African Journal of Aquatic Science

ISSN: (Print) (Online) Journal homepage: www.tandfonline.com/journals/taas20

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To cite this article: JJ Pearson, R Gerber, W Malherbe, NJ Smit & L de Necker (27 Sep 2024): A review of the reported and future potential ecological impacts of the invasive freshwater snail *Tarebia granifera* in South Africa., African Journal of Aquatic Science, DOI: 10.2989/16085914.2024.2357292

To link to this article: https://doi.org/10.2989/16085914.2024.2357292

African Journal of Aquatic Science 2024, 49(3): xxx–xxx
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AFRICAN JOURNAL OF
AQUATIC SCIENCE
ISSN 1608-5914 EISSN 1727-9364
https://doi.org/10.2989/16085914.2024.2357292

Review Article

A review of the reported and future potential ecological impacts of the invasive freshwater snail *Tarebia granifera* in South Africa.

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The Southeast Asian gastropod *Tarebia granifera* is an invasive freshwater snail across several continents. Our review summarises the impacts of this invasive snail on invaded aquatic ecosystems. The most important impacts are those related to their ability to reproduce quickly and reach high densities within invaded ecosystems. The snail has reportedly caused declines and local extinctions in native snail populations globally. They can further significantly reduce algal standing stocks and may have severe impacts on benthic biomass, resulting in decreased benthic biodiversity and disturbances in aquatic ecosystem function. These invasive snails also cause bioturbation that can lead to changes in the nutrient cycles of invaded aquatic ecosystems and affect food web dynamics, with unknown implications for ecosystem function. Furthermore, *T. granifera* is well known to harbour a diverse range of parasitic species of medical and veterinary importance both within and outside their native ranges. The effective control of invasive *T. granifera* remains challenging as they are not easily preyed upon, and potential control methods may have unintentional side effects on native biota. This review provides evidence that there is a need to control this invader to avoid further degradation of freshwater habitats and aquatic biodiversity.

Keywords: disease transmission, ecological risk, exotic species, invasion biology, management, native species, quilted melania

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Introduction

The loss of aquatic biodiversity attracts far less attention than that of terrestrial environments even though current trends indicate a more rapid loss of native biodiversity in aquatic environments (Cooke et al. 2016). The Living Planet Report of 2020 revealed that species in freshwater environments are at a higher risk of extinction than those in terrestrial environments, with almost a third of freshwater species at risk of extinction (Collen et al. 2014; WWF 2020). Despite the clear loss and great risk of extinction for freshwater biota, research and conservation efforts are still largely lacking (Thomaz et al. 2015; Di Marco et al. 2017).

Whether accidental or deliberate, the introduction and consequent establishment of non-native species remains a leading threat to, and cause of, global biodiversity loss (Meyerson et al. 2019; Reid et al. 2019; WWF 2020). This is particularly true for freshwater aquatic ecosystems, that have a far greater biodiversity per surface area than either marine or terrestrial environments (Dudgeon et al. 2006). Aquatic invasive species (AIS) are one of the most important threats to global freshwater biodiversity and it is thus critical to research and understand the factors leading to the introduction, establishment, spread and impact of AIS in these ecosystems (Havel et al. 2015; Reid et al. 2019; Jones et al. 2021). Despite their ubiquity and diversity, freshwater molluscs are one of the most threatened groups of animals in the world (Bogan 2007; Johnson et al. 2013; Lopes-Lima et al. 2021) and one of the primary threats to these biota is the introduction of alien species (Almeida et al. 2018).

Alien or non-native species are those introduced into new environments, outside of their native range (Facon et al. 2006; Richardson and Pyšek 2006). Some alien species have the ability to adapt, survive and reproduce in new environments, becoming established and often rapidly increasing their population (Pimentel et al. 2005; Richardson and Pyšek 2006; Prentis et al. 2008). Not all alien species become invasive as some will die off naturally in their introduced environment or survive without causing extensive harm to the environment or native species (Lovell et al. 2005). Invasive species are alien species that have been introduced, become established, and spread while often causing harm to the environment, native species and the economy (Lovell et al. 2005; Pimentel et al. 2005; Richardson and Pyšek 2006).

The introduction of alien species is considered one of southern Africa's most important threats to freshwater biodiversity after habitat modification and pollution (Snoeks et al. 2011; Weyl et al. 2020). South African freshwater biota are particularly vulnerable to the introduction of alien species since many already-threatened species occur in the country. These habitats are further under pressure from the

African Journal of Aquatic Science is co-published by NISC (Pty) Ltd and Informa UK Limited (trading as Taylor & Francis Group)

considerable levels of development taking place (Snoeks et al. 2011) and high rates of international trade between South Africa and other countries, thus increasing the risk of invasive species introduction (Faulkner et al. 2020). Knowledge of the alien species that are present and their distribution in South Africa should be monitored since management and control of invasive species are of national priority (Weyl et al. 2020; Makherana et al. 2022a).

As with global trends, the rate of alien species introduction to South Africa has been directly linked to an increase in international trade (Faulkner et al. 2020). The number of introduced species in South Africa increased in the 1950s along with the improvement of technology that allowed for more rapid international trade and, consequently, more pathways for the introduction of alien species (Faulkner et al. 2020). Aside from international transport and import through cargo and ships (Lovell et al. 2005; Faulkner et al. 2020), the aquarium industry, particularly the aquarium hobby sales and the trade in aquatic plants, is one of the most important methods of freshwater molluscan introductions globally (Walker 1978; Madsen and Frandsen 1989; Cowie 1998; Pointier 1999; Letelier et al. 2007; Strayer 2010; Preston et al. 2022).

Thirteen freshwater molluscan species were introduced into South Africa between 1942 and 2006. Seven of these species have established, and up to 40% of introduced freshwater molluscan species have become invasive (Appleton 2003; Appleton and Miranda 2015a). Almost all freshwater molluscan species introduced into South Africa before 1990 originated from the Americas, apart from one Australian species (*Physastra gibbosa*; Gould 1846) and one East African species (*Biomphalaria angulosa*; Mandahl-Barth 1957) that were unable to establish (Appleton 2003; Appleton and Miranda 2015a). Imports of products from Asia to South Africa doubled from 1998 to 2011 and this increase most certainly led to increased rates of alien species introduction (Appleton and Miranda 2015a; Miranda et al. 2022). Indeed, four Asian molluscan species have been introduced into South Africa since 1999, namely *Tarebia granifera* (Lamarck 1822), *Radix rubiginosa* (Michelin 1831), *Gyraulus chinensis* (Dunker 1848) and *Sinotaia quadrata* (Benson 1842). With increased international trade, the risk of further alien species introductions will also increase, and better control is required to prevent this (Appleton and Miranda 2015a; Miranda et al. 2022).

