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Distribution, drivers and population structure of the invasive alien snail *Tarebia granifera* in the Luvuvhu system, South Africa

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Abstract

Invasive alien species continue to spread and proliferate in waterways worldwide, but environmental drivers of invasion dynamics lack assessment. Knowledge gaps are pervasive in the Global South, where the frequent heavy human-modification of rivers provides high opportunity for invasion. In southern Africa, the spatio-temporal ecology of a widespread and high-impact invasive alien snail, *Tarebia granifera*, and its management status is understudied. Here, an ecological assessment was conducted at seven sites around Nandoni Reservoir on the Luvuvhu River in South Africa. The distribution and densities of *T. granifera* were mapped and the potential drivers of population structure were explored. *T. granifera* was widespread at sites impacted to varying extents due to anthropogenic activity, with densities exceeding 500 individuals per square meter at the most impacted areas. *T. granifera* predominantly preferred shallow and sandy environments, being significantly associated with sediment (i.e., chlorophyll-a, Mn, SOC, SOM) and water (i.e., pH, conductivity, TDS) variables. *T. granifera* seemed to exhibit two recruitment peaks in November and March, identified via size-based stock assessment. Sediment parameters (i.e., sediment organic matter, sediment organic carbon, manganese) and water chemistry (i.e., pH, total dissolved solids, conductivity) were found to be important in structuring *T. granifera* populations, with overall snail densities highest during the summer season. We provide important autecological information and insights on the distribution and extent of the spread of *T. granifera*. This may help in the development of invasive alien snail management action plans within the region, as well as modelling efforts to predict invasion patterns elsewhere based on environmental characteristics.

KEYWORDS
aquatic non-native invasions, environmental gradients, Global South, human-modified river, quilted melania, reservoir

1 | INTRODUCTION

Thousands of alien species have spread to non-native ranges around the world in recent decades (Seebens et al., 2017), precipitating ecological impacts from reductions in fitness, to population declines, to extinctions (Bellard, Cassey, & Blackburn, 2016; Nunes et al., 2019). Aquatic systems are regarded as most vulnerable, experiencing high rates of invasion, and marked ecological and socio-economic impacts (Bailey et al., 2020; Cuthbert et al., 2021). In freshwaters, high connectivity coupled with lacklustre biosecurity permits the rapid spread of invaders following their introduction (Coughlan, Cuthbert, & Dick, 2020), delaying management and potentially exacerbating control-related spending (Ahmed et al., 2021).

Molluscs are among the most notorious freshwater invaders (e.g., zebra mussel, *Dreissena polymorpha*; New Zealand mud snail, *Potamopyrgus antipodarum*) (Nentwig, Bacher, Kumschick, Pyšek, & Vilà, 2018). Globally they have been introduced through accidental and intentional vectors (Yanai, Dayan, Mienis, & Gasith, 2017) and often exhibit particularly high invasiveness due to their small size and difficulty of detection at low population sizes or immature life stages (Zieritz et al., 2017). The subtropics have the greatest diversity of freshwater molluscs globally (De Kock & Wolmarans, 2007). Mollusc invasions could homogenize this biodiversity, but status and risks remain understudied, especially in the Global South. Bivalves and gastropods are found in a wide range of freshwater habitats (Seddon, Appleton, Van Damme, & Graf, 2011), being essential for aquatic primary production and consumption, feeding on algae, bacteria, zooplankton, detritus, dissolved organic material, diatoms and plants (Alzurfi, Algburi, Taher, Alhachami, & Zwain, 2019). Despite these services, invading molluscs have driven shifts in the structure and functioning of aquatic ecosystems, by engineering environments and shifting trophic dynamics as well as other ecological processes (Emery-Butcher, Beatty, & Robson, 2020). For example, invasive snails can increase phytoplankton biomass through the release of nutrients via grazing activities and lead to exclusion of native species (Emery-Butcher et al., 2020; Miranda, Perissinotto, & Appleton, 2010).

In South Africa, molluscs are one of the largest groups of invertebrates (Weyl et al., 2020), although incursions of alien species are a growing but overlooked concern. So far, there are over 13 reported invasive snails in the country, most notably *Tarebia granifera* (Figure 1; Weyl et al., 2020). *T. granifera* is native to south-east Asia and has reportedly invaded several African countries, such as Mozambique, Eswatini, South Africa and Zimbabwe, among others (Miranda et al., 2010). This alien snail was possibly introduced to South Africa through the aquarium trade during the early 1990s as stowaways with aquarium plants (Appleton & Nadasan, 2002). *T. granifera* occurs in low-lying and shallow areas of lotic and lentic freshwater and estuarine systems, but is also found in artificial water bodies, such as irrigation channels and reservoirs (Weyl et al., 2020; Yakovenko, Fedonenko, Klimenko, & Petrovsky, 2018). Human-modified water ways can promote establishment and spread of *T. granifera* through disturbance, alongside canalisation for agricultural and industrial purposes (Jones et al., 2017; Miranda et al., 2010). The rapid spread of

FIGURE 1 Images of the quilted melania *Tarebia granifera*, with a shell length of 4–35 mm. *Source:* Gavin Snow [Color figure can be viewed at wileyonlinelibrary.com]

T. granifera has been through both passive (transferred through water or aquatic weeds that attach to the boat or trailers) and active (through attachment to waterfowl droppings or feathers) means (Jones et al., 2017).

Invasion by *T. granifera* can lead to biodiversity loss if it occurs in high densities, as it tends to dominate benthic aquatic communities, leading to competition for resources and loss or displacement of native species (Miranda et al., 2010; Weyl et al., 2020). Globally, *T. granifera* poses a major threat to resident communities, and it has been known to cause local extinction of native snails (Kesner & Kumschick, 2018; Zengeya, Kumschick, Weyl, & van Wilgen, 2020). For example, the native thiarid *Melanoides tuberculata* appears to be declining due to pressure from rapidly spreading *T. granifera* (Appleton, Forbes, & Demetriades, 2009). However, studies have not established the drivers behind the successful spread of this species in aquatic ecosystems (but see Raw, Miranda, & Perissinotto, 2013) and, centrally, which water or sediment chemistry drivers might promote invasion success. Thus, the spatiotemporal ecology of this widespread and high-impact invasive alien snail and its management status are largely understudied.

