Assessment of past and present distribution of freshwater molluscs in KwaZulu-Natal, South Africa, particularly at River Eco-Status Monitoring Programme sites

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ABSTRACT

Globally, freshwater biodiversity is declining in major river basins. As a whole, South Africa is not exempt from this trend; the rivers of KwaZulu-Natal Province are being impacted by various anthropogenic activities that threaten their sustainability, leading to the loss of natural land cover and the ultimate decline in environmental functionality and connectivity in KwaZulu-Natal. Across South Africa and KwaZulu-Natal, nearly 71% of freshwater ecosystems are considered either endangered or critically endangered because of anthropogenic activities.

Previous work on freshwater Mollusca in South Africa, especially in KwaZulu-Natal, is well-documented, including recent distribution range and taxonomic studies. Historically, ca. 69 freshwater mollusc species have been recorded for KwaZulu-Natal, supported by 124 years of historical collection data. However, most recent and ongoing surveys in the province have recorded fewer freshwater mollusc species than previously documented, suggesting a decline of mollusc diversity in KwaZulu-Natal. Additionally, ever since the River Eco-Status Monitoring Programme (REMP) was established in the last decade, aquatic macroinvertebrates, including 11 mollusc families, have been used for biomonitoring of freshwater ecosystems in South Africa, while historical records have reported 16 mollusc families, and no higher resolution has been used to assess mollusc diversity collected at the REMP sites in KwaZulu-Natal. Thus, updated information on the diversity of freshwater molluscs across major freshwater ecosystems of KwaZulu-Natal is needed to support conservation efforts and decision-making. The aim of this study was to analyse past and present changes in the diversity and distribution of freshwater molluscs in KwaZulu-Natal, particularly at REMP sites.

Historical records of 124 years were sourced from four databases of South African natural history collections housed at the Albany Museum in Makanda, Eastern Cape Province (AMM),

East London Museum in East London, Eastern Cape Province (ELM), KwaZulu-Natal Museum in Pietermaritzburg, KwaZulu-Natal (KZNM) and the National Freshwater Snail Collection (NFSC) of South Africa in Potchefstroom, North West Province. Specimen records were curated and validated against two independent online open data infrastructures. The number of collected individuals and diversity amongst collections were compared, and trends in the database were analysed. Additionally, historical mollusc taxa were mapped to the nearest 10 km radius, based on their locality descriptions and coordinates, to match the REMP sites in KwaZulu-Natal.

A total of 52 sites were sampled four times between February 2024 and September 2025, and were part of the REMP surveys conducted. The sampling sites belonged to the three water management areas, namely 'U', V', and 'W', of KwaZulu-Natal, and some of them overlapped with historical localities. Freshwater mollusc specimens were collected using the kick-stir-sweep methodology outlined in the South African Scoring System 5 (SASS5) and active search through hand-picking during each sampling event. The identification keys developed by Brown (1994), and Appleton (2002) were used to identify collected molluscs morphologically to species level. Water quality variables (pH, water temperature, dissolved oxygen (DO), total dissolved solids (TDS), electrical conductivity (EC) and salinity) were recorded *in situ* at each sampling site, and biotope availability was assessed.

This study found that 69 freshwater mollusc species in KwaZulu-Natal are presently preserved in natural history collections in South Africa (55 gastropods and 14 bivalves), belonging to 16 families (11 gastropods and five bivalves). The list of 69 mollusc species included historical records, online sources, and our latest sampling surveys from 2024 and 2025. The greatest increase in specimen collection and deposition occurred during the 1960s and 1970s, peaking at 77% before declining thereafter. A large proportion of specimens collected during this period were deposited

at the National Freshwater Snail Collection of South Africa (NFSC) in Potchefstroom, North West Province. Family Planorbidae amongst the gastropods was the most diverse (17 species), while Sphaeriidae was the most diverse within the bivalves (seven species). The 'U' WMA harbours the most diverse mollusc community, with a total of 54 species (43 gastropods and 11 bivalves). The gastropods *Tomichia natalensis* (Connolly, 1939) and *Tomichia tristis* (Morelet, 1889) are listed as Critically Endangered (CR), and *Tomichia ventricosa* (Reeve, 1842) Endangered (EN) on the International Union for Conservation of Nature (IUCN) Red List; while the vast majority of freshwater molluscs are listed as either Least Concern (LC) or Data Deficient (DD). In addition, this study found that there was a huge disconnection between museum specimens in natural history collections in South Africa and online data repositories such as the Global Biodiversity Information Facility (GBIF) and Freshwater Biodiversity Information System (FBIS), as most of the data used were not available on these two online data repositories.

The results of this study also revealed a higher number of invasive freshwater mollusc species than endemic species. Among biotopes and water quality variables measured, it was reported that the availability of vegetation and total dissolved solids (TDS), were the primary variables determining the number of collected individuals and the distribution of molluscs. Compared with recent studies and the ongoing freshwater mollusc surveys by FBIS, this study recorded 24 species during field samplings of February 2024 and September 2025, belonging to 11 families (seven gastropods and four bivalves). Although more species were recorded in this study than in recent studies and in the FBIS's ongoing surveys over the past five years (2020 – 2025), this study recorded 45 fewer species than historical data. Compared with historical records mapped to the nearest 10 km radius at the 52 REMP sites, 13 species were recorded, whereas this study recorded 24 species, with high or low diversity at some sites.

This study concludes that, firstly, the prevalence of invasive species in highly organic-polluted freshwater ecosystems may have contributed to the displacement of endemic species, which are less favoured by predation and competition. Secondly, this study suggests that the combination of climate change, in the form of natural disasters such as droughts and floods, in KwaZulu-Natal, with river pollution may have contributed to low mollusc diversity at certain sites. Finally, this study indicates that low mollusc diversity in KwaZulu-Natal may also be attributed to inadequate sampling and a lack of a long-term monitoring programme at selected sites over the past decade. Thus, an increase in financial and skill investment in natural history collections is advocated to facilitate wider geographical and temporal sampling, as well as taxonomic updates. Data mobilisation and sharing are also encouraged. The identification and integration of new sites into the REMP surveys are recommended. Ultimately, the results of this study may assist decision-makers in the district municipalities of KwaZulu-Natal, as well as those in South Africa as a whole, in establishing a sustainable balance in the management of freshwater resources and ecosystems.

PREFACE

The data described in this thesis were collected in KwaZulu-Natal, Republic of South Africa, from February 2024 to September 2025. Field sampling and data analyses were conducted while registered in the Discipline of Ecological Sciences, School of Agriculture and Sciences, University of KwaZulu-Natal, Pietermaritzburg, under the supervision of Prof Colleen T. Downs and co-supervision of Dr Matthew J. Burnett and Dr Igor Muratov.

This thesis, submitted for the degree of Doctor of Philosophy in the College of Agriculture, Engineering and Science, University of KwaZulu-Natal, Pietermaritzburg campus, represents original work by the author and has not otherwise been submitted in any form for any degree or diploma to any University. Where use has been made of the work of others, it is duly acknowledged in the text.



……

Matabaro Ziganira

November 2025

I certify that the above statement is correct, and as the candidate's supervisor, I have approved this thesis for submission.



……..

Prof Colleen T. Downs

Supervisor

November 2025

COLLEGE OF AGRICULTURE, ENGINEERING AND SCIENCE

DECLARATION 1 - PLAGIARISM

I, Matabaro Ziganira, declare that

1. The research reported in this thesis, except where otherwise indicated, is my original research.
2. This thesis has not been submitted for any degree or examination at any other university.
3. This thesis does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons.
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DECLARATION 2 - PUBLICATIONS

DETAILS OF CONTRIBUTION TO PUBLICATIONS that form part and/or include research presented in this thesis.

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Significant progress in the study of African freshwater snails over the past 260 years

M Ziganira & CT Downs

Author contributions:

MZ conceived the paper with CTD. MZ collected and analysed data, and wrote the paper. CTD contributed valuable comments to the manuscript.