Tarebia granifera (quilted melania) is a prosobranch gastropod native to Southeast Asia (Figure 1a) (Abbott 1952; Appleton et al. 2009; Appleton and Miranda 2015a). According to Sodeman (1991), *T. granifera* is also native to Madagascar, although Madhyastha and Dutta (2012) consider the presence of *T. granifera* in Madagascar uncertain. The native distribution for *T. granifera* was based on the IUCN Red-listing assessment completed by Madhyastha and Dutta (2012), while additional records of invasion were based on GBIF (2021) data. This mollusc has successfully invaded predominantly tropical and subtropical aquatic ecosystems across several continents (Figures 1b, c), including the Ukraine, Caribbean Islands, Texas (USA), Mexico, Hawaii, Israel, Egypt, Mozambique, Zimbabwe, Eswatini and South Africa (Chaniotis et al. 1980a; Contreras-Arquieta and Contreras-Balderas 1999; Appleton 2003; Pointier et al. 2003; Appleton et al. 2009; Karatayev et al. 2009; López-López et al. 2009; Miranda et al. 2010; Appleton and Miranda 2015a; López-Altarriba et al. 2019; Rico-Sánchez et al. 2020; Sullivan and Littrell 2020; Moustafa et al. 2021). This snail was first reported in Africa by Appleton and Nadasan (2002) from the northern parts of the South African province of KwaZulu-Natal in 1999, where it was discovered in a concrete reservoir at Mandeni. *Tarebia granifera* was most likely introduced into the country as a stowaway of the aquarium industry (Picker and Griffiths 2011). Since then, it has spread into numerous water bodies including several subtropical rivers and estuaries in southern Africa and throughout KwaZulu-Natal, and northwards into the Mpumalanga and Limpopo provinces of South Africa (Figure 1c; Appleton et al. 2009; Miranda et al. 2011b; Malherbe 2018). Appleton et al. (2009) collected *T. granifera* in 2006 from 13 rivers, five lakes, two impoundments and several estuaries in northern KwaZulu-Natal. Well-established populations have since been found in important conservation areas including the Kruger National Park, iSimangaliso Wetland Park and Ndumo Game Reserve (Appleton 2003; Wolmarans and de Kock 2006; Dube et al. 2017; Acosta et al. 2020; de Necker et al. 2021; Majdi et al. 2022).

Although reports have been published on the effects of *T. granifera* in invaded regions globally, there has been no comprehensive review or report of the current and potential future impacts of *T. granifera* in southern Africa. The aim of this review is thus to synthesise the reported effects of this invasive snail on invaded ecosystems globally and extrapolate these effects to South African environments and their associated aquatic biota. This is the first synthesis of the data on this ecologically important invader.

Biology and reproduction

Although *T. granifera* has been reported from rivers at an altitude of 983 m on Guam Island, Micronesia (Abbott 1952), it should be noted that temperatures at this altitude were consistently above 24 ˚C, suggesting that temperature, rather than altitude, plays the most important role in this mollusc's distribution patterns. Most localities invaded by *T. granifera* in South Africa lie below an altitude of 300 m above sea level (asl) (Appleton et al. 2009). Research has, however, found that *T. granifera* can survive extreme temperature ranges of 0–47.5 ˚C and may even be able to survive cold fronts if the temperature remains above −1 °C (Miranda et al. 2010). This is a much wider temperature range than previously proposed in the literature (7−40 °C) by Chaniotis et al. (1980c). This may make it possible for *T. granifera* to invade areas at elevated altitudes with colder climates, thus expanding their potential invasion range not only in southern Africa but other countries worldwide (Miranda et al. 2010). According to Albarrán-Mélzer et al. (2020), the harder and thicker shells of *T. granifera* not only offer better protection against harsh environmental conditions and predation, but also provide better thermoregulation performance in environments with high-temperature extremes (Figure 2). This may give them an advantage over native species and facilitate their

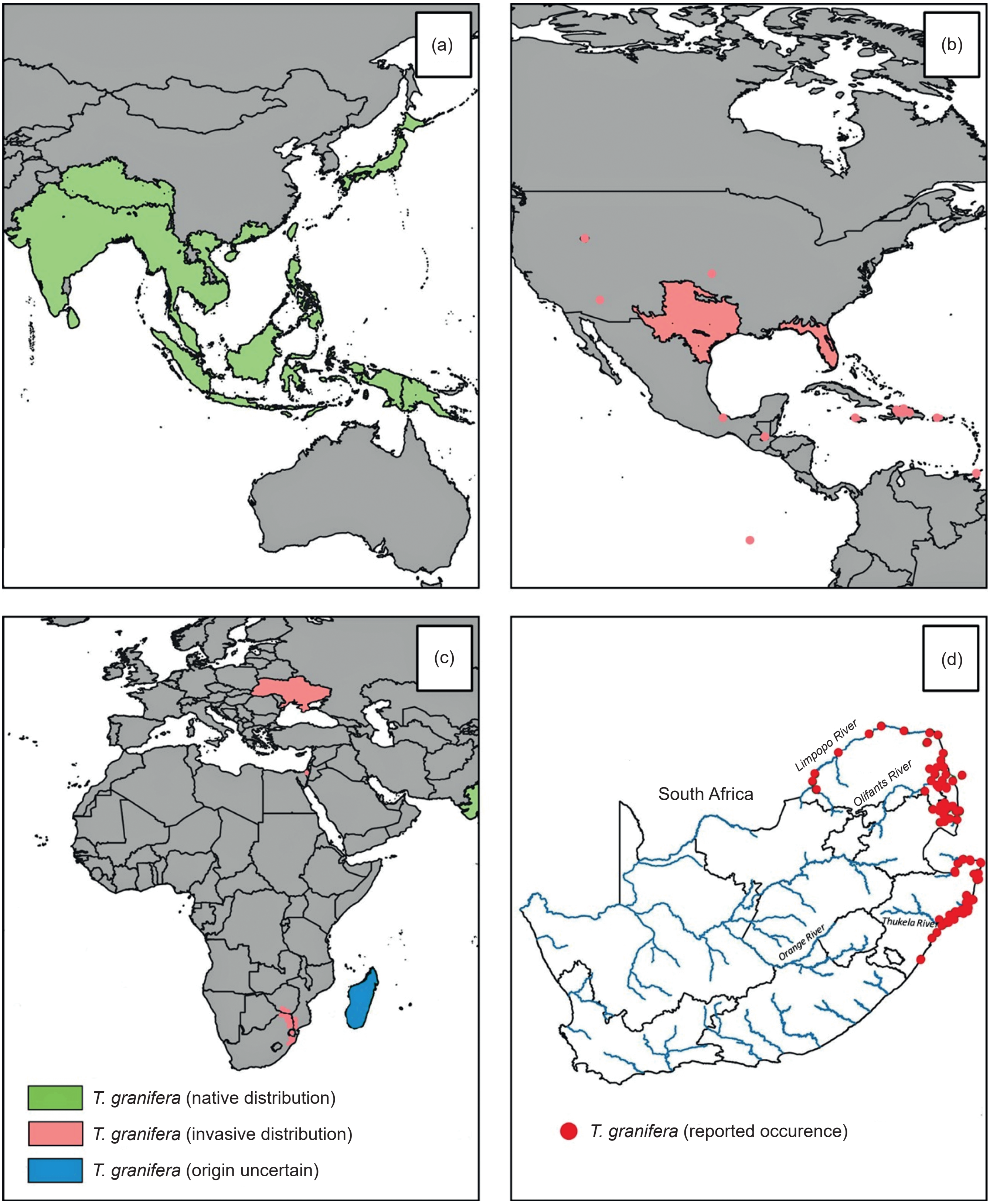

Figure 1: (a) – (c): Maps illustrating the global native and invasive distribution of *Tarebia granifera*. (d) Map of the reported occurrence of *T. granifera* in South Africa (Madhyastha and Dutta 2012; GBIF 2021)