This study assessed *T. granifera* distribution and size patterns in relation to environmental characteristics in a reservoir situated on the Luvuvhu River system in South Africa. The main aims of this study were to assess: (a) whether environmental variables and *T. granifera* population structure and composition differed among different reservoir sites subject to varying anthropogenic activity across seasons, (b) how the distribution of *T. granifera* related to physicochemical parameters in Nandoni reservoir and (c) the key water or sediment variable drivers structuring the population within the system.

2 | MATERIALS AND METHODS

2.1 | Study area

Nandoni reservoir (with a centroid of 22°59′11″ S, 30°36′16.19″ E) is situated in Thulamela Municipality, Vhembe District in the Limpopo Province of South Africa (Figure 2) and is approximately 10 km from the town of Thohoyandou (Mbedzi, Cuthbert, Wasserman, Murungweni, & Dalu, 2020). The reservoir lies along the Luvuvhu River with an earth-fill and concrete structure, with an approximate catchment area of 1,380 km^2, total length of 2,215 m and a total capacity of 16.4 million m^3. The average air temperature around the

reservoir is 23 and 17°C during the summer and winter, respectively (DWAF, 2012). The average annual precipitation for the entire catchment varies between 610 and 800 mm, with a mean annual runoff of 519 million m^3 (Heath & Claassen, 1999). The topography of the reservoir area is comprised of low−lying, undulating terrain which is underlain by a gneiss sequence of the Soutpansberg group. The soil in most parts has been eroded due to continuous agricultural activities.

The collection of samples occurred in spring (September 23, 2020), summer (November 23, 2020), autumn (March 18, 2021) and winter (June 4, 2021). Site selection was based on previous studies on the system (i.e., Dalu, Malesa, & Cuthbert, 2019; Mbedzi et al., 2020) and according to human population density along the reservoir shore lines. In total, seven sites were selected around the reservoir: four sites (site 2– Budeli village (estimated village population density [ePD] 2,362), site 4– Mulenzhe village (ePD 2,566), site 6– Dididi village (ePD 2,312) and site 7– Thohoyandou J (Muledane village: ePD 1,428), categorized as high ePD density sites; and three sites (site 1 – ePD0, close to an agricultural college, site 5 – ePD6, site 3– ePD4, at the outskirts of Mulenzhe village, in a bay adjacent to a fishing lodge) categorized as low ePD (Figure 2; see Mbedzi et al., 2020; https://census2011.adrianfrith.com/place/966). This reflects the human population gradient occurring at the reservoir, with no areas considered 'pristine' due to human alterations and
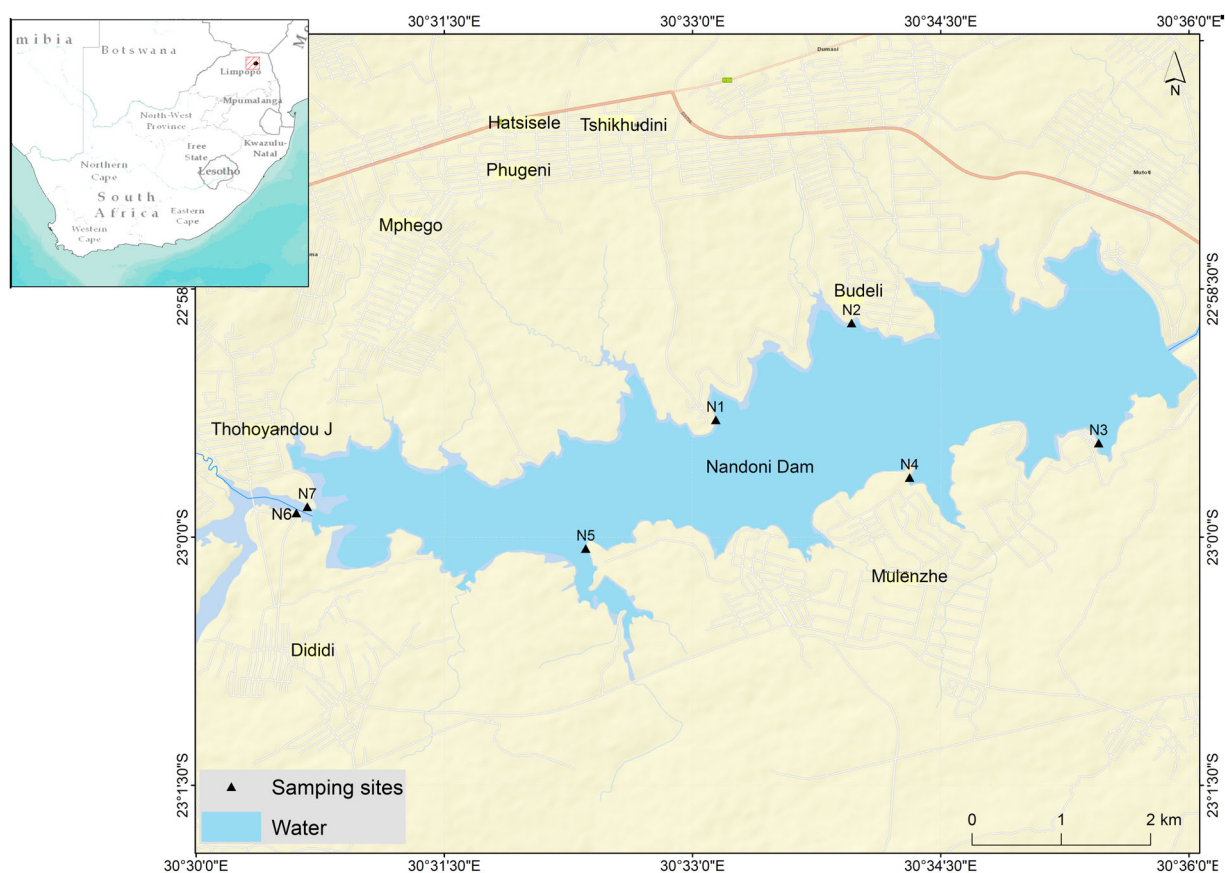