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Using natural history collections to determine the relative changes in diversity and distribution of freshwater molluscs in KwaZulu-Natal, South Africa

M Ziganira, JM Burnett, W Malherbe & CT Downs

Author contributions:

MZ conceived the paper with MJB and CTD. MZ collected and analysed data, and wrote the paper. WM donated NFSC data. MJB, WM and CTD contributed valuable comments to the manuscript.

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M Ziganira, JM Burnett, L Ngozi & CT Downs

Author contributions:

MZ conceived the paper with MJB and CTD. MZ and LN collected data. MZ analysed data, and wrote the paper. MJB, LN and CTD contributed valuable comments to the manuscript.

PUBLICATION 4 - not submitted

Updated checklist of freshwater molluscs to assess species diversity and distribution in freshwater ecosystems of KwaZulu-Natal, South Africa

M Ziganira, MJ Burnett & CT Downs

Author contributions:

MZ conceived the paper with MJB and CTD. MZ collected and analysed data, and wrote the paper. MJB and CTD contributed valuable comments to the manuscript.



Signed: ……

Matabaro Ziganira

November 2025

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DEDICATION

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CHAPTER 1

Introduction

1.1 Background

Freshwater ecosystems and their associated riparian habitats are amongst the most biologically diverse on Earth, and have inestimable economic, health, cultural, scientific and educational values (Wantzen et al., 2016; Albert et al., 2021; Vári et al., 2022). Studies have shown that freshwater ecosystems, such as rivers, lakes, and wetlands, and the organisms that inhabit them, provide essential ecosystem services (food and water) that support livelihoods (McClain, 2013; Kafumbata et al., 2014; Sayer et al., 2018; Danaher et al., 2022). Freshwater ecosystems also play a crucial role in preventing floods and droughts and are essential to human existence by transporting nutrients, providing health benefits, and offering recreational benefits (Dudgeon et al., 2006; Vörösmarty et al., 2010; Albert et al., 2021). Yet, the impact of human activities on lakes, rivers, streams, wetlands, and groundwater has accelerated changes in freshwater ecosystems over time (Böhm et al., 2020; Lopes-Lima et al., 2021). This is dramatically reducing freshwater biodiversity and depriving present and future generations of critical natural resources and services (Wantzen et al., 2016; Rodell et al., 2018; Vári et al., 2022).

Studies estimate that freshwater ecosystems are degrading more rapidly than terrestrial and marine ecosystems (Dudgeon et al., 2006; Darwall et al., 2011; Reid et al., 2019; van Klink et al., 2020). Africa is renowned for its diverse freshwater ecosystems (Masese et al., 2023). While many rivers in Africa are being dammed for hydropower and water supply for agricultural, forestry, and urban activities (McClain, 2013; O'Brien et al., 2021), lakes are being utilised for transportation, fishing, water supply, and cultural activities. Unfortunately, water withdrawal, pollution, invasive species, overfishing, and biomass harvesting around wetlands with human settlements cause threats to these ecosystems (Dalu and Wasserman, 2022).

As a whole, South Africa is not exempt from this trend, the rivers of KwaZulu-Natal are being impacted by various anthropogenic activities that threaten their sustainability (Agboola et al., 2020; Evans et al., 2022; Burnett et al., 2025), the leading causes of natural land cover loss and the ultimate decline in environmental functionality and connectivity in KwaZulu-Natal (Alexander et al., 2021).

1.2 Freshwater molluscs

Mollusca is the second largest phylum on Earth, comprising around 90,000 species, with up to 55,000 marine species, up to 30,000 terrestrial species and up to 7,000 freshwater species (Sousa, 2024; MolluscaBase, 2025). Molluscs are ubiquitous animals and can be found from the deep sea to the top of mountains, and they play a fundamental role in a wide range of ecosystem functions and services (Vaughn and Hoellein, 2018; de la Chesnais et al., 2019; Floyd et al., 2020; Sousa, 2024).

Molluscs are soft-bodied and unsegmented animals (Hodgson, 2018). Some of them have a body organised into a muscular foot, a head, a visceral mass containing most of the organ systems, and a fleshy mantle that secretes the calcareous shell (Hodgson, 2018). The phylum Mollusca comprises approximately 100,000 described species and potentially an additional 100,000 species yet to be described (Strong et al., 2008). The phylum is divided among seven classes and is present on every continent (Ruppert et al., 2004). Freshwater molluscs are classified into gastropods (snails and freshwater “limpets”) and several groups of bivalves (mussels and clams) that have repeatedly colonised freshwater (Brown, 1994; Hodgson, 2018). Gastropods have a univalve shell and possess a file-like radula used to feed on the periphyton covering rocks or plants (Brown, 1994; Hodgson, 2018). Mussels and clams have a hinged, bivalved shell and are generally suspension and/or deposit feeders (Brown, 1994; Hodgson, 2018). Freshwater molluscs are distributed globally, occurring on all

continents except Antarctica (Graf and Cummings, 2007; Strong et al., 2008; Cummings et al., 2016; Atkinson et al., 2023).

1.3 Significance of freshwater molluscs

Freshwater molluscs (bivalves and gastropods) are found in a wide range of freshwater ecosystems (Seddon et al., 2011), contribute to bioturbation and biofiltration in freshwater lotic and lentic environments (Bogan, 2008; Palmer et al., 1997; Covich et al., 1999). Also, freshwater molluscs play an important role in stabilising the food web by feeding on algae, bacteria, zooplankton, detritus, dissolved organic matter, diatoms and plants (Alzurfi et al., 2019), and some provide a source of protein and income to local communities (Köhler, 2012; Shivambu et al., 2020). Besides the ecosystem services, freshwater molluscs are constantly used as proxies in biodiversity research because of their wide range of distribution in freshwater habitats, varied life-history strategies and complex ecological interactions (Seddon et al., 2011); and important vectors of parasitic diseases (Chimbari et al., 1997; 2020; Chimbari, 2012; Kapour et al., 2024; Muzarabani et al., 2024).

However, freshwater ecosystems are under threat, and their biodiversity is declining in major global river basins (Vörösmarty et al., 2010; Turak et al., 2017; Böhm et al., 2020; Lopes-Lima et al., 2021; Ziganira and Downs, 2025). Freshwater molluscs are poorly documented, extremely threatened and have the highest number of recorded extinctions of any major taxonomic group (Vaughn and Taylor, 1999; Lydeard et al., 2004; Lopes-Lima et al., 2021)**.** The decline in freshwater molluscs goes unnoticed because of poor documentation and monitoring, as only a small fraction of molluscan species (<2%) have had their conservation status accurately assessed (Lydeard et al., 2004; Reckendorfer et al., 2006; Kemp et al., 2016; Lopes-Lima et al., 2021). It is therefore important to understand the crucial role of freshwater

molluscs in the functioning of freshwater ecosystems and the ecological services they provide (Atkinson et al., 2023).

1.3.1 Provisioning services

Humans have used molluscs as food and as tools for millennia (Atkinson et al., 2023). There is evidence that freshwater mussels were used extensively as food in prehistoric times worldwide (Parmalee and Klippel, 1974; Nicodemus, 2011; Garvey, 2017). In Southeast Asia, freshwater molluscs remain an important food source and a common commodity in markets (Zieritz et al., 2018; Dee et al., 2019). In Africa, several lakes support molluscivorous fish that rely on molluscs as their primary food source (Seddon et al., 2011). Freshwater molluscs native to South Africa are an essential food source for aquatic and terrestrial predators and are vital in maintaining ecosystem function (Brown and Lydeard, 2010).

In Chinese traditional medicine, freshwater molluscs such as *Corbicula fluminea* have long been used to treat liver disease and the effects of alcoholism (Bai et al., 2020).

Between the mid-1800s and the mid-1900s, the mollusc shell button industry was a lucrative business in North America (Coker et al., 1919; Haag, 2012). In 1912, a harvest of 50,000 tons of mussels was removed from rivers in North America, and the total value of buttons was approximately US $6 billion between 1897 and 1963 (Haag, 2012; Strayer, 2017). As tools, Native American tribes use freshwater mollusc shells in pottery (Rafferty and Peacock, 2008). In Japan and across Asia, beads from freshwater mussel shells are used as nuclei to produce cultured pearls in marine bivalves (Haag, 2012). Also, in many parts of the world, freshwater molluscs are used for making utensils and jewellery (Serrand and Cummings, 2014; Cummings et al., 2016).