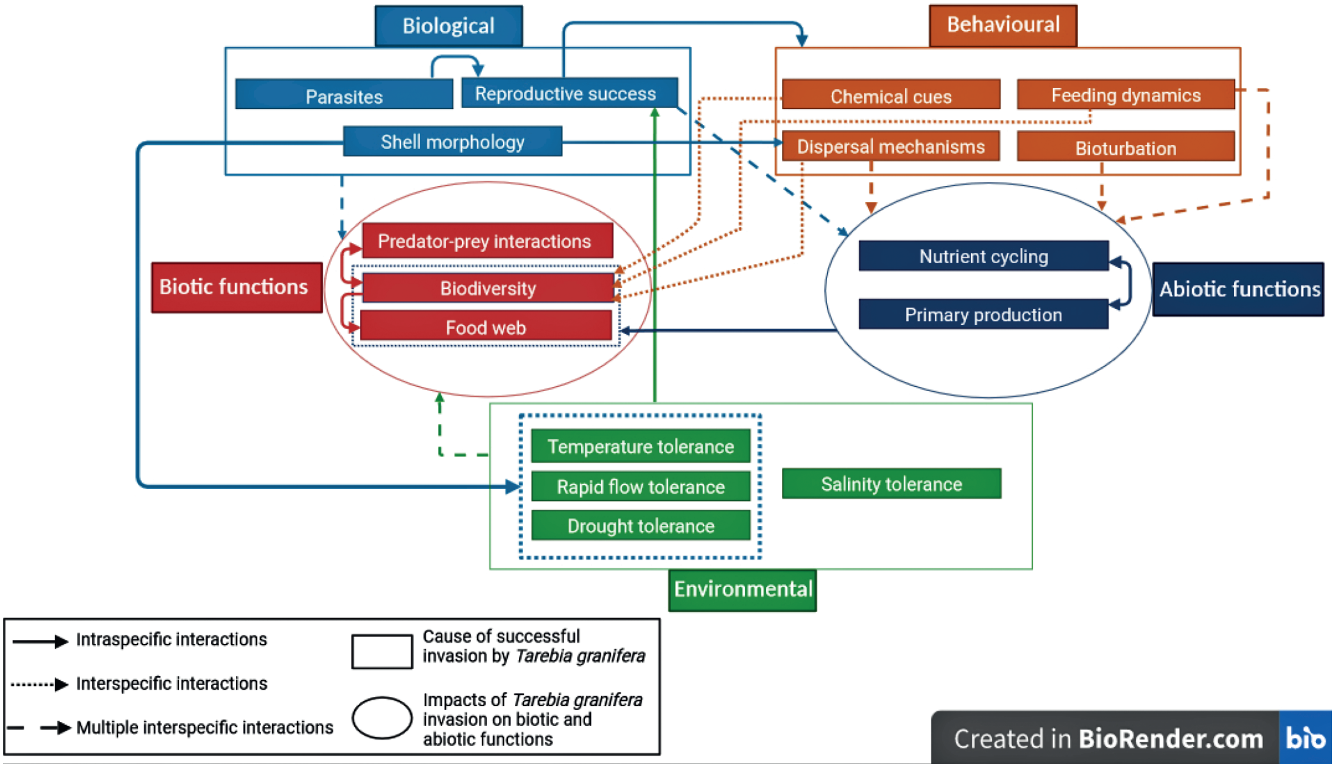

Figure 2: Summative infographic of reported causes of successful invasion by *Tarebia granifera* including biological, behavioural, and environmental causes and reported and proposed impacts of this species on both biotic and abiotic functions of invaded habitats

invasion success, especially since climate change will likely contribute to the spread of *T. granifera* in the future (Albarrán-Mélzer et al. 2020).

While *T. granifera* is considered a freshwater species, experiments have indicated that it can tolerate and survive at much higher levels of salinity than other freshwater species and for several weeks at a time (Figure 2) (Miranda et al. 2010). The snails achieve this by reducing their physical activity, closing their operculum, and burying into sediment until freshwater returns (Chaniotis et al. 1980a; Miranda et al. 2010). Miranda et al. (2010) found that lethal salinity for 50% of the population was reached at 30 PSU (Practical Salinity Unit) between 65 to 75 days and 40 PSU between 15 to 25 days. Indeed, the snail has been reported in highly saline and estuarine environments in South Africa, including the natural saline Lake Nyamithi (Acosta et al. 2020; de Necker et al. 2021) and the St Lucia estuary (Miranda et al. 2010). However, *T. granifera* are reportedly unable to survive acute increases in salinity as was evidenced by a salinity shock experiment by Miranda et al. (2010), as well as a study of the aquatic invertebrates of Lake Nyamithi. These studies determined that although *T. granifera* was able to live in the lake under natural saline conditions, they were unable to survive in the lake once salinity tripled for an extended period during a supraseasonal drought (de Necker et al. 2021).

Moreover, laboratory experiments have reported that this invasive snail can tolerate desiccation (air exposure) for two to three days at temperatures of 25 to 30 °C and 76 to 92% relative humidity (Chaniotis et al. 1980c; Facon et al. 2004; Miranda et al. 2011b). Furthermore, *T. granifera* can tolerate fast-flowing currents due to their streamlined shape and ability to hold their position well during sudden flow changes (Sodeman 1991). They have been found migrating upstream in streams discharging up to 0.05 $m^3\ s^{-1}$ in the Caribbean islands (Prentice 1983) and up to 1.2 $m^3\ s^{-1}$ in KwaZulu-Natal (Appleton et al. 2009). Upstream migration was shown to be dependent on snail size, food distribution and habitat variety (Snider and Gilliam 2008).

The ability of *T. granifera* to tolerate wide temperature extremes, high salinity, desiccation and fast-flowing water facilitates its success as an invader and significantly increases the range of aquatic ecosystems it is capable of invading (Wolmarans and de Kock 2006; Appleton et al. 2009; Miranda et al. 2010; Jones et al. 2017). Invaders with high ecological flexibility are likely to reach much higher population densities and inhabit larger regions, which play an essential role in their impact on the environment because of their ability to survive more diverse environmental conditions and outcompete native biota (Nentwig et al. 2010; Kesner and Kumschick 2018; Sirza et al. 2020).

