org/10.1111/j.1365-294X.2008.03984.x

Ihlow, F., Courant, J., Secondi, J., Herrel, A., Rebelo, R., Measey, G.J. et al., 2016, 'Impacts of climate change on the Global Invasion Potential of the African Clawed Frog *Xenopus laevis*', *PLoS One* 11, e0154869. https://doi.org/10.1371/journal.pone.0154869

Jennings, M.R. & Hayes, M.P., 1985, 'Pre-1900 overharvest of California red-legged frogs (*Rana aurora draytonii*): The inducement for bullfrog (*Rana catesbeiana*) introduction', *Herpetologica* 41, 94–103.

Kaiser, B.A. & Burnett, K.M., 2006, 'Economic impacts of *E. coqui* frogs in Hawaii', *Interdisciplinary Environmental Review* 8, 1–11. https://doi.org/10.1504/IER.2006.053951

Kraus, F., 2008, *Alien reptiles and amphibians: A scientific compendium and analysis*, Springer Science & Business Media, Berlin.

Kraus, F., 2015, 'Impacts from invasive reptiles and amphibians', *Annual Review of Ecology, Evolution, and Systematics* 46, 75–97. https://doi.org/10.1146/annurev-ecolsys-112414-054450

Kolby, J.E., Kraus, F., Rabemananjara, F., Rabesihanaka, S., Rabibisoa, N. & Rafanomezantsoa, J., 2014a, 'Stop Madagascar's toad invasion now', *Nature* 509, 563–563. https://doi.org/10.1038/509563a

Kolby, J.E., Smith, K.M., Berger, L., Karesh, W.B., Preston, A., Pessier, A.P. et al., 2014b, 'First evidence of amphibian chytrid fungus (*Batrachochytrium dendrobatidis*) and ranavirus in Hong Kong amphibian trade', *PLoS One* 9, e90750. https://doi.org/10.1371/journal.pone.0090750

Kumschick, S., Vimercati, G., de Villiers, F.A., Mokhatla, M., Davies, S.J., Thorp, C.J. et al., 2017, 'Impact assessment with different scoring tools: How well do alien amphibian assessments match?', *Neobiota* 33, 53–66 https://doi.org/10.3897/neobiota.33.10376

Lever, C., 2001, *The cane toad: The history and ecology of a successful colonist*, Westbury Academic & Scientific Publishing, Otley, West Yorkshire.

Low, T., 2002, *The new nature: Winners and losers in wild Australia*, Viking, Melbourne.

McGeoch, M.A., Genovesi, P., Bellingham, P.J., Costello, M.J., McGrannachan, C. & Sheppard, A., 2016, 'Prioritizing species, pathways, and sites to achieve conservation targets for biological invasion', *Biological Invasions* 18, 299–314. https://doi.org/10.1007/s10530-015-1013-1

Measey, G. & Davies, S., 2011, 'Struggling against domestic exotics at the southern end of Africa', *Froglog* 97, 28–30.

Measey, G.J., 2004, '*Xenopus laevis*', in L.R. Minter, M. Burger, J.A. Harrison, H.H. Braack, P.J. Bishop & D. Knoepfer (eds.), *Atlas and red data book of the frogs of South Africa, Lesotho and Swaziland*, pp 264–266. SI/MAB Series No 9, Smithsonian Institution Press, Washington, DC.

Measey, G.J., Roedder, D., Green, S.L., Kobayashi, R., Lillo, F., Lobos, G., et al., 2012, 'Ongoing invasions of the African clawed frog, *Xenopus laevis*: A global review', *Biological Invasions* 14, 2255–2270. https://doi.org/10.1007/s10530-012-0227-8

Measey, G.J., Vimercati, G., de Villiers, F.A., Mokhatla, M., Davies, S.J., Thorp, C.J. et al., 2016, 'A global assessment of alien amphibian impacts in a formal framework', *Diversity and Distributions* 22, 970–981. https://doi.org/10.1111/ddi.12462

Measey, J., 2016, 'Overland movement in African clawed frogs (*Xenopus laevis*): A systematic review', *PeerJ* 4, e2474. https://doi.org/10.7717/peerj.2474

Measey, J., in press, 'Where do African clawed frogs come from? An analysis of trade in live *Xenopus laevis* imported into the USA', *Salamandra*.

Measey, J., Annecke, W., Davies, S.J., Dorse, C., Stafford, L., Tolley, K. et al., 2014, 'Cape collaborations for amphibian solutions', *FrogLog* 22, 46–47.

Mecke, S., 2014, 'Invasive species: Review risks before eradicating toads', *Nature* 511, 534. https://doi.org/10.1038/511534c

Minter, L.R., Burger, M., Harrison, J.A., Braack, H.H., Bishop, P.J. & Knoepfer, D., 2004, *Atlas and red data book of the frogs of South Africa, Lesotho and Swaziland*, SI/MAB Series No. 9, Smithsonian Institution Press, Washington, DC.

Mokhatla, M.M., Rödder, D. & Measey, G.J., 2015, 'Assessing the effects of climate change on distributions of Cape Floristic Region amphibians', *South African Journal of Science* 111, 2014–0389. https://doi.org/10.17159/sajs.2015/20140389

Pessier, A.P., Nichols, D.K., Longcore, J.E. & Fuller, M.S., 1999, 'Cutaneous chytridiomycosis in poison dart frogs (*Dendrobates* spp.) and White's tree frogs (*Litoria caerulea*)', *Journal of Veterinary Diagnostic Investigations* 11, 194–199. https://doi.org/10.1177/104063879901100219

Picker, M.D., 1985, 'Hybridization and habitat selection in *Xenopus gilli* and *Xenopus laevis* in the south-western Cape Province', *Copeia* 1985, 574–580. https://doi.org/10.2307/1444746

Picker, M.D. & de Villiers, A.L., 1989, 'The distribution and conservation status of *Xenopus gilli* (Anura, Pipidae)', *Biological Conservation* 49, 169–183. https://doi.org/10.1016/0006-3207(89)90034-7

Pimentel, D., 2011, *Biological invasions: Economic and environmental costs of alien plant, animal, and microbe species,* CRC Press. Boca Raton, Florida USA.