1.3.2 Regulating services

Freshwater molluscs provide essential regulatory services, such as water purification, through their filter-feeding and grazing habits (Atkinson et al., 2023). For instance, mussels, through their filter-feeding, remove particles and associated nutrients from the water column, thereby improving water quality (Vaugh et al., 2008; Newton et al., 2011; Kreeger et al., 2018). Similarly, some groups of freshwater gastropods, such as Viviparidae and Bithynidae, are filter feeders, thereby improving water quality and removing toxic particles in freshwater ecosystems (Brown and Lydeard, 2010). Freshwater mussels also improve drinking water quality by filtering out pathogens and contaminants, such as coliform bacteria, pharmaceuticals, personal care products, and algal toxins, and sequestering these in their soft tissue and shell (Downing et al., 2014; Archambault, 2020; Hwang et al., 2021). Freshwater gastropods, through their grazing habit, can substantially reduce algal and biofilm biomass (Hill et al., 1992; Rosemond et al., 1993; Atkinson et al., 2023). The grazing patterns of freshwater gastropods can also control nuisance cyanobacteria and toxic algae in freshwater ecosystems (Zhang et al., 2012).

1.3.3 Supporting services

Freshwater molluscs play a crucial role in nutrient recycling, translocation, and storage (Atkinson et al., 2023). When freshwater molluscs filter-feed or graze, they convert energy and associated nutrients into their soft tissues, shells, and faeces, releasing bioavailable dissolved nutrients that support primary producers (Strayer, 2014; Atkinson and Vaughn, 2015). Nutrient storage by freshwater molluscs is potentially a valuable ecosystem service for nutrient abatement (Atkinson et al., 2023). Also, freshwater molluscs indirectly affect nutrient cycles by altering biogeochemical reactivity, microbial communities, and redox gradients (Atkinson et al., 2023).

Freshwater molluscs enhance denitrification and anaerobic ammonium oxidation (anammox) rates in benthic sediments because of their interactions with the benthic sediments and their high ammonia excretion (Hoellein et al., 2017; Trentman et al., 2018; Atkinson and Forshay, 2022). This process benefits water quality in freshwater ecosystems because denitrification permanently removes nitrogen from aquatic ecosystems (Atkinson et al., 2023).

Freshwater molluscs physically engineer aquatic ecosystems through their shell production and movement across and within the benthic substrate, thereby provisioning habitat for other organisms, such as algae, macroinvertebrates, and fish (Abbott and Bergey, 2007; Lukens et al., 2017; Hopper et al., 2019). For instance, high densities of freshwater mollusc shells in mussel beds increase the potential for strong hydrodynamic refugia and/or stabilise sediments (Mason and Sanders, 2021). It is also believed that the sturdy shell, gripping foot and mucus trails of freshwater gastropods might stabilise sediment (Atkinson et al., 2023).

As prey for other organisms, such as crayfish, fish, turtles and birds, freshwater molluscs have bottom-up effects on the food web (Atkinson and Vaughn, 2015). They are also food for humans and for small- to medium-sized mammals such as river otters (*Lutra* spp.) and muskrats (*Ondatra zibethicus*) (Cummings et al., 2016). Beyond the obvious direct habitat provisioning provided by the shell, molluscs can increase habitat availability through their grazing and bioturbation (Lukens et al., 2017). For example, filter-feeding freshwater bivalves can increase the photic zone in lakes and rivers, thereby enhancing benthic substrate organic matter and allowing colonisation by benthic macrophytes and aquatic insects (Strayer, 2020). The grazing pattern of the invasive snail *Pomacea canaliculata* can have strong top-down effects by reducing the biomass of aquatic plants, especially in shallow lakes with high nutrient loads, possibly leading to shifts from clear to turbid stable states (Gao et al., 2021; Liu et al., 2021). These state shifts can reduce light penetration in littoral zones and visibility for sight-feeding predators, with cascading effects on food webs (Liu et al., 2021).

1.3.4 Cultural services

Large and durable freshwater mussel shells are particularly important in pottery production by pottery-using hunter-gatherer communities in northern Europe (Bĕrzinš et al., 2014). In Africa, the Americas, and Asia, freshwater beads and other shell ornaments are widely used in rituals and ceremonies (Claassen, 2008; CTUIR, 2020). For example, the Winnebago tribe in Wisconsin, United States of America (USA), used shell beads in rituals and produced utensils and fishing hooks from shells, and used powdered shell to temper pottery (Kuhm, 2007). In the southern USA, freshwater mollusc shells are sometimes used to ornament graves (Haag, 2012).

In the USA, for example, the abundance of freshwater mussels in some places evokes a sense of place that is reflected in the names of river reaches (e.g., Muscle Shoals and Iˇsa´axuyi; Haag 2012; Hunn et al., 2015; Vaughn, 2018). Some live molluscs are kept as pets by humans and can be purchased in stores nationally and internationally through the aquarium and ornamental pet trade (Ng et al., 2016; Patoka et al., 2017). In some cases, this practice has led to the accidental introduction of alien freshwater molluscs into new ecosystems (Karatayev, et al., 2009).

Freshwater molluscs are also utilised in research and education to address various questions related to our understanding of ecosystem health and the biomonitoring of contaminants and pathogens in freshwater ecosystems (Mersch and Johansson, 1993; Giari et al., 2017). Eco-toxicological research has evaluated the sensitivities of freshwater molluscs to various contaminants, which have been used to assess water quality criteria (Augspurger, 2003; Wang et al., 2007). Educational outreach programmes for schools and ordinary citizens around the world have all benefited from the cultural services of freshwater molluscs, driven by people's desire to enjoy and preserve the natural environment for future generations.

1.4 Freshwater molluscs of medical importance

Some species of freshwater molluscs are highly invasive and can change the functioning of ecosystems, cause considerable damage to crops (e.g., some *Pomacea* species), spread diseases like schistosomiasis or liver flukes, are biofoulers that impact industry (e.g., zebra, quagga and golden mussels in the genera *Dreissena* and *Limnoperna*), or are detrimental to other wildlife (e.g., New Zealand mudsnails, *Potamopyrgus antipodarum* impacting trout) (Bequaert 1928; Strayer, 2010; Van Bocxlaer et al., 2014; Sousa et al., 2014; Cummings and Graf, 2015; Pyron and Brown, 2015). Freshwater molluscs are known to host a wide variety of parasites. Most digenetic trematode species, commonly referred to as flukes, appear to require a molluscan host to complete their life cycles and at least one, and possibly as many as three, additional hosts (Dillon, 2000).

Schistosomiasis is a significant public health concern in the tropics worldwide (WHO, 2016). Human schistosomiasis (bilharzia) is the second most important tropical parasitic disease after malaria and is ranked the most important waterborne disease (Steinmann et al., 2006; WHO, 2016). Over 700 million people in 78 countries worldwide are at risk of infection, especially in sub-Saharan Africa (WHO, 2016), where up to 90% of rural communities are affected (Bergquist et al., 2017). Schistosomiasis is also probably one of the most neglected diseases, as funding priorities were redirected to HIV/AIDS, malaria and other new viruses (Hotez et al., 2007; Utzinger et al., 2009). Therefore, it is crucial to continually monitor the diversity and distribution of freshwater molluscs in Africa, particularly in South Africa (Wolmarans et al., 2002; King, 2010; Adekiya et al., 2020).

1.5 Historical records of freshwater molluscs for KwaZulu-Natal

Significant advances have been made in freshwater Mollusca research in KwaZulu-Natal Province, South Africa (Brown, 1994). However, there are still knowledge gaps regarding

taxonomy, distribution, abundance, and population dynamics, as well as the application and effectiveness for conservation and decision-making. These shortfalls can be covered by analysing historical records in the natural history collections. Natural history collections have been utilised beyond their traditional taxonomic and systematic roles, generating data that inform present and future research (Hilton, 2021; Li et al., 2023). These collections and their associated data provide a foundation for present and future research addressing national and global relevance issues. Each unique specimen record contains information regarding the name of the organism and the collector(s), as well as the date and place of collection (Figure 1.1). These attributes make specimen records valuable for studying ecological changes over time (Shochat et al., 2006; Ward et al., 2015; Li et al., 2023; Alofs et al., 2025).