Tarebia granifera are parthenogenetic (capable of reproduction without fertilisation) as well as ovoviviparous (eggs hatch within the parent). These are traits that are also key to its success as an invader (Figure 2) (Appleton et al. 2009; Sirza et al. 2020). Shell length in adult snails ranges from 6 to 40 mm, but the most common size is ~25 mm (Abbott 1952; Chaniotis et al. 1980a). Sexual maturity is reached at a size between 5.5−8 mm, typically within 122 days of age (Chaniotis et al. 1980a; Prentice 1983), although observations made by Appleton et al. (2009) from snails collected in invaded regions in South Africa indicated that snails as small as 8 mm could reproduce, although most juveniles were born to snails >14 mm. New-born snails, 0.7−2.1 mm (Appleton et al. 2009) emerge through a birth opening on the righthand side of the head (Abbott 1952). These juveniles (0.5~1.25 mm) have a survival rate approaching 100% (Chen 2003) and can grow at a rate of about 0.16 mm per month (Chaniotis et al. 1980a). *Tarebia granifera* can give birth to an average of one juvenile every 12 hours and would therefore be able to rapidly reach high densities in newly invaded areas (Abbott 1952; Chaniotis et al. 1980a; Sodeman 1991; Appleton et al. 2009). Invasive snail species have been reported to have higher probabilities of causing economic and environmental harm due to their ability to reproduce rapidly (Keller et al. 2007; Rumi et al. 2010; Nash and Hoffmann 2012; Kesner and Kumschick 2018). Their ability to adapt to environmental changes, as well as their ability to reproduce quickly and rapidly reach high densities, enable *T. granifera* to often become the dominant invertebrate species in invaded aquatic habitats (Appleton 2003; de Kock and Wolmarans 2007; Appleton et al. 2009; Miranda et al. 2011a; Miranda and Perissinotto 2014; Makherana et al. 2022a; Sirza et al. 2020; Weyl et al. 2020; Purnama et al. 2021). Indeed, *T. granifera* has been reported to reduce native molluscan abundances due to their dominance in invaded aquatic habitats and this has made them uncontrollable in several ecosystems globally (Chuboon et al. 2013; Veeravechsukij et al. 2018a; Oliveira et al. 2020; Purnama et al. 2020, 2021; Sirza et al. 2020; Malatji et al. 2021; Nguyen et al. 2021; Makherana et al. 2022a; Yin et al. 2022). Similar trends have been reported in South Africa, where *T. granifera* may dominate molluscan and aquatic invertebrate abundances in invaded habitats (de Kock and Wolmarans 2007; Miranda and Perissinotto 2014; Jones et al. 2017; Majdi et al. 2022) and outcompete native molluscan species.

Disease transmission

Thiarid snails pose a severe threat to public health and are of veterinary importance as they transmit parasites of fishes, birds and mammals (Sodeman 1991; Mitchell et al. 2000; McKoy et al. 2011; Veeravechsukij et al. 2018a, b). These snails act as the first intermediate hosts for trematodes that have been reported to affect the respiratory, intestinal and hepatic systems of both wildlife and humans (Sodeman 1991; McKoy et al. 2011; Veeravechsukij et al. 2018a, b; Yin et al. 2022).

Tarebia granifera are well known to harbour diverse and prevalent species of trematodes both within and outside their native ranges (Bosma 1934; Abbott 1952; Grabda 1960; Giboda et al. 1991; Ditrich et al. 1992; Wang et al. 2002; Dechruksa et al. 2007; Ukong et al. 2007; Tolley-Jordan and Owen 2008; Chontananarth and Wongsawad 2010, 2013; McKoy et al. 2011; Heneberg et al. 2014; Le et al. 2017; Veeravechsukij et al. 2018a; Doanh et al. 2019; Tolley-Jordan and Chadwick 2019; Chalkowski et al. 2021; Paller et al. 2021; Manh Hung 2022; Yin et al. 2022). These trematodes include: *Haplorchis pumilio* Looss 1896 (Veeravechsukij et al. 2018a), *Haplorchis taichui* Nishigori 1924 (Ditrich et al. 1992; Chontananarth and Wongsawad 2010, 2013; Le et al. 2017; Veeravechsukij et al. 2018a), *Loxogenoides bicolor* Kaw 1945 (Dechruksa et al. 2007; Veeravechsukij et al. 2018a), *Centrocestus formosanus* Nishigori 1924 (Dechruksa et al. 2007; Veeravechsukij et al. 2018a), *Acanthatrium histaense* Koga 1953 (Dechruksa et al. 2007; Veeravechsukij et al. 2018a), *Haematoloechus similis* Looss 1899 (Grabda 1960; Dechruksa et al. 2007), *Transversotrema laruei* Velasquez 1958 (Veeravechsukij et al. 2018a), *Cardicola alseae* Meade and Pratt 1965 (Ukong et al. 2007; Veeravechsukij et al. 2018a), *Alaria mustelae* Bosma 1931 (Bosma 1934; Veeravechsukij et al. 2018a) and *Philophthalmus gralli* Mathis and Léger 1910 (Tolley-Jordan and Owen 2008; Heneberg et al. 2014; Veeravechsukij et al. 2018a).

Tarebia granifera has also been reported to serve as a host for invasive parasites in Jamaica (McKoy et al. 2011) and Texas (Tolley-Jordan and Owen 2008; Tolley-Jordan and Chadwick 2019). In Jamaica, *T. granifera* has been found to be infected with two species of invasive trematodes: a *Notocotylus* sp. and a *Philophthalmus* sp. (oriental avian eye fluke). This was also the first report of a *Notocotylus* sp. in *T. granifera* and a *Philophthalmus* sp. occurring in Jamaica (McKoy et al. 2011). In Texas, invasive oriental avian eye flukes (*Philophthalmus gralli* Mathis and Leger 1910) have also been found to infect *T. granifera* (Tolley-Jordan and Owen 2008; Tolley-Jordan and Chadwick 2019; Chalkowski et al. 2021).

Wading birds are definitive hosts for notocotylids (Skirnisson et al. 2004) and many species of birds, including birds of the orders Galliformes (ground-feeding birds) and Anseriformes (waterfowl), harbour philophthalmids (Murray 1964; Nollen and Murray 1978). Humans have been reported as incidental hosts for philophthalmids in Yugoslavia, Sri Lanka, Thailand, Mexico and the United States (Rajapakse et al. 2009), where these infections cause swelling of the semilunar fold in the eyes (Mimori et al. 1982).

The trematodes *H. pumilio* and *H. taichui* are widely distributed, occurring in at least 14 countries worldwide (Ditrich et al. 1992; Huston et al. 2014; Veeravechsukij et al. 2018a), and are known to infect *T. granifera* (Chontananarth and Wongsawad 2010, 2013; Le et al. 2017; Veeravechsukij et al. 2018a) and *Melanoides tuberculata* (O.F.Müller, 1774) (Tolley-Jordan and Owen 2008; Krailas et.al. 2011, 2014; Huston et al. 2014; Lopes et al. 2020; Pulido-Murillo et al. 2018). Invasion by these parasites can have severe pathological consequences for a broad range of intermediate fish hosts (Huston et al. 2014) since the penetration and migration of large numbers of cercaria can be lethal to fry and adult fish species (Sommerville 1982; Umadevi and Madhavi 2006). Natural definitive hosts are fish-eating animals, including humans (Chai et al. 2009; Giboda et al. 1991).