FIGURE 2 Study map highlighting the sites (N1–N7) surveyed in Nandoni Reservoir, South Africa [Color figure can be viewed at wileyonlinelibrary.com]

widespread invasion. The sites were highly variable in terms of substrate embeddedness, with site 1 being dominated by silt and sand, site 2 by clay, silt and boulders, site 3 by clay, silt, sand and stones/rocks, site 4 by silt and clay, site 5 by clay, site 6 by silt and clay and site 7 by sand and stones/rocks. While not assessed formally, other snail species encountered were the invasive *Physa acuta*, as well as small Planorbidae and large Physidae taxa, with the latter two being found in very low densities.

2.2 | Physiochemical parameters

2.2.1 | In-situ measurements

At each sampling site and season, conductivity (μS cm^{-1}), pH, total dissolved solids (mg L^{-1}) and water temperature ($^{\circ}$C) were measured in-situ using a portable handheld Cyberscan Series multiparameter meter (Eutech Instruments) from three different locations spaced at least 2 m apart.

2.2.2 | Sediment chemistry variables

Two integrated 1.5 kg sediment samples ($n = 2$) from three random areas within each site were collected across the different study sites and seasons. The sampling was done using acid-washed wooden splints and each integrated sample was placed in new polyethylene ziplock bags to avoid cross contaminates. The composite samples were immediately packed in a cooler box with ice, and transported to the University of Venda Pollution laboratory for analysis within 24 hr (Wang, Hamilton, & Kang, 2014). In the laboratory, the samples were oven-dried at 60°C for 72 hr to a constant weight before being disaggregated in a porcelain mortar. The dried sediment samples were then homogenized using a riffle splitter, and thereafter a sediment subsample of 0.5 kg was separated and sent to BEMLAB, Cape Town for further analysis.

Triplicate benthic algal core samples were collected at each station using a perspex sediment corer of 20 mm internal diameter, inserted by hand into the sediment for benthic chlorophyll-*a* concentration determination (following Human et al., 2018). Cation element (i.e., boron [B], calcium [Ca], magnesium [Mg], potassium [K], sodium [Na]), heavy metals (i.e., copper [Cu], iron [Fe], zinc [Zn]), sediment phosphorus (sed-P) and phosphate (sed-PO$_4^{3-}$) concentrations, sediment organic matter (SOM) and organic carbon (SOC), sediment pH, resistivity and stone count (<5 cm) were quantified for each site and season as described in detail in Dalu et al. (2021).

2.3 | Sampling of *Tarebia granifera*

T. granifera were collected from the seven different sites in each season, using two integrated samples collected from 3 quadrats (30 cm × 30 cm, sediment depth of 5–10 cm) each, to quantify density and size characteristics. Snails were collected by randomly placing a quadrat in the shallow, littoral zone of the reservoir at each site, with the entire contents of the quadrat collected using a handheld plastic spade and placed inside a plastic zip-lock bag. The samples were taken to the University of Venda Pollution Laboratory for further analyses. The collected samples were then sieved through a 2 mm mesh to separate *T. granifera* from sediments, before all snails were counted and measured (shell height [H] and breadth), to the nearest 0.1 mm using a Vernier calliper. The samples were then placed in a labelled polyethylene bottles containing a 90% ethanol solution. All field densities were quantified as individuals per m^2.

2.4 | Data analysis

To determine whether the ecosystem health based on water and sediment quality (log [$x + 1$] transformed) variables differed among sites (i.e., sites N1–N7) and seasons (i.e., spring, summer, autumn, winter), we used a distance-based PERMutational Analysis of VAriance (PERMANOVA; Anderson, 2001) in PRIMER v6 add-on package PERMANOVA+ (Anderson, Gorley, & Clarke, 2008). Each term in the analysis was tested using 9999 permutations (Anderson & ter Braak, 2003), with significant terms being investigated using a posteriori pair-wise comparison based on the PERMANOVA t-statistic (Anderson et al., 2008). We further tested whether there were significant differences in water and sediment chemistry variables and *T. granifera* densities among the study sites and seasons using two-way ANOVA in SPSS v16.0 for Windows software (SPSS Inc. 2007). Before the ANOVA analyses, all data were assessed for normality and homogeneity of variance and were found to conform to parametric assumptions using the Shapiro–Wilk's W and Levene's tests, respectively.

Geographical positions of study locations were used to produce distribution maps based on the estimated densities of invasive alien *T. granifera* using geographical information systems (ESRI, 2011). The programme FAO-ICLARM Stock Assessment Tool (FiSAT) was adopted to analyse *T. granifera* length frequency data (Sparre & Venema, 1993). The computer models incorporated in FiSAT were used to estimate the von Bertalanffy growth function (VBGF) parameters, that are K (growth coefficient, which is the relative growth rate of the species) and $L\infty$ (asymptotic length, which is the mean maximal length the snails would reach over an infinite period).