There are ca. 69 species of freshwater Mollusca occurring in KwaZulu-Natal, South Africa (Brown, 1967, 1994; Chapter 3). Freshwater molluscs' distribution is influenced by the availability of suitable aquatic biotopes, and depends on water quality (Dallas, 2007; De Kock and Wolmarans, 1998; Zeybek et al., 2012). The relationships amongst freshwater molluscs and biotopes such as marginal and aquatic vegetation and sediment are well documented (Brown, 1978, 1994; Dallas, 2007; Odume et al., 2015; Kemp et al., 2016). These biotopes are constantly under threat because of anthropogenic activities (Vaughn and Taylor, 1999; De Klerk et al., 2012; DWA, 2012; Kemp et al., 2016). In South Africa, nearly 71% of freshwater ecosystems are considered endangered or critically endangered because of anthropogenic activities (Nel et al., 2004; Kemp et al., 2016). In KwaZulu-Natal, rivers are being impacted by various anthropogenic activities that threaten their sustainability (Agboola et al., 2020; Evans et al., 2022; Burnett et al., 2025). In the South African context, water quality monitoring is conducted by measuring core variables, including system variables (phosphate, nitrate, and nitrite) and toxic substances (substances listed in the South African Water Quality Guidelines for Aquatic Ecosystems) (DWAF, 1996; Raphahlelo et al., 2022).



Family	Genus	Species	Species	Locality	Lat	Long
Ampullariidae	Pomacea	bridgesii	Pomacea bridgesii	Uvongo, Dooling's Fish farm	-30.835	30.393
Ampullariidae	Pomacea	bridgesii	Pomacea bridgesii	Shelly Beach, High-cliff fish farm	-30.800	30.414
Ampullariidae	Lanistes	ovum	Lanistes ovum	Ndumo Game Res., around Nyamithi	-26.888	32.275
Ampullariidae	Lanistes	ovum	Lanistes ovum	Ndumo Game Res.	-26.883	32.275
Ampullariidae	Lanistes	ovum	Lanistes ovum	Ndumo area	-26.870	32.217
Ampullariidae	Lanistes	ovum	Lanistes ovum	Ndumo Game Res.	-26.888	32.275
Ampullariidae	Lanistes	ovum	Lanistes ovum	Ndumo Game Res., Nyamithi Pan	-26.883	32.283
Ampullariidae	Lanistes	ovum	Lanistes ovum	Ndumo Game Res., Banzi Pan	-26.872	32.288
Ampullariidae	Lanistes	ovum	Lanistes ovum	Ndumo Game Res., Banzi Pan	-26.872	32.288
Ampullariidae	Lanistes	ovum	Lanistes ovum	Ndumo Game Res., Nyamathi Pan	-26.890	32.301
Ampullariidae	Lanistes	ovum	Lanistes ovum	Ndumo Game Res., Mahemane	-26.876	32.250
Bulinidae	Bulinus	tropicus	Bulinus tropicus	Utrecht, Balelesberg 'Skurwekoppie'	-27.516	30.225
Bulinidae	Bulinus	tropicus	Bulinus tropicus	Utrecht, Balelesberg	-27.533	30.223
Bulinidae	Bulinus	tropicus	Bulinus tropicus	Wakkerstroom area, Kromellenboog	-27.470	30.272
Bulinidae	Bulinus	tropicus	Bulinus tropicus	Wakkerstroom area, Engelbrechts Dr	-27.448	30.047
Bulinidae	Bulinus	tropicus	Bulinus tropicus	Utrecht	-27.666	30.316
Bulinidae	Bulinus	tropicus	Bulinus tropicus	Wakkerstroom area	-27.399	30.107
Bulinidae	Bulinus	tropicus	Bulinus tropicus	Mkomazi River, Lundy's Hill Store bri	-30.200	30.802
Bulinidae	Bulinus	tropicus	Bulinus tropicus	Sani Pass summit , near top police pc	-29.656	29.445
Bulinidae	Bulinus	tropicus	Bulinus tropicus	Himeville	-29.738	29.558
Bulinidae	Bulinus	tropicus	Bulinus tropicus	Pietermaritzburg area, Mpushini Rive	-29.696	30.442
Bulinidae	Bulinus	tropicus	Bulinus tropicus	Park Rynie area, Rocky Bay	-30.35	30.717
Bulinidae	Bulinus	tropicus	Bulinus tropicus	Ndumo Game Res., Nyamithi Pan	-26.883	32.283
Bulinidae	Bulinus	tropicus	Bulinus tropicus	Lotheni area, near base of Redi Pass	-29.418	29.504
Bulinidae	Bulinus	tropicus	Bulinus tropicus	Mkhuze Game Res.	-27.59846	32.30149
Bulinidae	Bulinus	tropicus	Bulinus tropicus	Pietermaritzburg, Pentrich area, Slan	-29.671	30.363
Bulinidae	Bulinus	tropicus	Bulinus tropicus	Cathedral Peak	-28.947	29.205

Figure 1.1: Workflow showing the procedures natural history collections follow to create a collection database: (a) Sampling of mollusc specimens in a river by hand-picking, or by kick-stir-sweep methodology according to the South African Scoring System 5 (SASS5) (Dickens and Graham, 2002), (b) Deposition of specimens that are preserved and identified ideally to the species level. Collection records reflect the fact that all specimens of the same species and sampling event are stored together as a single lot, and (c) Digitised collection records in a spreadsheet to allow data analyses.

Although freshwater mollusc surveys in South Africa and KwaZulu-Natal in particular are ongoing and well documented (Conolly, 1939; Mandahl-Barth, 1958, 1960; Kuiper, 1964; 1966; Van Eeden and Brown, 1966; Brown, 1967; Appleton, 1996; Herbert, 1998; FBIS, 2022), low diversity has been reported, suggesting a possible decline of species diversity. To reconstruct long-term changes in freshwater mollusc communities in KwaZulu-Natal, records from the Albany Museum in Makanda (AMM), East London Museum (ELM), KwaZulu-Natal

Museum (KZNM) and the National Freshwater Snail Collection (NFSC), South Africa, a university collection with extensive freshwater mollusc specimens were used in this study. The department of freshwater invertebrates at Albany Museum, Makanda (AMM) (Grahamstown), Eastern Cape, focuses on freshwater molluscs of Southern Africa (Cole, 2021). This collection benefited from the national surveys of the 1950s, which significantly contributed to its growth (Cole, 2021). The Malacology department at the East London Museum (ELM), East London, Eastern Cape Province, specialises in both molluscs of Eastern Cape Province and terrestrial molluscs of South Africa (Cole, 2021). The KwaZulu-Natal Museum in Pietermaritzburg, KZN, has the Mollusca collection ranked among the 15th-largest in the world, with the oldest dry shell dated to 1897 (Kilburn and Herbert, 1994; Ziganira, 2018; Cole, 2021). The National Freshwater Snail Collection (NFSC), South Africa, was initiated in the 1950s, and most specimens were collected between the 1960s and the 1980s by local health authorities and government staff of the former Mollusc Research Unit, housed at Potchefstroom University (now North-West University) (De Kock and Wolmarans, 2008; Hadfield, 2020).

1.6 River Eco-Status Monitoring Program (REMP)

The River Eco-Status Monitoring Program (REMP) evolved from the River Health Programme (RHP) in 2016, and is a component of the South African National Aquatic Ecosystem Health Monitoring Programme (NAEHMP) mandated by the Department of Water and Sanitation (Dallas et al. 2008, 2010; DWS 2016; Evans et al., 2022; Burnett et al., 2025). The purpose of REMP is to monitor the ecological conditions in river ecosystems, as reflected by the system drivers and biological responses (instream and riparian) (DWS, 2016). The REMP and RHP programme divides rivers in South Africa into nine water management areas (WMAs), categorised from A to X for national water resource management purposes (Kleynhans and

Louw, 2007; Meissner et al., 2016; Evans et al., 2022). In KwaZulu-Natal, the 16 major rivers are allocated to three of the nine WMAs, namely ‘U’, ‘V’ and ‘W’ (Evans et al., 2022).