In some cases, biological invaders have immunity against predators, pathogens or parasites within invaded habitats; or these threats are missing from invaded habitats, thus giving the invader advantage over native species (Genner et al. 2008). Field evidence from Lake Malawi indicated that trematodes were absent from a highly invasive morph of *M. tuberculata* and that the invader was resistant to trematodes found in native *M. tuberculata* (Genner et al. 2008). It is suspected that the parasites naturally infecting the invasive morph may not have migrated with the host or were unable to survive in the invaded habitat due to the absence of suitable intermediate or final hosts (Keane and Crawley 2002; Torchin et al. 2003; Genner et al. 2008). Trematodes are known to play a vital role in host snail populations as they can affect changes in survivorship, behaviour and morphology, and cause reduced fecundity and growth (Sorensen and Minchella 2001; Lafferty and Kuris 2009; McKoy et al. 2011). Genner et al. (2008) report that certain native trematodes act as parasitic castrators of snails and cause reduced population growth within the snail populations.

To date, no trematodes have been reported in *T. granifera* from South Africa, likely giving it an advantage over native molluscan species (Figure 2), including *M. tuberculata* (Miranda et al. 2011b; Weyl et al. 2020) and contributing to their rapid population expansion. It may be that *T. granifera* has immunity to parasites in invaded areas of South Africa and the native parasites may be unable to infect this species due to their evolutionary adaptations to native host species (Ebert 1994, 1998; Prenter et al. 2004; Fromme and Dybdahl 2006).

Classical hypotheses such as the "spillover" and "spillback" hypotheses are important to consider with regard to invasive host species (Chalkowski et al. 2018). Spillover of parasites occurs when parasites from invasive host species are introduced into a new environment and subsequently infect native species, therefore posing a health risk to native species (Daszak et al. 2000; Lymbery et al. 2014; Iglesias et al. 2015; Chalkowski et al. 2018). Parasite spillback occurs when native parasites from a native host infect an invasive host, while also increasing the risk to infect other native species (Hoberg et al. 2002; Kelly et al. 2009; Chalkowski et al. 2018). Appleton et al. (2009) suggests that the rapid spread of *T. granifera* and the resultant replacement of native *M. tuberculata* in South Africa, may worsen this problem. Based on the many possible ways invasive and native host-parasite species can interact, it might be possible that *T. granifera* can (a) dilute native parasite populations via host displacement, (b) serve as a host to invasive parasites introduced via migratory birds, or (c) eventually serve as a host for native parasite taxa that spillover from native hosts (Chalkowski et al. 2018). Even though no parasites have been reported from *T. granifera* in South Africa, the native thiarid *M. tuberculata* was previously reported to be infected with at least nine unidentified cercariae (Faust 1921; Porter 1938), which have been described under the generic collective group *Cercaria* (Müller 1773). The last reports describing parasites from *M. tuberculata* in South Africa were, however, in 1921 by Faust and in 1938 by Porter. It is, therefore, quite likely that the estimated trematode diversity in this snail might be higher than expected considering *M. tuberculata* is known to be a host for diverse groups of trematodes worldwide (Pinto and de Melo 2011). Since *T. granifera* can reach high densities within invaded habitats, and may replace *M. tuberculata* and several other native snail species, studies on the parasitic diversity of both these thiarid species in South Africa will be of great significance (Malatji et al. 2021). Experimental studies may further our understanding of the suitability of *T. granifera* and *M. tuberculata* as hosts for native and/or invasive trematode species in South Africa (Malatji et al. 2021). This will contribute not only to a better understanding of the biodiversity and biology of the snail hosts, but also to their evolutionary relationships with parasitic trematodes.

Dispersal mechanisms

Alien species with the ability to spread through a variety of mechanisms are able to become highly invasive over a wide distribution area and have a higher probability of causing environmental changes in newly invaded areas (Moodley et al. 2013; Novoa et al. 2016; Kesner and Kumschick 2018). *Tarebia granifera* may be able to spread successfully from one waterbody to another through a variety of mechanisms (Figure 2). One of these includes the digestive system of birds where aquatic birds eat snails whole in one habitat, and then may pass them out unharmed in another habitat (Appleton et al. 2009). Indeed, small individuals of *T. granifera* (5−7 mm) have been reported in the droppings of aquatic birds in the Mhlali River in KwaZulu-Natal (Appleton et al. 2009). As some of the shells were still intact, the snails may have been alive when they passed through the bird's digestive system, and it is thought that they would perhaps have survived if they had been dropped in water (Appleton et al. 2009). Thiarid snails, including *M. tuberculata*, are known to form part of the diet of birds (Appleton 2002), including the White-faced Duck, *Dendrocygna viduata* (Linnaeus 1766; Hockey et al. 2005). According to Halse (1984), food is retained in the gut of aquatic birds for between two and six hours, and thus dispersal of snails (that survive in the gut) is likely to occur as these birds move over short distances from one aquatic ecosystem to the next (Appleton et al. 2009).

Tarebia granifera have also been found attached to floating clumps of macrophytes in rivers, thus making dispersal downstream rapid and easy (Appleton et al. 2009). Another mode of dispersal may be through drying mud on large mammals, such as elephant (*Loxodonta africana* Blumenback 1797) and buffalo (*Syncerus caffer* Sparrman 1779), particularly in conservation areas such as the Kruger National Park (Vanschoenwinkel et al. 2008, 2011; van Leeuwen et al. 2013). It is likely that *T. granifera* is also dispersed between habitats by anthropogenic means, including on boats or mud attached to footwear or vehicle wheels. Although this has not specifically been determined for *T. granifera*, many aquatic species are reportedly transported this way including mussels, bivalves, invasive aquatic plants, such as *Salvinia molesta*, and large branchiopods (Ricciardi and MacIsaac 2000; Leuven et al. 2009; Waterkeyn et al. 2010).

Mechanisms underlying impacts of *Tarebia granifera*

The introduction of invasive species to aquatic ecosystems has become a key ecological factor, as invading organisms increasingly alter aquatic communities (Gurevitch and

Padilla 2004; Almeida et al. 2018). Species that establish themselves outside of their native ranges usually achieve densities higher than they would in their native areas and often have negative impacts on native species as a result (Carlton et al. 1990; Gurevitch and Padilla 2004; Gallardo et al. 2016; Majdi et al. 2022). *Tarebia granifera* populations can reach incredibly high densities, up to 10 000 m^{-2}, and are often the dominant invertebrate species in invaded aquatic communities (Pillay and Perissinotto 2008; Appleton et al. 2009; Jones et al. 2020; Scharler et al. 2020; Mujiono and Isnaningsih 2021; Purnama et al. 2021; Majdi et al. 2022; Nwoko et al. 2022). Appleton et al. (2009) reported an average density of 20 764 m^{-2} from the Nseleni River in KwaZulu-Natal, while Weyl et al. (2020) reported on a snail community from the Phongolo River, indicating that 93% of the biomass consisted of *T. granifera*. It is, therefore, likely that this snail negatively impacts the indigenous benthos and community structures in invaded water bodies, resulting in a decline in the abundance of native species (Hillebrand et al. 2002; Appleton et al. 2009; Jones et al. 2017; Miranda et al. 2011a; Miranda and Perissinotto 2014; Sirza et al. 2020; Purnama et al. 2021; Majdi et al. 2022; Nwoko et al. 2022; Oetama and Purnama 2022). Native aquatic species may be particularly vulnerable to interference from dense populations of *T. granifera.* For example, high densities of *T. granifera* may cause decreased growth rates in native snail species, leading to delays in sexual maturity (reduced reproduction) and causing an increase in mortality and displacement or total eradication (Hillebrand et al. 2002; de Kock and Wolmarans 2008; Appleton et al. 2009; Jones et al. 2017; Miranda et al. 2011a, b; Miranda and Perissinotto 2012, 2014; Rico-Sánchez et al. 2020). Numerous studies, both globally and in South Africa, suggest that *T. granifera* may have severe negative impacts on native aquatic snail communities (Hillebrand et al. 2002; Appleton et al. 2009; López-López et al. 2009; Jones et al. 2017; Pointier et al. 2010; Miranda et al. 2011a; Miranda and Perissinotto 2014; Purnama et al. 2021; Nwoko et al. 2022; Oetama and Purnama 2022) although few studies have assessed the specific impacts. Further research on the ecological impact of this invader on aquatic community structures and biodiversity is urgently needed (Appleton et al. 2009; Weyl et al. 2020; Purnama et al. 2022; Majdi et al. 2022; Raphahlelo et al. 2022).