A Detrended Canonical Correspondence Analysis (DCCA) was used to determine whether unimodal or linear methods were most appropriate for ordination analysis. The gradient lengths from the DCCA analysis were examined, and since the longest gradient was shorter than 3.0, a linear constrained Redundancy Analysis (RDA) method was found to be the most appropriate for the data. The RDA, based on significant ($p < 0.05$) forward selected environmental variables, was used for analysis using 9999 Monte Carlo Permutations in Canoco version 5.1 (ter Braak & Šmilauer, 2012). To evaluate changes in *T. granifera* densities among study sites and seasons, a hierarchial cluster analysis was carried out in PRIMER v6 (Anderson et al., 2008),

in autopilot mode so as to allow the program to choose the best solution for each dimensionality (Kruskal & Wish, 1978).

3 | RESULTS

3.1 | Habitat characteristics

Nandoni reservoir ecosystem health based on the water and sediment chemistry variables differed significantly among study sites (Pseudo-$F_{6,55} = 4.115$, $p = .0001$) and seasons (Pseudo-$F_{3,55} = 9.450$, $p = .0001$). Significant pairwise differences ($p < .050$) were found across all season combinations, however, for sites no significant differences ($p > .050$) were observed for N2 versus N1, N3 and N4, N3 versus N4, N6 versus N4 and N7, N7 versus N4 and N5 versus N4 combinations, with system health deteriorating towards the winter season (Table 1). While variable, the summer often had high sediment and water concentrations and autumn had low concentrations (Table 2).

Sediment variables in summer, autumn and winter had pH values that were slightly acidic, and lowest in spring (Table 2). High sediment metal concentrations were recorded during summer (Table 2). Benthic chlorophyll-a concentration varied throughout the seasons, with a mean value of 139.5 g m^{-2} in winter and decreasing to a low concentration mean of 61.8 g m^{-2} in spring (Table 2). For water variables, temperature varied among all seasons (Table 2). In autumn, water pH was very low (mean 6.4) and peaked in spring (mean 8.6). Conductivity and TDS were generally very high in summer (Table 2).

Sediment and water variables displayed considerable heterogeneity among sites and seasons (Tables 2 and 3). All sediment variables except B, S, SOC and SOM differed significantly among sites, whereas

pH, resistivity, stone count, Mn, S, SOM and chl-a differed among seasons (Table 3). Significant site-season interactions were evidenced for resistivity, Fe, and chl-a in addition. For water variables, temperature, pH and TDS differed consistently significantly among sites and seasons singularly (Table 3), while conductivity differed among seasons alone; temperature and pH also exhibit significant site-season interactions (Table 3).

3.2 | Snail distribution and size patterns

T. granifera densities per m^2 were found to be significantly different across study seasons ($F_{3,55} = 41.824$, $p < .001$), but not among sites ($F_{6,55} = 1.614$, $p = .179$) or in interaction between these terms ($F_{18,55} = 0.967$, $p = .513$). Autumn snail densities were low (range = 44–206 individuals m^{-2}, mean = 104 individuals m^{-2}) and peaked during the summer season (range = 161–517 individuals m^{-2}, mean = 368 individuals m^{-2}) (Figure 3). In general, sites associated with low population/household densities (i.e., N1, N3, N5) nearby had variable mean *T. granifera* densities per m^{-2} (Figure 3).

Considering length frequency distributions (Figure 4), size cohorts were clearly identifiable across seasons, with FiSAT identifying at least 6 size classes and two recruitment peaks in November and March. Thus, clear indications of growth were obtained from the length frequency distributions for all seasons. The growth coefficient (K) and asymptotic length ($L\infty$) were 0.46 and 36.75 mm, respectively.

3.3 | Influence of physicochemical variables on *Tarebia granifera* densities

RDA first and second axes of the selected exploratory variables accounted for 36.4% of the total *T. granifera* density variance. Of the 21 physicochemical variables, the density of *T. granifera* across the seven study sites and four seasons was found to be significantly associated with sediment (i.e., chlorophyll-a, Mn, SOC, SOM) and water (i.e., pH, conductivity, TDS) variables (Figure 5). Water pH, TDS and conductivity, SOC and Mn were positively associated with the first axis while, SOM and benthic chlorophyll-a were negatively associated with the first axis (Figure 5). Summer sites were clearly separated along the first axis from the rest of the sites/seasons, whereas the spring sites showed a slight overlap with the autumn and winter sites. Summer site samples were associated with high *T. granifera* densities which were associated to high pH, conductivity, TDS, Mn and SOC (Figure 5). Whereas, most of the autumn and winter site samples were associated with low *T. granifera* densities.

4 | DISCUSSION

This study assessed the invasion ecology of *T. granifera* in a tropical river-fed reservoir in southern Africa, across four seasons in relation to human densities, sediment and water chemistry variables. While

TABLE 1 Pairwise comparison results for the PERMANOVA highlighting the t (white) and p values (grey) for the seasons and sites

Seasons				
	Spring	Summer	Autumn	Winter
Spring	1.000	0.014	0.0002	0.0001
Summer	1.925	1.000	0.0001	0.0001
Autumn	3.026	3.512	1.000	0.0001
Winter	3.203	3.728	2.914	1.000

Sites							
	N1	N2	N3	N4	N5	N6	N7
N1	1.000	0.290	**0.007**	**0.023**	**0.0001**	**0.001**	**0.004**
N2	1.107	1.000	0.336	0.263	**0.015**	**0.026**	**0.045**
N3	**2.397**	1.001	1.000	0.233	**0.001**	**0.011**	**0.026**
N4	**1.970**	1.161	1.208	1.000	0.057	0.055	0.253
N5	**4.669**	**2.449**	**3.241**	1.702	1.000	**0.022**	**0.024**
N6	**2.976**	**1.943**	**2.175**	1.667	**1.893**	1.000	0.367
N7	**2.874**	**1.876**	**1.909**	1.170	**1.853**	1.050	1.000

Note: Bold values indicate significant differences at $p < .05$.