In South Africa, the South African Scoring System (SASS) is commonly used in field settings for rapid bioassessment of water quality and the general condition of riverine ecosystems (Dallas and Day, 2004). Aquatic macroinvertebrates are usually used during SASS and have been the backbone of REMP (Dallas, 2000a; Dickens and Graham, 2002). The SASS is a scoring system based on macroinvertebrates, in which each macroinvertebrate taxon is assigned a sensitivity/tolerance score based on the water quality conditions it is known to tolerate (Dallas et al., 1995; Dallas, 1997). However, the SASS method was designed as a field-based monitoring system and does not permit higher resolution of the taxa assessed (Dallas et al. 1995), as the collected taxa are only identified to the family level. Additionally, the SASS 5 Score sheet lists only 11 families of freshwater molluscs (eight gastropods and three bivalves), whereas historical records have reported 16 families (11 gastropods and five bivalves). As a result, five freshwater mollusc families have been left out of the SASS 5 Score sheet, and using microscopic identification of collected molluscs through the SASS 5 method has not been evaluated. The field surveys of this study were conducted at 52 established REMP sites in the three WMAs of KwaZulu-Natal. The methodologies applied at each sampling site were SASS 5 and active search (hand-picking), and freshwater molluscs were monitored for two years (2024 – 2025).

1.7 Study area

The province of KwaZulu-Natal is the only region in South Africa that can truly be described as not being water-scarce under present or possible future climatic conditions (Rivers-Moore et al., 2007) and is the best place to study freshwater molluscs (Brown, 1967, 1994). KwaZulu-Natal is situated in the coastal region of eastern South Africa between latitudes 27° and 31°.

Bounded by the Drakensberg escarpment in the west and the Indian Ocean in the east, the ecological conditions at the northern and southern boundaries are similar to those in the neighbouring Mozambique and Eastern Cape Province, respectively (Brown, 1967; 1994). Maputaland–Pondoland–Albany, South Africa, has been identified as a biodiversity hotspot and centre for endemism (Hart et al., 2014; Parera et al., 2021). This hotspot covers the eastern coast of southern Africa and extends from Maputo in Mozambique to Gqeberha (Port Elizabeth) in the Eastern Cape Province of South Africa, and inland along the south-east of the Great Escarpment (Steenkamp et al., 2004; Parera et al., 2021). For this study, we selected freshwater mollusc taxa whose historical distribution overlapped with the REMP sites that manage the 16 major rivers in KwaZulu-Natal in three WMAs (Evans et al., 2022). The three WMAs are (1) from the Mvoti River catchment south to the uMzimkulu River catchment, which is managed under the WMA 'U' and makes up southern KwaZulu-Natal, (2) the Thukela River catchment is managed as the WMA 'V, and (3) from the Amatigulu River catchment north to the Usuthu River catchment makes up northern KwaZulu-Natal, is managed as the WMA'W' (Evans et al., 2022).

1.8 Problem statement

In South Africa, nearly 71% of freshwater ecosystems are considered as either endangered or critically endangered because of anthropogenic activities (Nel et al., 2004; Kemp et al., 2016). In KwaZulu-Natal, rivers are being impacted by various anthropogenic activities that threaten their sustainability (Agboola et al., 2020; Evans et al., 2022; Burnett et al., 2025). Previous work on freshwater Mollusca in South Africa, especially in KwaZulu-Natal, is well documented, including recent distribution range and taxonomic studies (Connolly, 1939; Mandahl-Barth, 1958, 1960; Kuiper, 1964, 1966; Van Eeden and Brown, 1966; Brown, 1967; Appleton, 1996; Herbert, 1998; Nwoko et al., 2022). Additionally, significant advances have

been made in all the main fields of freshwater Mollusca research, and research using natural history collections to track anthropogenic activities has recently been on the rise (Brown, 1994; Li et al., 2023).

Historically, ca. 69 freshwater mollusc species have been recorded for KwaZulu-Natal, supported by years of historical collection data (Brown, 1967; 1994). However, recent and ongoing surveys in KwaZulu-Natal (FBIS, 2022; Nwoko et al., 2022), have recorded fewer freshwater mollusc species than previously documented, suggesting a possible decline of mollusc diversity. While the importance of natural history collections for research is generally appreciated (Shultz et al., 2021), the use of museum collections to analyse the relative changes in diversity and distribution of freshwater molluscs over time in KwaZulu-Natal is lacking. Additionally, aquatic macroinvertebrates and other aquatic organisms, such as molluscs, are usually exposed to anthropogenic disturbance and are important agents in biomonitoring (Rosenberg and Resh, 1993; Mooraki et al. 2009). However, ever since REMP was established in the last decade, aquatic macroinvertebrates, including 11 mollusc families, have been used for biomonitoring of freshwater ecosystems in South Africa (DWS, 2016), while historical records have reported 16 families (Ziganira et al., 2026), and no higher resolution has been used to assess mollusc diversity at REMP sites in KwaZulu-Natal. Thus, updated information on the diversity of freshwater molluscs across major freshwater ecosystems of KwaZulu-Natal is needed to support conservation efforts and decision-making.

1.9 Aim and objectives

The overall aim of this study was to analyse past and present changes in the diversity and distribution of freshwater molluscs in KwaZulu-Natal, particularly at REMP sites. MolluscaBase was used for all taxonomic validation. Historical records from four natural history collections (Albany Museum in Makanda (AMM), East London Museum in East

London (ELM), KwaZulu-Natal Museum in Pietermaritzburg (KZNM), and National Freshwater Snail Collection of South Africa in Potchefstroom (NFSC) were analysed in order to determine the relative changes in diversity and distribution of freshwater molluscs of KwaZulu-Natal (Chapter 3). Validation of the results was conducted by comparing the historical data with online data repositories of the Freshwater Biodiversity Information System (FBIS) and the Global Biodiversity Information Facility (GBIF) to assess relative trends. Additionally, historical mollusc taxa were mapped to the nearest 10 km radius using GEOLocate Web Application tool (https://www.geo-locate.org/), based on their locality descriptions and coordinates, to match the REMP sites in KwaZulu-Natal. A total of 52 sites were surveyed. The sampling events were part of the River Eco-Monitoring Programme (REMP) surveys because the study specifically targeted those sites. Additionally, we sampled seasonally across two years (2024 – 2025, four samples) to account for annual and seasonal changes. The sampling sites belonged to the three water management areas 'U', V', 'W' (WMAs) of KwaZulu-Natal, and some of them overlapped with historical localities (Chapter 4). Freshwater mollusc specimens were collected using the kick-stir-sweep methodology as outlined in the South African Scoring System 5 (SASS 5), and hand picking during each sampling event (Chapter 4). The collected freshwater molluscs were identified to species level, and trends and relationships among species were analysed using different statistical and numerical methods. An up-to-date checklist of freshwater molluscs in KwaZulu-Natal was generated to support conservation efforts for freshwater ecosystems and to inform decision-making in the province.

To achieve the aim, the following objectives were established:

1. Document the significant progress in the study of African freshwater molluscs over the past 260 years of research on the African continent.

2. Analyse the information on specimen records provided by natural history collections to determine the relative changes in diversity and distribution of freshwater molluscs of KwaZulu-Natal.
3. Assess the diversity, composition and distribution of freshwater malacofauna in major freshwater ecosystems of KwaZulu-Natal in relation to water quality and whether they have changed with time.
4. Update and review of freshwater mollusc checklist to assess diversity and distribution across major freshwater ecosystems of KwaZulu-Natal.