Pyron, R.A., 2014, 'Biogeographic analysis reveals ancient continental vicariance and recent oceanic dispersal in amphibians', *Systematic Biology*, syu042. https://doi.org/10.1093/sysbio/syu042

Reiß, C., Olsson, L. & Hoßfeld, U., 2015, 'The history of the oldest self-sustaining laboratory animal: 150 years of axolotl research', *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution* 324, 393–404. https://doi.org/10.1002/jez.b.22617

Richardson, P., 1982, 'The Natal Sugar Industry, 1849–1905: An Interpretative Essay', *The Journal of African History* 23, 515–527. https://doi.org/10.1017/S0021853700021332

Rueda-Almonacid, J., 1999, 'Situación actual y problemática generada por la introducción de "rana toro" a Colombia', *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales* 23, 367–394.

Schlaepfer, M.A., Helenbrook, W.D., Searing, K.B. & Shoemaker, K.T., 2009, 'Assisted colonization: Evaluating contrasting management actions (and values) in the face of uncertainty', *Science* 231, 611–613. https://doi.org/10.1016/j.tree.2009.05.008

Siegfried, W.R., 1962, *Introduced vertebrates in the Cape province*, Cape Department of Nature Conservation Annual Report 4, pp. 1–16.

Shoemaker, V.H., Baker, M.A. & Loveridge, J.P., 1989, 'Effect of water balance on thermoregulation in waterproof frogs (*Chiromantis* and *Phyllomedusa*)', *Physiological Zoology* 62, 133–146. https://doi.org/10.1086/physzool.62.1.30160002

Sin, H., Beard, K.H. & Pitt, W.C., 2008, 'An invasive frog, *Eleutherodactylus coqui*, increases new leaf production and leaf litter decomposition rates through nutrient cycling in Hawaii', *Biological Invasions* 10, 335–345. https://doi.org/10.1007/s10530-007-9133-x

Smith, A.M. & Green, D.M., 2005, 'Dispersal and the metapopulation paradigm in amphibian ecology and conservation: Are all amphibian populations metapopulations?' *Ecography* 28, 110–128. https://doi.org/10.1111/j.0906-7590.2005.04042.x

Tingley, R., Romagosa, C.M., Kraus, F., Bickford, D., Phillips, B.L. & Shine, R., 2010, 'The frog filter: Amphibian introduction bias driven by taxonomy, body size and biogeography', *Global Ecology and Biogeography* 19, 496–503. https://doi.org/10.1111/j.1466-8238.2010.00530.x

Tolley, K.A., Davies, S.J. & Chown, S.L., 2008, 'Deconstructing a controversial local range expansion: Conservation biogeography of the painted reed frog (*Hyperolius marmoratus*) in South Africa', *Diversity and Distributions* 14, 400–411. https://doi.org/10.1111/j.1472-4642.2007.00428.x

Van Bocxlaer, I., Loader, S.P., Roelants, K., Biju, S., Menegon, M. & Bossuyt, F., 2010, 'Gradual adaptation toward a range-expansion phenotype initiated the global radiation of toads', *Science* 327, 679–682. https://doi.org/10.1126/science.1181707

Van Rensburg, B.J., Weyl, O.L., Davies, S.J., van Wilgen, N.J., Spear, D., Chimimba, C.T. et al., 2011, 'Invasive vertebrates of South Africa', in D. Pimentel (ed.), *Biological invasions: Economic and environmental costs of alien plant, animal, and microbe species,* pp. 326–378, CRC Press.

Van Sittert, L. & Measey, G.J., 2016, 'Historical perspectives on global exports and research of African clawed frogs (*Xenopus laevis*)', *Transactions of the Royal Society of South Africa* 71, 157–166. https://doi.org/10.1080/0035919x.2016.1158747

Van Wilgen, N.J., Richardson, D.M. & Baard, E.H., 2008, 'Alien reptiles and amphibians in South Africa: Towards a pragmatic management strategy', *South African Journal of Science* 104, 13–20.

Van Wyk, G.F., 1953, 'Contributions to the knowledge of *Xenopus laevis* (Daudin)', *Div Inland Fish* 1953, 47–50.

Vimercati, G., Hui, C., Davies, S.J., Measey, G.J., In press, 'Integrating age structured and landscape resistance models to disentangle invasion dynamics of a pond-breeding anuran'. *Ecological Modelling*. https://doi.org/10.1016/j.ecolmodel.2017.03.017

Weldon, C., Villiers, A.L.D. & Preez, L.H.D., 2007, 'Quantification of the trade in *Xenopus laevis* from South Africa, with implications for biodiversity conservation', *African Journal of Herpetology* 56, 77–83. https://doi.org/10.1080/21564574.2007.9635553

Wilson, J.R., Dormontt, E.E., Prentis, P.J., Lowe, A.J. & Richardson, D.M., 2009, 'Something in the way you move: Dispersal pathways affect invasion success', *Trends in Ecology & Evolution* 24, 136–144. https://doi.org/10.1016/j.tree.2008.10.007

Yap, T.A., Koo, M.S., Ambrose, R.F., Wake, D.B. & Vredenburg, V.T., 2015, 'Averting a North American biodiversity crisis', *Science* 349, 481–482. https://doi.org/10.1126/science.aab1052