Variables	Units	Spring	Summer	Autumn	Winter
Sediment					
pH		6.1 ± 0.3	6.7 ± 0.3	6.7 ± 0.6	6.5 ± 0.3
Resistivity	ohms	1912 ± 314	1,127 ± 240	1981 ± 515	1,675 ± 379
Stone	%	34.7 ± 17.4	53.3 ± 12.4	39.7 ± 12.3	36.3 ± 7.3
P	mg kg^{-1}	15.2 ± 9.3	12.2 ± 6.4	26.1 ± 10.4	17.5 ± 2.8
K	mg kg^{-1}	63.1 ± 27.0	55.1 ± 13.8	57.1 ± 19.8	46.3 ± 6.5
Ca	cmol(+) kg^{-1}	4.2 ± 1.1	5.1 ± 2.0	3.3 ± 0.7	3.5 ± 0.6
Mg	cmol(+) kg^{-1}	1.4 ± 0.6	1.88 ± 0.6	1.14 ± 0.5	1.1 ± 0.1
Na	cmol(+) kg^{-1}	0.15 ± 0.04	0.21 ± 0.1	0.18 ± 0.1	0.16 ± 0.03
Cu	mg kg^{-1}	5.1 ± 0.8	5.5 ± 2.7	4.6 ± 1.5	4.5 ± 0.8
Zn	mg kg^{-1}	5.6 ± 1.5	2.8 ± 0.8	4.3 ± 1.7	3.6 ± 1.0
Mn	mg kg^{-1}	91.1 ± 34.0	139.5 ± 72.9	109.4 ± 32.6	63.1 ± 15.3
B	mg kg^{-1}	0.3 ± 0.1	0.20 ± 0.04	0.20 ± 0.06	0.19 ± 0.04
Fe	mg kg^{-1}	161.1 ± 29.8	246.0 ± 85.8	200.1 ± 55.4	151.6 ± 15.0
SOC	%	1.2 ± 0.5	1.4 ± 0.4	0.75 ± 0.19	0.97 ± 0.12
S	mg kg^{-1}	18.8 ± 8.8	38.6 ± 16.9	15.7 ± 5.7	21.1 ± 5.0
SOM	%	4.6 ± 2.6	13.7 ± 3.2	13.6 ± 5.5	15.4 ± 11.8
Chlorophyll-*a*	g m^{-2}	61.8 ± 12.4	100.3 ± 40.7	118.0 ± 49.5	139.5 ± 32.5
Water					
Temperature	°C	29.8 ± 0.6	29.8 ± 0.9	31.2 ± 0.2	21.2 ± 0.2
pH		8.6 ± 0.2	8.5 ± 0.1	6.4 ± 0.2	7.4 ± 0.2
Conductivity	μS cm^{-1}	273.9 ± 0.6	268.7 ± 9.4	140.5 ± 4.1	159.6 ± 2.5
TDS	mg L^{-1}	165.9 ± 2.8	167.2 ± 1.0	70.3 ± 2.0	79.6 ± 1.4

TABLE 2 Physicochemical variables measured (±SD) in Nandoni reservoir in September 2020 to June 2021

Abbreviations: B, boron; Ca, calcium; Cu, copper; Fe, iron; K, potassium; Mg, magnesium; Mn, manganese; Na, sodium; P, phosphorus; S, sulphur; SOC, sediment organic carbon; SOM, sediment organic matter; TDS, total dissolved solids; Zn, zinc.

based on a single impoundment in South Africa, we found that *T. granifera* was heterogeneously distributed among all four seasons, with peak littoral densities in summer which corresponded to changes in water and sediment variables. This summer peak corroborates other studies which recorded high densities seasonally as the temperature peaked (Miranda, Perissinotto, & Appleton, 2011b; Yong, Sanchez, Perera, Ferrer, & Amador, 1987). In our study system, the summer peak could thus be associated with greater rainfall and water temperatures (Appleton & Nadasan, 2002). Further, peak densities were associated with significant decreases in benthic chl-*a* concentrations, which could be related to grazing by the snails, with implications for food web transfer (Moslemi, Snider, MacNeill, Gilliam, & Flecker, 2012). As such, the *T. granifera* invasion of Nandoni reservoir has potentially altered a suite of ecosystem properties within the study system. Further research on the basic biology of this species is required to elucidate the invasion patterns in this study system (e.g., reproduction and feeding ecology), and particularly the implications of biotic interactions for invasion success in such human-modified habitats.

We did not find significant differences in densities among sites (while all were human-impacted and invaded), suggesting that the invasion is widespread and ubiquitous in this study system, and relatively unimpeded by human disturbances, such as car and laundry washing, bathing/swimming and water abstraction on a daily basis that occur in densely-population areas. A lack of comparable uninvaded sites prohibited direct analysis of ecosystem-level effects of invasion here (Moslemi et al., 2012), with no uninvaded sites found in the reservoir. We speculate that, since the species is abundant within the Limpopo River system on which the study site is located, it likely migrated from the main stem up to the current location, or has been dispersed by water birds and via passive dispersal through boats or fishing gear (see Appleton & Nadasan, 2002). How this species interacts with or impacts other native snails in this study system is yet to be determined, but this study provides a preliminary assessment of intra-specific population dynamics.