1.10 Structure of the thesis

The main body of this thesis is organised as manuscripts prepared for publication in peer-reviewed journal articles. The first chapter (Chapter 1) is the Introduction, which provides the literature review of the concepts covered in this study. The next four chapters (Chapters 2, 3, 4, and 5) are empirical chapters, each addressing a specific objective. Each chapter is formatted according to the journal it is intended to be (or has been) submitted to. Because of this thesis format, a certain degree of repetition, especially in the methods section, was unavoidable. However, this is deemed of little concern, as this format allows the reader to read each chapter separately without losing the overall context of the thesis. Chapter 2 investigated the significant progress in the study of African freshwater snails over the past 260 years. Chapter 3 sourced data from natural history collections databases to determine the relative changes in diversity and distribution of freshwater molluscs in KwaZulu-Natal. Chapter 4 assessed the diversity, composition, and distribution of molluscan species across major freshwater ecosystems in KwaZulu-Natal, in relation to water quality and whether these patterns had changed over time. Chapter 5 updated and reviewed the checklist of freshwater molluscs to assess diversity and

distribution in freshwater ecosystems of KwaZulu-Natal. Finally, Chapter 6 provides the general discussion, findings, conclusions and management recommendations.

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CHAPTER 2

Significant progress in the study of African freshwater snails over the past 260 years

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Running header: A systematic review of African freshwater snail research

2.1 Abstract

Globally, freshwater ecosystems are threatened. Research progress concerning African freshwater snails was reviewed using a systematic review process. Since 1757, the number of publications produced has increased, particularly in the last decade. In the first 50 years (1757-1800), 0.1% of publications on freshwater snails in Africa were conducted, followed by 0% (1801-1850), 3.3% (1851-1900), 3.5% (1901-1950), and 48.7% (1951-2000). The last 23 years (2001-2024) exhibited a large increase (44.3%) in publications of the total conducted. Studies on freshwater snails varied in number across the ten major African water basins, with the majority of studies in the Nile (21.7%), followed by the Congo Basin (17.6%), and the Niger (12.4%). The Orange Basin and Lake Tanganyika also received a high number of studies (10.9%) and (7.2%), respectively. Most freshwater snail study objectives related to conservation and taxonomy (70%), followed by disease vector (20.5%), with genetics/genomic/DNA barcoding/eDNA receiving significant focus as well (5.2%). Studies focusing on geology and palaeontology (2.5%), followed by climate change (1.5%), and machine learning (0.4%). The modern phase in the study of African freshwater snails began in the early 20th century with the discovery of Bulinus truncatus and Biomphalaria alexandrina as intermediate hosts for the parasites that cause human schistosomiasis. African freshwater malacology has since then benefited from African and overseas malacologists based at universities and medical laboratories across Africa and overseas. In addition to taxonomic studies, there was a steady rise in contributions relating to ecology, disease vectors, palaeontology and genetics. These contributed knowledge on local endemism and speciation, invasive species, species origins and distribution across African water basins, as well as the spread of infectious diseases and impacts of climate change. In the last decade, there have been shifts in methods, including the application of DNA barcoding, genomics, environmental DNA, and, most recently, machine learning.

KEYWORDS: Africa; freshwater ecosystems; literature review; malacology; snails

2.2 Introduction

Africa is the second largest continent in the world, both in size (~ 30 million km^2) and population (1.4 billion inhabitants as of 2022) (Guttal, 2021; United Nations, 2019). The African continent hosts some of the largest freshwater ecosystems in the world, including the Nile, the longest river in the world, and the Congo River, the world's second-largest basin both in terms of drainage area and discharge to the Atlantic Ocean (Dai et al., 2009; Laraque et al., 2020; Papa et al., 2023). In terms of area and volume, Africa also has three of the ten largest freshwater lakes on Earth, including Lake Victoria, Lake Tanganyika and Lake Malawi (Hernegger et al., 2021).

The rivers and other surface water bodies in sub-Saharan Africa are often shared by two or more countries (Table 2.1). Drainage basins with more than five basin countries include Chad, Volta, Zambezi, Niger, Congo, and the Nile, which are of global significance for biodiversity and the carbon and nutrient cycles (Hastie et al., 2021; Lunt et al., 2019; Simaika et al., 2021; Figure 2.1). The African landscapes are also made of smaller water systems, such as streams, reservoirs, ponds and tanks, which provide drinking water and agricultural resources to rural populations (Gardelle et al., 2010).

Table 2.1: The ten largest surface water bodies in sub-Saharan Africa shared by two or more countries (IPCC, 2001).

Basin name	**Number of countries**	**Basin area (1000 km^2)**	**Basin countries**
Congo	9	3,720	Congo, Tanzania, Cameroon, Burundi, Rwanda, Zambia, DRC*, Central African Republic, Angola
Nile	11	3,031	Sudan, South Sudan, Ethiopia, Egypt, Uganda, Tanzania, Kenya, Rwanda, Burundi, DRC, Eritrea
Niger	9	2,200	Mali, Nigeria, Niger, Guinea, Cameroon, Burkina Faso, Benin, Cote d'Ivoire, Chad
Lake Chad	6	1,910	Chad, Niger, Central African Republic, Nigeria, Sudan, Cameroon
Zambezi	8	1,385	Zambia, Angola, Zimbabwe, Mozambique, Malawi, Botswana, Tanzania, Namibia
Orange	4	950	South Africa, Namibia, Botswana, Lesotho
Okavango	4	529	Botswana, Angola, Namibia, Zimbabwe
Limpopo	4	385	South Africa, Botswana, Mozambique, Zimbabwe
Volta	6	379	Burkina Faso, Chana, Togo, Cote d'Ivory, Benin, Mali
Senegal	4	353	Mali, Mauritania, Senegal, Guinea

*Democratic Republic of the Congo

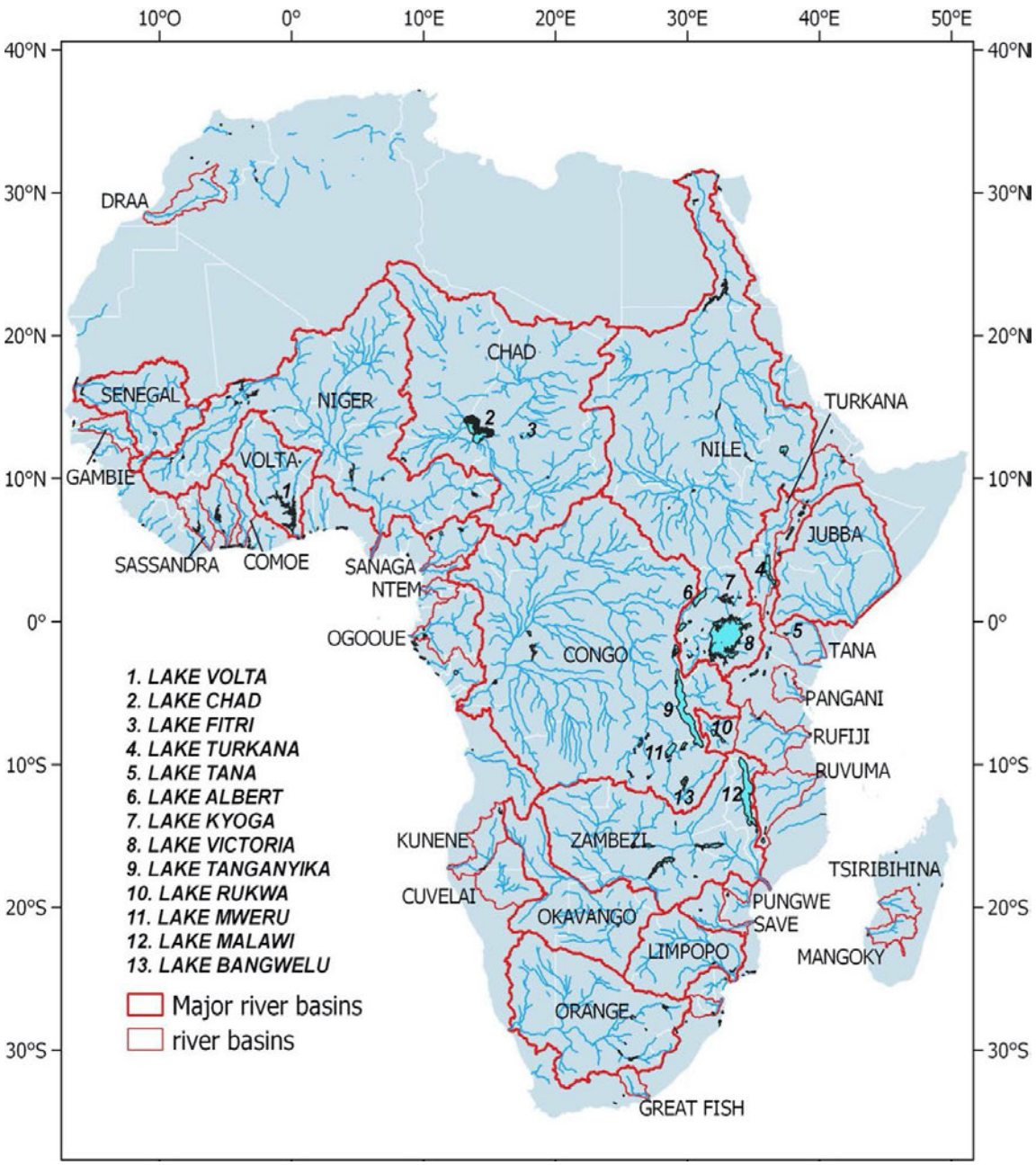


Figure 2.1: River basins and Lakes in Africa (Adapted from Papa et al., 2023).