The invasion success of *T. granifera* may be directly related to the release of chemical cues that repel native gastropods (Figure 2) (Raw et al. 2013, 2015). Although chemoreception in snails is well researched (Wollerman et al. 2003; Picker and Griffiths 2011; Raw et al. 2013, 2015), it was assumed, until quite recently, that competition for food and space are the main mechanisms by which *T. granifera* displace native snail populations. A study by Raw et al. (2013), however, found that three snails native to South Africa, *Assiminea* cf. *capensis* (Bartsch 1915), *Coriandria durbanensis* (Tomlin 1916) and *M. tuberculata*, responded by moving away from food sources, due to chemical cues released by *T. granifera*. In the Dominican Republic, *T. granifera* was introduced to *Biomphalaria glabrata* (Say 1818) habitats, and within 14 months *T. granifera* was displacing *B. glabrata* (Perez et al. 1991). This displacement was not due to competition for food or space, but possibly due to chemicals secreted by the invader. These chemical cues have the potential to impact native snail behaviour, causing them to vacate optimal habitat, reducing biotic resistance and thus further facilitating invasion success (Raw et al. 2013, 2015). Although the mechanism is not fully understood, this has led to intentional introductions of *T. granifera* and *M. tuberculata* as biocontrol agents for *Schistosoma* host snails in several countries globally (Prentice 1983; Perez et al. 1991; Sodeman 1991; Pointier and Jourdane 2000; Appleton et al. 2009; Pointier et al. 2010; Hewitt and Willingham 2019). Schistosomiasis infects approximately 4.5 million people in South Africa annually (Lothe et al. 2018), and the displacement or eradication of native snails that transmit schistosomiasis by *T. granifera* may, therefore, reduce the risk of infection to people; although, this may in turn have severe ecological consequences for invaded habitats.

Tarebia granifera have reportedly caused local extinctions of native snail populations in Cuba (Pointier and Jourdane 2000; Karatayev et al. 2009), Venezuela (Pointier and Giboda 1999), Puerto Rico (Giboda et al. 1997; Chaniotis et al. 1980a, b) and South Africa (de Kock and Wolmarans 2008; Appleton et al. 2009; Miranda et al. 2011a, b; Miranda and Perissinotto 2012, 2014; Jones et al. 2017; Kesner and Kumschick 2018; Zengeya et al. 2020). Native molluscs, such as *Chambardia wahlbergi* (Krauss 1848), *Corbicula fluminalis* (Krauss 1848), *Cleopatra ferruginea* (Lea 1850), *Thiara amarula* (Linnaeus 1758*), Lanistes ovum* (Troschel 1845) and *M. tuberculata*, are considered vulnerable in South Africa (Appleton et al. 2009) and *T. granifera* poses a considerable risk to these species. It has already been reported that, once introduced, *T. granifera* rapidly outnumbers *M. tuberculata* in terms of density (Pointier et al. 1998). Further, *M. tuberculata* and *T. amarula* have become less common in South Africa in areas with higher densities of *T. granifera* (Miranda et al. 2011a).

Apart from its environmental impacts and the role as an intermediate host for medically and economically important trematodes, *T. granifera* may also pose a risk to important infrastructure (Appleton et al. 2009; Yakovenko et al. 2018; Oleh et al. 2018; Yesipova et al. 2022). The snail is abundant in reservoirs of three large industrial plants in northern KwaZulu-Natal. The shells block pipes and damage equipment and have also interfered with water circulation at a nearby fish hatchery (Appleton et al. 2009). In addition, *T. granifera* and *M. tuberculata* have been reported to threaten the hydraulic cooling structures in the Zaporizhia Nuclear Power Plant (ZNPP), Ukraine (Yakovenko et al. 2018; Oleh et al. 2018; Yesipova et al. 2022). Snails reached densities of up to 5 200 individuals m^{-2} in the basins and metal pipes, and shells created obstacles which decreased effectiveness of pumping stations, meaning such infrastructure needs constant mechanical cleaning (Yesipova et al. 2022).

Feeding dynamics and food web interactions

Tarebia granifera may have severe impacts on benthic biomass that could have implications on food availability for native aquatic species and result in decreased benthic biodiversity, as well as cause disturbances to aquatic ecosystem function (Figure 2) (March and Pringle 2003; Miranda et al. 2010, 2011a; Moslemi et al. 2012; Raw et al. 2013; Miranda and Perissinotto 2014; Hill et al. 2015; Rico-Sánchez et al. 2020; Majdi et al. 2022). This invasive snail feeds mainly on algae (mostly diatoms) and semi-decomposed organic matter, and its feeding impact can be much higher than that of other invertebrates (Miranda et al. 2011a). Miranda et al. (2011a) reported that *T. granifera* utilised up to 35% of available microphytobenthos (photosynthetic diatoms, cyanobacteria, flagellates and green algae) per day, and up to 68% of the daily primary benthic production in coastal and estuarine lakes in South Africa, with similar findings reported for zooplankton species (Perissinotto, 1992; Kibirige and Perissinotto 2003). This mollusc thus poses a significant threat to algal and zooplankton communities, potentially causing direct bottom-up and cascading effects on an ecosystem and its associated food web (Miranda et al. 2010; Miranda and Perissinotto 2014). According to Miranda et al. (2011a), the ingestion rate of *T. granifera* is comparable to that of the Golden apple snail (*Pomacea canaliculata* Lamarck 1822), among the world's most destructive invasive species (Lowe et al. 2000; Baker et al. 2010).

As invasive species disrupt trophic functioning, native species also tend to shift their dietary preference (Vander Zanden et al. 1999). This was evident in coastal lakes from KwaZulu-Natal where the native snail *Assiminea ovata* (Krauss 1848) started feeding less on microphytobenthos and more on branching algae after *T. granifera* became established (Miranda and Perissinotto 2012). Invasive *T. granifera* populations in the San Marcos River (Texas) have also been reported to consume the eggs of the threatened Fountain Darter fish (*Etheostoma fonticola* Jordan and Gilbert 1886) with potential negative consequences (Phillips et al. 2010). The widespread diet of *T. granifera* has likely contributed to its successful establishment in southern Africa (Miranda and Perissinotto 2012).