T. granifera of different size classes (i.e., potential age groups) were recorded using stock assessments, which identified at least six different groups varying across the study seasons. In general, the shell height observed in Nandoni reservoir in this study was of a greater range compared to that observed in the KwaZulu Natal province of South Africa (range 0.8 to 22 mm) (Appleton & Nadasan, 2002), Havana (range 0–16 mm) (Yong et al., 1987) and the St. Lucia Estuary (range <1–29 mm) (Miranda et al., 2011b). Furthermore, larger size groups (>18 mm) or older cohorts dominated, whereas in the studies

TABLE 3 Two-way analyses of variance (ANOVA) based on sediment and water variables for sites and seasons

Parameter	Site F	Site p	Season F	Season p	Site × season F	Site × season p
Sediment						
pH	**6.057**	**<.001**	**4.430**	**.011**	0.526	.911
Resistivity	**4.176**	**.004**	**7.506**	**.001**	**3.769**	**.001**
Stone	**2.900**	**.024**	**3.277**	**.035**	1.313	.255
P	**3.836**	**.006**	2.733	.062	1.628	.123
K	**3.124**	**.017**	0.689	.566	0.659	.808
Ca	**5.310**	**.001**	1.734	.182	1.865	.070
Mg	**6.769**	**<.001**	1.452	.248	0.572	.879
Na	**4.830**	**.002**	1.081	.373	0.857	.618
Cu	**7.869**	**.000**	0.235	.871	1.811	.080
Zn	**2.436**	**.050**	1.028	.395	1.516	.161
Mn	**3.461**	**.011**	**2.958**	**.049**	0.558	.890
B	1.625	.176	1.536	.226	0.762	.711
Fe	**3.764**	**.007**	2.619	.070	**3.752**	**.001**
S	0.593	.733	**8.110**	**<.001**	1.627	.124
SOC	2.094	.085	2.468	.082	1.179	.339
SOM	0.568	.752	**3.189**	**.038**	1.377	.220
Benthic chl-*a*	**2.638**	**.036**	**9.405**	**<.001**	**3.147**	**.004**
Water						
Temperature	**4.822**	**.001**	**6.564**	**<.001**	**7.966**	**<.001**
pH	**13.678**	**<.001**	**20.297**	**<.001**	**9.851**	**<.001**
Conductivity	0.927	.490	**7.657**	**<.001**	1.139	.366
TDS	**6.958**	**<.001**	**42.233**	**<.001**	1.665	.111

Note: Bold values indicate significant differences at $p < .05$. See abbreviations in Table 2 for the parameters.

highlighted above, smaller snails and younger age groups were dominant. These differences could be attributed to favourable climate, flow conditions and resource availability (Miranda et al., 2011b), allowing older cohorts to dominate in Nandoni reservoir, or larger cohorts being competitively superior and smaller sizes moving to deeper waters that we did not survey. The implications of these parameters should be further determined in-field, as well as other habitat characteristics (e.g., vegetation, wave exposure and substrate) and biotic interactions. The growth coefficient of 0.46 (estimated at 1.41 mm/month based on an $L∞$ of 36.75 mm) was double that observed in other studies (e.g., Chaniotis, Butler, Ferguson, & Jobin, 1980). Contrastingly, the densities (max of 544 individuals per m²) observed in Nandoni reservoir were generally lower than those observed in other parts of South Africa of >1,000 individuals per m² (Appleton & Nadasan, 2002; Miranda et al., 2011b). This might reflect a relatively early invasion stage, or the rich population dynamics that have been reported in invasive snails due to 'boom-bust' trends as populations grow and deplete resources (Perissinotto, Miranda, Raw, & Peer, 2014); such trends cannot be appreciated with irregular snapshot surveys in time. Alternatively, the system could have a relatively low carrying capacity. Nevertheless, this study provides a basis for

understanding snail invasions, as little is known of the seasonal population fluctuations of *T. granifera* in relation to their environment.

In the present study, *T. granifera* densities were significantly associated with sediment (i.e., benthic chlorophyll-*a*, Mn, SOC, SOM) and water (i.e., pH, conductivity, TDS) chemistry variables. The high benthic chl-*a*, SOC and SOM levels, observed especially during the summer months, might explain the high densities and sizes of *T. granifera* observed in the study area, since *T. granifera* sizes are mostly influenced by food availability and quality (Miranda et al., 2011a ,2011b; Yong et al., 1987). The breaking down of SOM and SOC might have resulted in the release of nutrients that facilitated the growth of benthic algae which *T. granifera* feed on. Positive effects of rising pH could be attributed to the fact that *T. granifera* shells are eroded at low pH, as has been observed in other study systems where acidity precluded high population levels (Miranda et al., 2011b). The high conductivity and TDS levels observed, especially during spring and summer, may have contributed to high *T. granifera* densities, as in previous studies (e.g., Larson, Dewey, & Krist, 2020; Vazquez, Ward, & Sepulveda, 2016). Low conductivity tends to reduce the growth and survival of snails (Larson et al., 2020), which might explain some of the low densities observed during
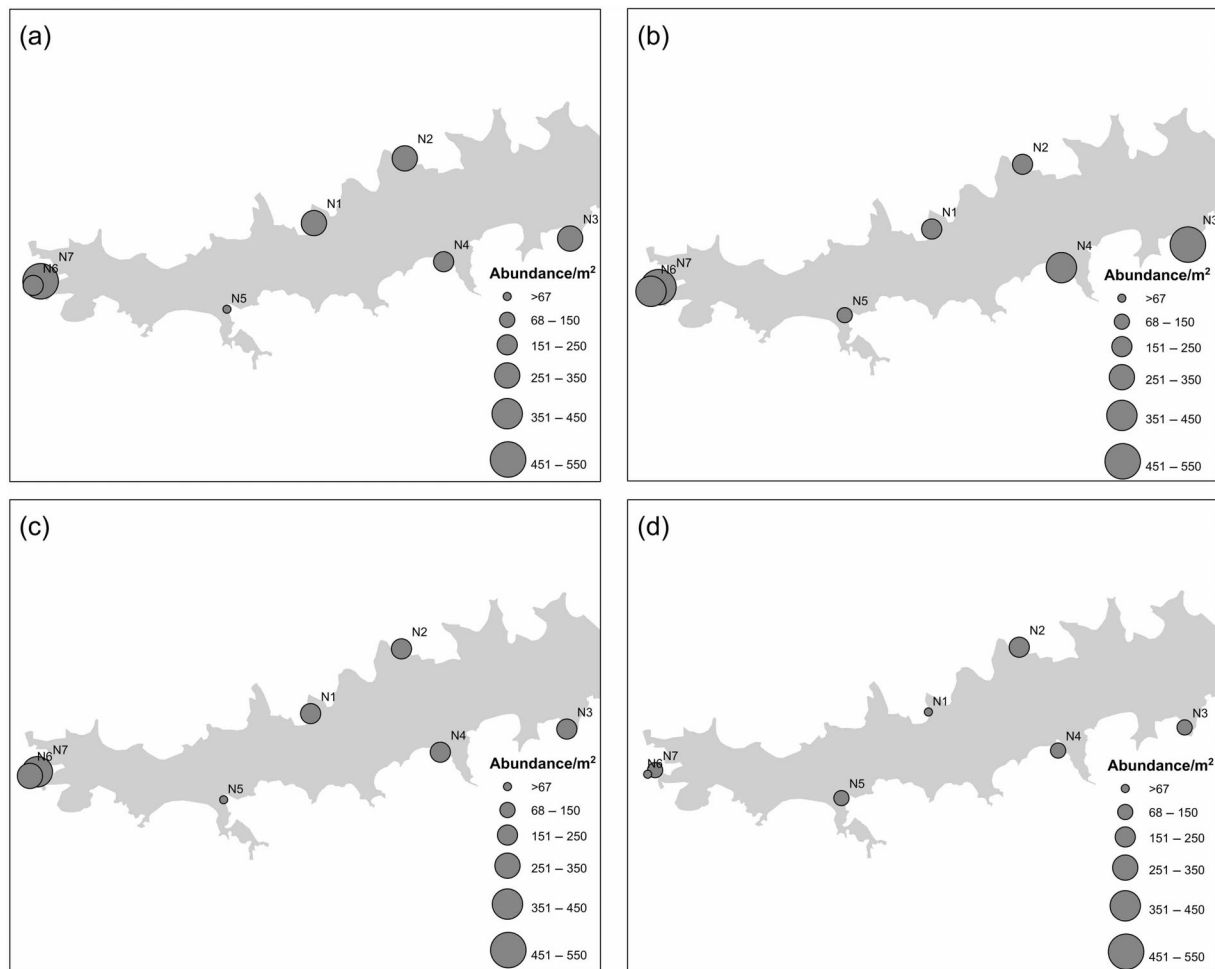
FIGURE 3 Distribution map of *Tarebia granifera* in the Nandoni reservoir of South Africa from (a) spring (September 2020), (b) summer (November 2020), (c) autumn (March 2021) and (d) winter (June 2021)