The Afrotropical region encompasses a diverse range of ecosystems, characterised by varying degrees of species diversity (Davis et al., 1994; Klopper et al., 2002; Lindsey et al., 2022; Stuart et al., 1990). Biodiversity is not evenly distributed on Earth, and the Afrotropical region is no exception. Species distribution within ecosystems in the Afrotropical region is influenced by climate, soil type and topography and has been recorded as higher in lowland

equatorial rainforests (Aquilas et al., 2022; Stuart et al., 1990) than in other ecoregions/zones. In Africa, topography and rainfall affect species richness and abundance, with more species recorded in regions with a wide variety of ecosystems (Papa et al., 2023; Stuart et al., 1990; Tumwebaze et al., 2022; Figure 2.1). The Democratic Republic of the Congo (DRC), for instance, is probably regarded as the richest nation in Africa for biodiversity because of its extensive lowland rainforests, northern and southern savannahs, large areas of wetlands, lakes, and mountains (Aquilas, 2022; Stuart et al., 1990). While South Africa is considered the second richest country for biodiversity, mainly because of its unique rich flora of the Cape regions, other African countries with internationally important biodiversity include Cameroon, Kenya, Nigeria, Tanzania, Uganda and Madagascar (Aquilas, 2022; Griffiths et al., 2010; Skowno et al., 2019; Stuart et al., 1990).

Globally, freshwater ecosystems are under threat (Vörösmarty et al., 2010; Böhm et al., 2020; Lopes-Lima et al., 2021), and studies estimate a rapid degradation compared with terrestrial and marine ecosystems (Darwall et al., 2011; Dudgeon et al., 2006; Reid et al., 2019; van Klink et al., 2020). Africa is well known for its renowned freshwater ecosystems (Masese et al., 2023; Figure 2.1). While many rivers in Africa are being dammed for hydropower and water supply for agriculture, forestry, and urban activities (McClain, 2013; O'Brien et al., 2021), lakes are used for transportation, fishing, water supply, and cultural activities. Unfortunately, water withdrawal, pollution, invasive species, overfishing, and biomass harvesting around wetlands with human settlements cause threats to these ecosystems (Dalu and Wasserman, 2022).

Studies have shown that freshwater ecosystems such as rivers, lakes, and wetlands provide essential ecosystem services (food and water) that support livelihoods (Danaher et al., 2022; Kafumbata et al., 2014; McClain, 2013; Sayer et al., 2018). Freshwater ecosystems also play an important role in preventing floods or droughts, and are crucial to human existence by

transporting nutrients and providing health as well as recreational benefits (Albert et al., 2021; Dudgeon et al., 2006; Vörösmarty et al., 2010). Molluscs (bivalves and gastropods) are found in a wide range of freshwater ecosystems (Seddon et al., 2011), contribute to bioturbation and biofiltration in freshwater lotic and lentic environments (Bogan, 2008; Covich et al., 1999; Palmer et al., 1997). Also, molluscs play an important role in stabilising the food web by feeding on algae, bacteria, zooplankton, detritus, dissolved organic matter, diatoms and plants (Alzurfi et al., 2019), and some provide a source of protein and income to local communities (Köhler et al., 2012; Shivambu et al., 2020). Besides the ecosystem services, freshwater molluscs are constantly used as proxies in biodiversity research because of their wide range of distribution in freshwater habitats, varied life-history strategies and complex ecological interactions (Seddon et al., 2011); and important vectors of parasitic diseases (Chimbari et al., 1997; 2020; Chimbari, 2012; Kapour et al., 2024a,b; Muzarabani et al., 2024).

It is imperative to gain an understanding of mollusc species diversity and distribution, and to prevent snail-transmitted parasitic diseases in communities dependent on freshwater resources (Chingwena et al., 2004; EI-Gindy, 1957; Genner et al., 2007; Krings et al., 2021). In terms of molluscs, Lake Tanganyika belongs to the East African Great Lakes and is well known for harbouring a high proportion of endemic and morphologically distinct genera, and a natural laboratory to study speciation (Krings et al., 2021). Compared with Europe and North America, freshwater molluscs of Africa are less diverse, with an estimated 560 species, while North America and Europe have an estimated 880 and 780 species, respectively (Bogan, 2008; Seddon et al., 2011). It is estimated that freshwater molluscs in Africa are approximately represented by 75% gastropods and 25% bivalves (Seddon et al., 2011). Species diversity of freshwater molluscs in Africa varies with subregion, with the highest diversity recorded in the East African Great Lakes (Lake Victoria, Lake Tanganyika and Lake Malawi), the Upper Congo catchment around Lake Mweru, the river rapids regions of western Africa, and the

Lower Congo Rapids (Seddon et al., 2011). The regions of North-western Africa (the Maghreb), the East African coastal rivers, the Lower Nile River, the Lake Chad basin and the Malebo Pool in the Congo Basin are also considered important for freshwater mollusc biodiversity (Seddon et al., 2011).

However, like most other tropical regions, the freshwater snail diversity of Africa has drawn interest from both foreign and local scientists and collectors. Scientific study of African freshwater snails began nearly 260 years ago, with the arrival of European traders and explorers (Brown, 1994). Presently, significant advances have been made in all the main fields of research, including conservation, taxonomy, genetics, climate change, ecology, public health and more. Despite these, there are still gaps that need to be addressed, including (1) a lack of snail life history studies with regard to freshwater basin-connectivity on the continent; (2) a lack of categorisation of fields of study in publication records over the past four centuries. It could be suggested that research on freshwater snails is under-represented in some African regions and has been largely sidelined compared with terrestrial and marine molluscs. To date, little has been done to document the significant progress in the study of African freshwater snails over the past 260 years. The aim of this literature review was to assess the significant research progress in the study of African freshwater snail biology over the past four centuries. We believe that understanding the historical and present research efforts on freshwater snails across the continent is fundamental for addressing various challenges associated with biodiversity conservation, sustainable development and climate change.

2.3 Methods

2.3.1 Data collection

We conducted a literature search on research on freshwater snails in rivers, lakes, wetlands and ponds across Africa and its islands. We compiled data from international peer-reviewed

published journals and conference proceedings of freshwater snail research across all African countries. Because of the geopolitical reasons on the continent, not all literature was in English. Because of this, literature in French, Portuguese and Spanish were included (Ailly, 1896; Ancey, 1906; Azevedo et al., 1961; Bacci, 1951; Baluku et al., 1989; Barré et al., 1982; Binder, 1957; 1968; Bourguignat, 1885; 1886; 1889; 1890; Casaca and de Carvalho, 1955; Dupouy et al., 1980; Germain, 1908; 1920; 1923; 1925; Julvez et al., 1990; Kristensen, 1985; Leloup, 1953; Lévêque, 1967; Morais, 1975; Sellin et al., 1980). Editorials, letters, comments, and books were also included. Article titles were found using the Biodiversity Heritage Library, Google Scholar, Scopus and Web of Science ™ online search engine databases using the search phrase 'Freshwater snails in Africa' with the following keyword (*) basin name, ancient and new name of lakes, rivers, wetlands, snails, gastropod, bivalve, and individual country in Africa (new and ancient names). The search string used was not limited to publication date, ensuring all freshwater snail publications conducted in Africa were included, with the first being published in 1757 (Adanson, 1757). Publications were incorporated in the review if they represented malacology-based research focused on African water basins, including rivers, lakes, wetlands and ponds. We recorded the results for each publication in a Microsoft Excel© spreadsheet, and the data were refined/ sorted by year of publication.