As native snail species are replaced by *T. granifera* in South Africa, native predators such as shrimps (*Macrobrachium* sp. Spence Bate 1868), crabs (*Potamonautes* sp. Macleay 1838) and dragonflies (Libellulidae) may also be impacted as many of these predators are unable to break the harder shells of *T. granifera*, increasing the likelihood of indirect bottom-up effects on invaded ecosystems (Appleton et al. 2009; Miranda et al. 2016). Hermit crabs in Tobago, (*Clibanarius tricolor* Gibbes 1850 and *Clibanarius vittatus* Bosc 1802) have started making use of *T. granifera* shells that washed downstream (Van Oosterhout et al. 2013). This may make hermit crabs less vulnerable to predators and have additional indirect bottom-up effects on aquatic food webs.

Tarebia granifera are important bioturbation agents and at high densities affect nutrient cycles of invaded aquatic ecosystems (Figure 2) (Arnott and Vanni 1996; Hall et al. 2003; Carlsson et al. 2004). Moslemi et al. (2012) found riparian cover influenced the effect of *T. granifera* on nitrogen (N) cycling in West Indian streams. This study found that snail densities were up to eight times higher, and nitrogen excretion up to nine times higher, in open-canopy habitats compared to habitats with extensive riparian vegetation. Changes to the availability of nutrients may influence primary production and the growth and community structures of primary producers (Vanni 2002), with unknown implications for ecosystem function (Moslemi et al. 2012). Comprehensive research on the effects of *T. granifera* on aquatic food webs in invaded habitats are limited, but greatly needed, as *T. granifera* is a globally problematic invader.

Tarebia granifera as prey

Alien species often have higher competitive abilities in invaded areas due to the enemy release hypothesis, e.g. resistance to predation, parasites and pathogens (Elton 1958; Tilman 1999). Although *T. granifera* can be preyed upon by birds, fish and invertebrates, it does not seem to have many successful predators in South Africa (Miranda and Perissinotto 2012; Miranda et al. 2016; Whitfield et al. 2021). Predators will often feed on the most abundant prey (known as frequency-dependent predation), but prey preference is also determined by energy gained from the prey relative to the energy cost of catching the prey (Morrison et al. 2019). *Potamonautes sidneyi* (Rathbun 1904), a crab native to South Africa, preys upon *T. granifera* in Lake Sibaya, KwaZulu-Natal (Peer et al. 2015). Miranda et al. (2016) reported that *P. sidneyi* and *P. perlatus* (Milne Edwards 1837) were, however, often unable to successfully crush the rigid shell of *T. granifera* compared to the native *M. tuberculata*. Although some large male crabs were able to crush the shells of *T. granifera*, successful attacks were less frequent compared with attacks on native *M. tuberculata.* In cases when alien prey species are harder to consume, predators will be more likely to select native species, giving the invasive species further advantage (Figure 2) (Shinen et al. 2009; López et al. 2010).

Morrison et al. (2019) suggest that Eastern musk turtles *Sternotherus odoratus* (Latreille 1802) in Texas may have shifted their diets to include invasive snails over the last three decades. *Melanoides tuberculata*, *T. granifera*, and the Giant Ramshorn Snail *Marisa cornuarietis* (Linnaeus 1758), all invasive in the USA, were the most abundant species identified from *S. odoratus* faecal samples and *T. granifera* was found in half the samples investigated during the study (Morrison et al. 2019).

Interactions with other invasive species

Ecosystems are frequently invaded by multiple invasive species, and interactions among species may amplify negative impacts on native communities and ecosystems (Johnson et al. 2009; Makherana et al. 2022b). A mesocosm study in the USA examined interactions between invasive Rusty crayfish *Orconectes rusticus* (Girard 1852) and Chinese Mystery snails *Cipangopaludina chinensis* (Gray 1834). Both invaders had weak negative impacts on one another, but both negatively affected native snail biomass and abundance (Johnson et al. 2009). These invasive species drove one native snail to local extinction and reduced a second species by more than 95%. Rusty crayfish (a snail predator) were also significantly more likely to consume native snails compared to the thicker shell and larger sized invader (Johnson et al. 2009).

Three molluscan species (*Corbicula fluminea* (Müller 1774), *M. tuberculata* and *T. granifera*) invasive in the

Tuxpan and Tecolutla Rivers in Mexico have negatively impacted native molluscan abundances (López-López et al. 2009). *Melanoides tuberculata* and native molluscan species in these areas have reportedly been confined to narrow habitats with a limited distribution range, and occurred in low densities, while *T. granifera* and *C. fluminea* indicated strong dominance and wider distribution. López-López et al. (2009) further indicated that *T. granifera* reached higher population densities than the other invasive species, likely by out-competing the other species and by rapidly recolonising ecosystems after pronounced depletions in snail density during the heavy rainy season. *Tarebia granifera* populations grew quickly during the dry season and were more successful than both other invasive snails and native snails (López-López et al. 2009).

Negative interactions between native and invasive species may also be due to differences in habitat use rather than direct competition (Tolley-Jordan and Owen 2008). A study conducted in Texas found that the invasive snails *M. tuberculata* and *T. granifera* co-occurred in lentic habitats while *M. tuberculata* and the native *Elimia comalensis* (Pilsbry 1890) did not co-occur (Tolley-Jordan and Owen 2008). In lentic habitats, the invaders had similar densities and even though *E. comalensis* had the highest densities of the native species, it was still 200 times less than the densities of the invaders (Tolley-Jordan and Owen 2008). Conversely, in lotic habitats *T. granifera* and *E. comalensis* distributions positively co-occurred and they had similar densities, while the density of *M. tuberculata* was ten times lower (Tolley-Jordan and Owen 2008). This is possibly because *T. granifera* is able to tolerate faster water flow than *M. tuberculata* (Dussart and Pointier 1999). The preference of *E. comalensis* for lotic habitats allowed it to occur in densities similar to that of *T. granifera* (Tolley-Jordan and Owen 2008).

Intense competitive interactions occur among exotic species with similar ecological traits. For instance, the invasion of *T. granifera* and a new morph of *M. tuberculata* (MA strain) seriously impacted other morphs of *M. tuberculata* in Guadeloupe and Martinique, Caribbean Islands (Pointier et al. 2010). These invasions led to the extinction of one morph of *M. tuberculata* (FDF strain) while others became scarce. Similar findings have been reported in the Great African Lakes where the invasion of Asian morphs of *M. tuberculata* threatens native thiarid diversity (Genner et al. 2004). In systems where endemic thiarid diversity is high, similar threats can be expected from invasive thiarid species (Pointier et al. 2005; Simone 2006; Pointier et al. 2010). Although *M. tuberculata* is native to South Africa, invasive morphs may be present due to the complex global invasion history of the snail (Genner et al. 2004; Van Bocxlaer et al. 2015; Miranda et al. 2016).

Invasive snail populations should not be regarded as genetically depauperate (Pointier et al. 2010). Introductions of *M. tuberculata* to Martinique and Guadeloupe gave rise to rare sexual events between introduced morphs, forming natural hybrids which have high levels of genetic variation and ecologically important traits (Facon et al. 2008). Different morphology and life history traits allow these hybrids to be very successful (Facon et al. 2005).