autumn and winter. Thus, at high conductivity and TDS levels, particularly during spring and summer, *T. granifera* will likely increase its growth and survival as it can adapt to acute high salinity stress and maintain a hypo-osmotic haemolymph (Larson et al., 2020); it has been found in very large densities in estuaries in South Africa of high conductivity levels. Nevertheless, as we did not assess biotic interactions or wider habitat characteristics here, population dynamics could relate to a broader suite of variables that we did not capture, while certain physico-chemical parameters may be relatively benign in effect.

While *T. granifera* was widespread in the focal sites in our study, and thus relatively unimpeded by disturbances associated with human activity, no *T. granifera* have been recorded on the more polluted Mvudi River which joins the Luvuvhu River before entering the reservoir. This could be attributed to contaminants and/or fast flowing waters due to wastewater runoff and discharge, which either impedes population growth through poor water quality or prevents population establishment and upstream spread due to high velocity; despite potential adaptations in invasive snails to different flow conditions

(Kistner & Dybdahl, 2013). As with other invasive snails, adaptabilities to human disturbance and rates of parthenogenetic reproduction promote establishment in a range of conditions (Miranda et al., 2016). Despite a lack of impact studies in our study system, the rapid spread of *T. granifera* has reportedly displaced native gastropods. For example, Raw et al. (2013) also showed that native gastropods *Assiminea* cf. *capensis*, *M. tuberculata* and *Coriandria durbanensis* exhibited negative taxis response to chemical cues released by *T. granifera* at invaded sites in St. Lucia Estuary, South Africa. Similarly, Appleton et al. (2009) make anecdotal reports on *M. tuberculata* declines in many sites where *T. granifera* now occur in South Africa. Given the link between population dynamics and ecological impact (Parker et al., 1999), the factors that shape density and size structures in the present study may thus be the same which mediate impact. These results thus provide insights into population dynamics according to environmental variables in a heavily human-altered environment, but could be furthered by more resolute, widespread and longstanding investigations into the species and particularly wider biotic interactions such as competition and predation.
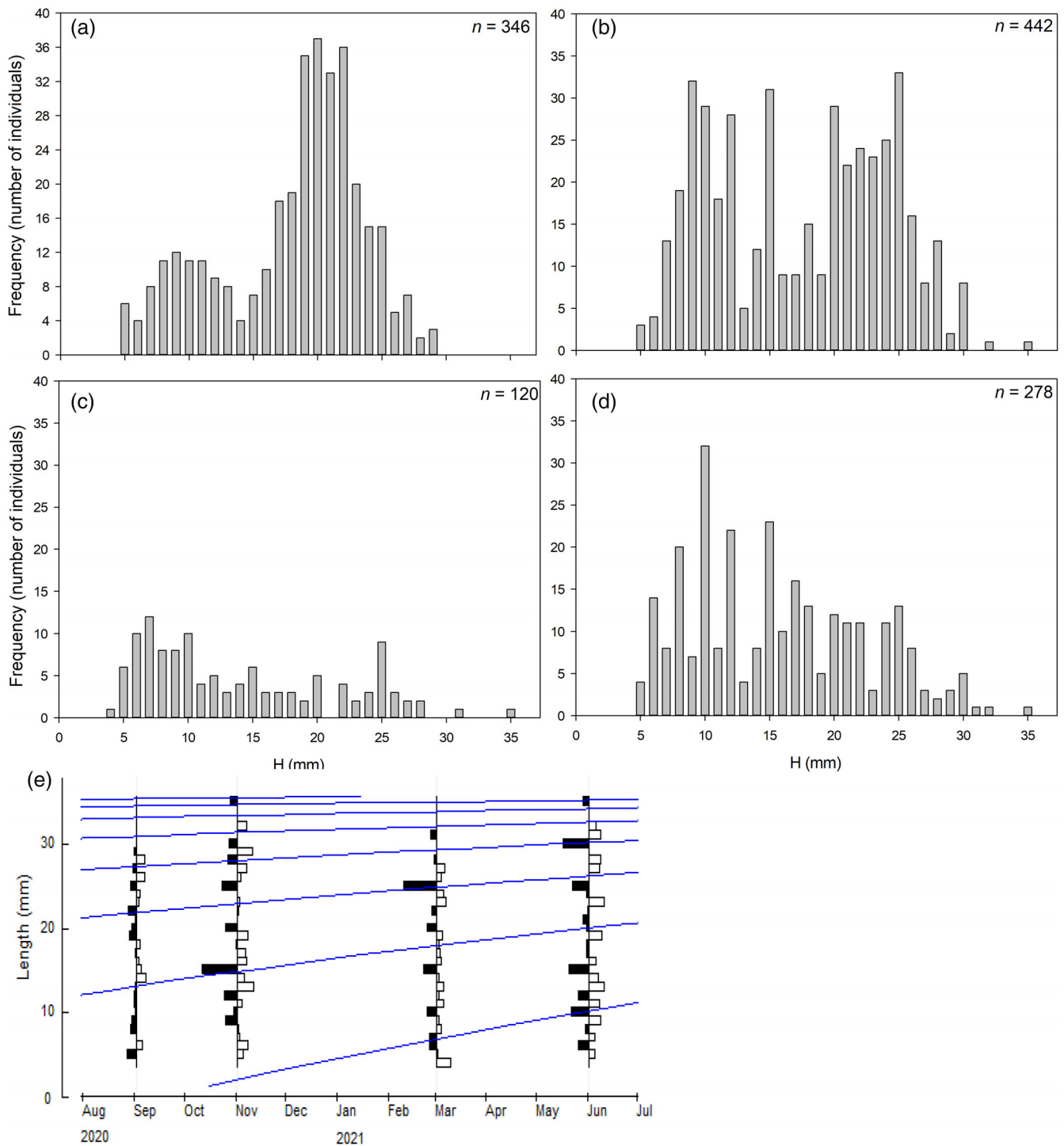