Control measures

The complete eradication of *T. granifera* from an environment is particularly difficult due to its parthenogenic life history (Miranda et al. 2010). The use of molluscicides in the natural environment is not a practical method of control as non-target species may be adversely affected (McCullough et al. 1980; Miranda et al. 2010). A 'salinity shock experiment' by Miranda et al. (2010) indicated that *T. granifera* were vulnerable to sudden increases in salinity. This led to suggestions that snails could be controlled in some estuaries by artificially breaching barriers and elevating salinity (Miranda et al. 2010). The manipulation of natural environments on such a scale may, however, also have unintended and negative consequences on non-target species and these ecosystems as a whole (Miranda et al. 2010).

The black carp *Mylopharyngodon piceus* (Richardson 1846) is a freshwater snail predator that has been effectively used as a biological control of *M. tuberculata* and *T. granifera* in several parts of the world (Ben-Ami and Heller 2001; Manh Hung et al. 2013; Yakovenko et al. 2018). The Assassin snail *Anentome helena* (von dem Busch 1847) has also been reported to be an effective biological control of *M. tuberculata* in Malaysia, Indonesia, Thailand and Laos (Schiffbauer 2009; Yakovenko et al. 2018), and a potential control agent of *T. granifera* (Yakovenko et al. 2018). The introduction of biological control agents, however, has numerous environmental risks that need to be considered, and extensive research needs to be done before attempting to use these measures in new environments (Howarth 1991; Simberloff and Stiling 1996; Hoddle 2004; Louda and Stiling 2004). As previously mentioned, trematodes play a vital role in the natural control of snail populations due to their ability to affect snail survivorship, behaviour and morphology, causing reduced fecundity and growth (Sorensen and Minchella 2001; Genner et al. 2008; Lafferty and Kuris 2009; McKoy et al. 2011). In a study conducted by McKoy et al. (2011), only 3% of *T. granifera* infected with trematodes had reproductive stages (eggs, embryos or juveniles) compared to 90% of snails that were not infected. Though potentially significant, the ecological impact of trematodes on the fecundity of *T. granifera* and the environment needs to be investigated further (McKoy et al. 2011). Unfortunately, the control of *T. granifera* with trematodes in natural environments may also have unintended negative effects on native species and the environment. Moreover, due to a lack of invasive species monitoring and management (Makherana et al. 2022a) and the large area already occupied by *T. granifera* in the eastern and northern parts of southern Africa (Appleton et al. 2009), this snail will probably continue to expand its range (Kesner and Kumschick 2018).

In the Ukraine, Yakovenko et al. (2018) found that thiarid snails were unequally distributed in the ZNPP, with an average abundance of 3.3 *T. granifera* to one *M. tuberculata*. Experimental trials using Marbled crayfish *Procambarus virginalis* (Lyko 2017), Pumpkinseed fish *Lepomis gibbosus* (Linnaeus 1758), and the loach *Botia lohachata* (Chaudhuri 1912) were found to be unsuccessful at controlling snail populations. The Assassin snail was a successful control agent but when this predatory mollusc has more accessible food, such as organic matter, it consumes smaller quantities of the thiarid snails (Oleh et al. 2018). According to Oleh et al. (2018), the most successful method to control *T. granifera* populations in power plant intakes was using snail traps, which attract snails with bait. Snails fall into the traps as they move towards the bait and are unable to escape (Oleh et al. 2018). The authors found that traps were also effective at catching sexually mature snails, thereby removing reproductive individuals from the population. Yakovenko et al. (2018) also suggested that the power plant should stock their cooling ponds with the molluscivorous black carp and Assassin snails. This research may lead to the development of control measures to reduce accidental introductions of snails into reservoirs of importance (Yakovenko et al. 2018; Oleh et al. 2018). Laboratory investigations on biological and biomechanical methods to control snails are ongoing (Yakovenko et al. 2018; Oleh et al. 2018; Yesipova et al. 2022) but effective control of established *T. granifera* populations in a natural setting remains challenging. The most effective method to prevent snail invasions in the future, to date, is to implement strict policies that regulate the global trade of freshwater molluscs (Preston et al. 2022).

Concluding remarks

Tarebia granifera is a highly resilient and opportunistic species that is able to flourish in disturbed environments. This enables individuals to rapidly disperse and invade a wide variety of aquatic habitats in a relatively short time. The snail has been reported to cause declines and local extinctions in native snail populations on a global scale due to their ability to reproduce quickly and reach high densities.

Furthermore, high densities of *T. granifera* may have significant impacts on benthic biomass that could have implications on food availability for native aquatic species, resulting in decreased benthic biodiversity as well as changes in the food web dynamics and nutrient cycles of invaded ecosystems (Figure 2). Apart from their environmental impacts and their role as intermediate hosts for diverse and prevalent species of medically and veterinary important trematodes on a global scale, *T. granifera* have been reported to pose an important economic threat to infrastructure in Ukraine and South Africa.

Management and remediation of biological invasions in southern Africa need a more complete understanding of *T. granifera*'s impact and the mechanisms through which they occur. Previous studies have investigated the impacts and population structures of *T. granifera* in coastal lakes and estuaries in KwaZulu-Natal. However, less is known about the current distribution, population dynamics and impacts *T. granifera* have on the native biodiversity and aquatic community structures of freshwater ecosystems in southern Africa. Given that the current distribution and densities of native as well as invasive freshwater snail species are underreported, it is critical to understand impacts of this ubiquitous invader. In addition, because this invader may also act as a potential intermediate host for parasitic trematodes in southern Africa, there is a need to investigate the potential impacts of *T. granifera* on both native ecosystems and human health.

Acknowledgements — The Water Research Commission (WRC) is hereby acknowledged for providing a Postgraduate MSc Scholarship to J.J. Pearson. The National Research Foundation (NRF)–Department of Science and Innovation (DSI) Professional Development Programme is further acknowledged for the use of infrastructure provided by the NRF–SAIAB Research Platform and for funding provided to L de Necker. We also thank the two anonymous referees for their time to review the manuscript.

Funding — JJ Pearson received scholarship funding from the Water Research Commission (Project number: C2019/2020-00151) under the supervision of Dr L de Necker, Dr R Gerber and Dr W Malherbe. L de Necker received research funding from the National Research Foundation (NRF)–Department of Science and Innovation (DSI) Professional Development Programme (Grant No. 127549) and funding channelled through the NRF-SAIAB Institutional Support system. All subsequent authors declare that they have no financial interests.

Competing interests — The authors have no known competing financial interests or personal relationships to declare that are relevant to the content of this paper or that could have appeared to influence the work reported in this paper.

Author contributions — JJ Pearson: conceptualisation, data curation (literature search, investigation); writing (original draft); writing (editing). R Gerber: conceptualisation; project administration; supervision; validation; writing (review and editing). W Malherbe: conceptualisation; project administration; supervision; validation; writing (review and editing). NJ Smit: project administration; supervision; validation; writing (review and editing). L de Necker: conceptualisation; funding acquisition; project administration; supervision; writing (original draft); writing (editing).

Data availability — Data sharing is not applicable as no datasets were generated or analysed as part of this paper.

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Received 09 February 2023; revised 22 April 2024; accepted 12 May 2024
Associate Editor: J Ewart-Smith