FIGURE 4 Frequency distributions of *Tarebia granifera* in Nandoni Reservoir from (a) spring (September 2020), (b) summer (November 2020), (c) autumn (March 2021) and (d) winter (June 2021), as well as (e) von Bertalanffy growth function plot and length frequencies, with the blue lines indicating the relative size (zonation of size classes) in time, i.e. growth curve, and black and white bars the running average frequencies to emphasize positive and negative peaks (recruitment peaks shown by larger bars), respectively. Note that plot (e) is made with same data as plots (a)–(d), by dividing each of the frequency values by the corresponding running mean frequency, and via the subtraction of 1 from each of the resulting quotients to remove potential sources of bias [Color figure can be viewed at wileyonlinelibrary.com]

5 | OUTLOOK

While the present study identified population characteristics and abiotic determinants of *T. granifera* densities and sizes, it is still unclear

what the ecological impacts are, and which species are being adversely affected in the region. There should thus be further studies on *T. granifera* in lakes and rivers to determine if and how native species assemblages are compromised, as well as assessments of
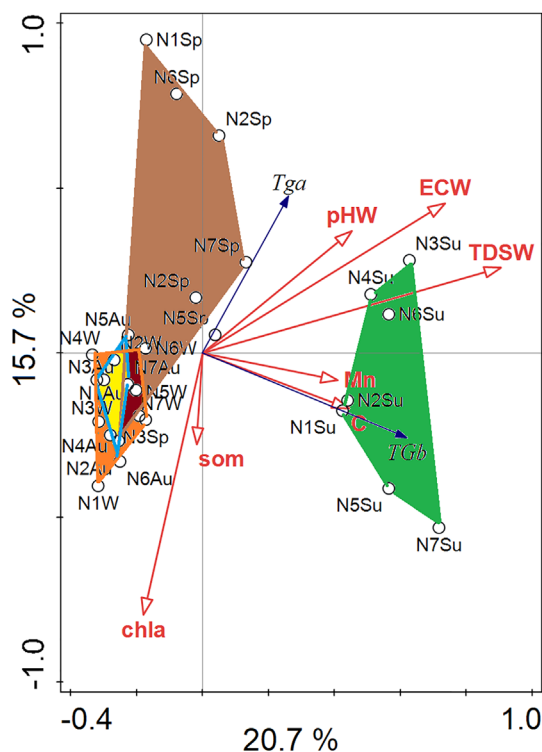
FIGURE 5 Redundancy analysis ordination biplot showing the relationship between measured significant environmental variables with *Tarebia granifera* densities. Sites N1–N7, letters after the site names: Au, autumn; Sp, spring; Su, summer; W, winter; TGa, *T. granifera* adults; TGb, *T. granifera* juveniles; chla, benthic chlorophyll-*a*; som, sediment organic matter; pHW, water pH; ECW, electrical conductivity in water; TDSW, water total dissolved solids; Mn, manganese; C, sediment organic carbon [Color figure can be viewed at wileyonlinelibrary.com]

populations at different depths and habitats of the system through time. Future work should also focus on improving monitoring of aquatic ecosystems that have not been invaded (e.g., through use of environmental DNA) and determining pathways, to ensure improved biosecurity such that further ecosystems are not invaded in future. Similarly, studies on physico-chemical drivers and thresholds of *T. granifera* are necessary, as well as biotic interactions. Finally, environmentally-sound ways to manage invasive snail populations should be assessed.

CONFLICT OF INTEREST

The authors certify that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

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