2.3.2 Analyses of research focus on freshwater snails

To investigate the various interdisciplinary fields of study, we recorded and summarised a range of variables. These included the year of publication, the water basin or country in which the study was conducted and the fields of study. We used the year of publication of each study to assess temporal trends in research (Figure 2.2). The year of publication dates ranged from 1757 (18th century) to 2024 (21st century). Research publications were assessed in the ten

largest surface water basins in sub-Saharan Africa and their associated countries (Figure 2.3; Table 2.1).

To better understand knowledge gaps, we assessed each publication against six primary fields of study. Studies were grouped into a maximum of six primary fields of study, as some publications covered multiple aspects of biology, conservation, or ecology. The six primary fields of study identified were: 1. taxonomy and conservation (biodiversity, ecology-related studies). 2. geology and palaeontology (paleoecology, palaeogeography), 3. disease vector studies on parasitic infections such as schistosomiasis (bilharzia), *Hepatic distomatosis*, and *Paramphistomum daubneyi*. 4. climate change, 5. genetic/genomic and DNA barcoding/ eDNA, and 6. machine learning approaches (Figure 2.4).

2.3.3 Statistical analyses

We collated all these data and used descriptive statistics to show trends. We used regression analysis and percentages generated using Microsoft Excel© 2013 to show trends.

2.4 Results and discussion

2.4.1 Publications

Our literature research generated 791 publications from books, editorials and peer-reviewed journals (Supplementary information Table S2.1; Ziganira and Downs, 2024). Since 1757, the number of subsequent publications produced has increased rapidly, particularly in the last decade (Figure 2.1, Table 2.2). In the first 50 years (1757-1800), 0.1% of publications on freshwater snails in Africa were conducted, followed by 0% (1801-1850), 3.3% (1851-1900), 3.5% (1901-1950), and 48.8% (1951-2000). The last 23 years (2001-2024) exhibited a large increase in publications, with 44.3% of publications on freshwater snails of the total conducted in Africa during this time (Figure 2.2, Table 2.2).

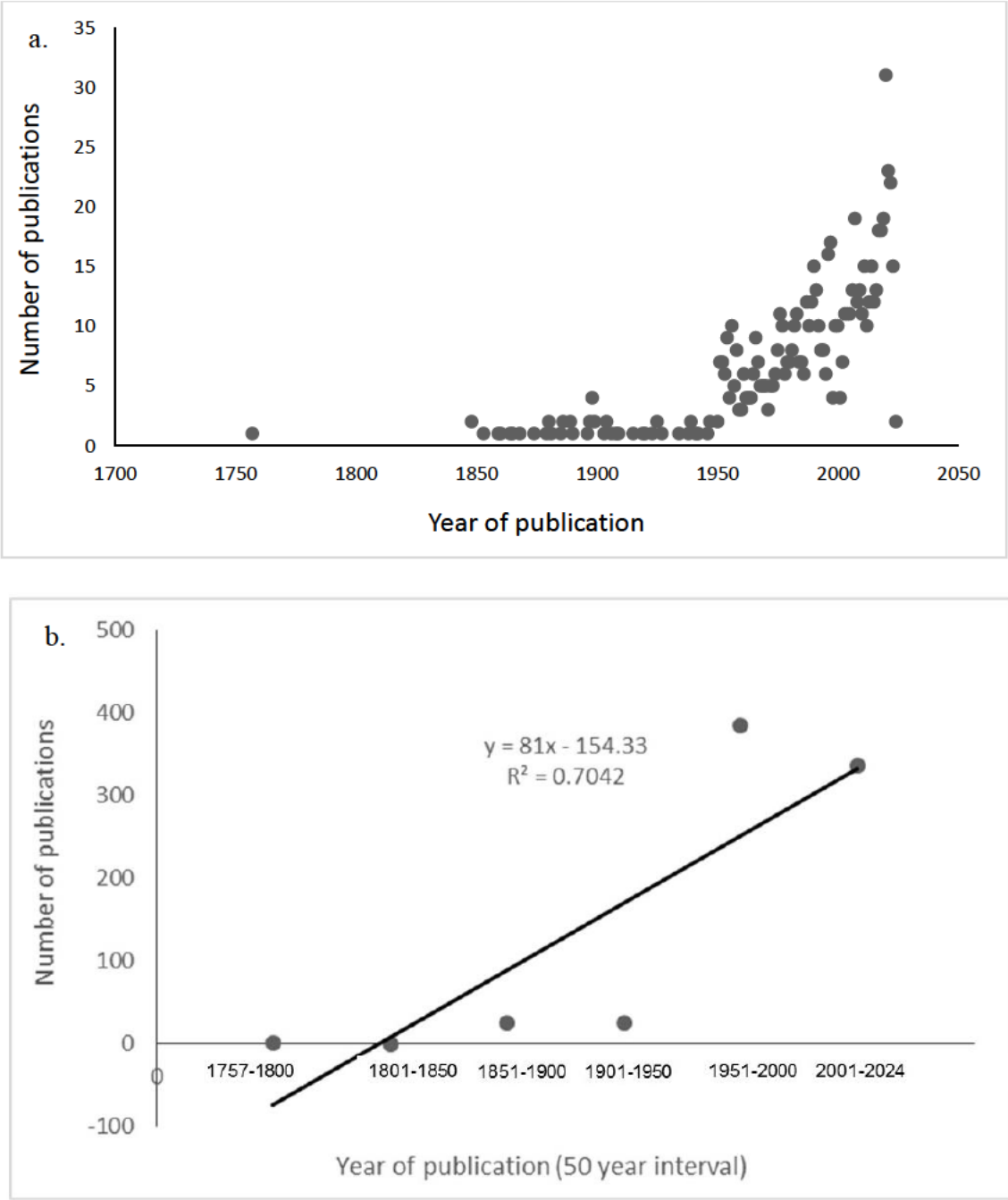


Figure 2.2: Number of published studies on freshwater snails conducted in Africa between 1757 and 2024. Data are grouped at 50-year intervals in both a. and b. The last 23 years (2001-2024), as shown in b. exhibited a large increase in publications, with 44.3% of publications on freshwater snails of the total conducted in Africa during this time.

Table 2.2: Total number of freshwater snail studies conducted in Africa for each field of study between 1757 and 2024, and also presented as a percentage of the total number of studies.

Year interval	Total number of studies conducted for each field of study	Percentage of total studies (%)
1757-1800	1	0.1
1801-1850	0	0
1851-1900	26	3.3
1901-1950	28	3.5
1951-2000	385	48.7
2001-2024	351	44.3

2.4.2 Distribution of research on freshwater snails in Africa

Studies on freshwater snails varied in number across major African water basins between 1757 and 2024, with several water basins displaying considerably higher numbers of freshwater snail publications than the rest. Out of the 54 African countries, studies on freshwater snails were conducted in seven major water basins (625/791, 79%), with studies (21%) occurring across multiple water basins and countries (Figure 2.3; Supplementary information Table S2.2, Ziganira and Downs, 2024). To determine the percentage contribution made by each African water basin, we treated each basin and associated countries (Table 2.1) listed in those publications. We found that 166 publications were shared with more than one basin or country, and were treated as separate. The result brought the total to 625 publications across all the African water basins. The majority of studies on freshwater snails in Africa were conducted in the Nile (136/625, 21.7%), followed by the Congo Basin (110/625, 17.6%), and the Niger

(78/625, 12.4%). The Orange Basin and Lake Tanganyika also produced a high number of studies (67/625, 10.7%) and (45/625, 7.2%), respectively. The number of studies on freshwater snails conducted across African water basins was disproportionate, with the top five water basins contributing 436 (69.7%) of the total studies of freshwater snails (Figure 2.3; Supplementary information Table S2.2, Ziganira and Downs, 2024).

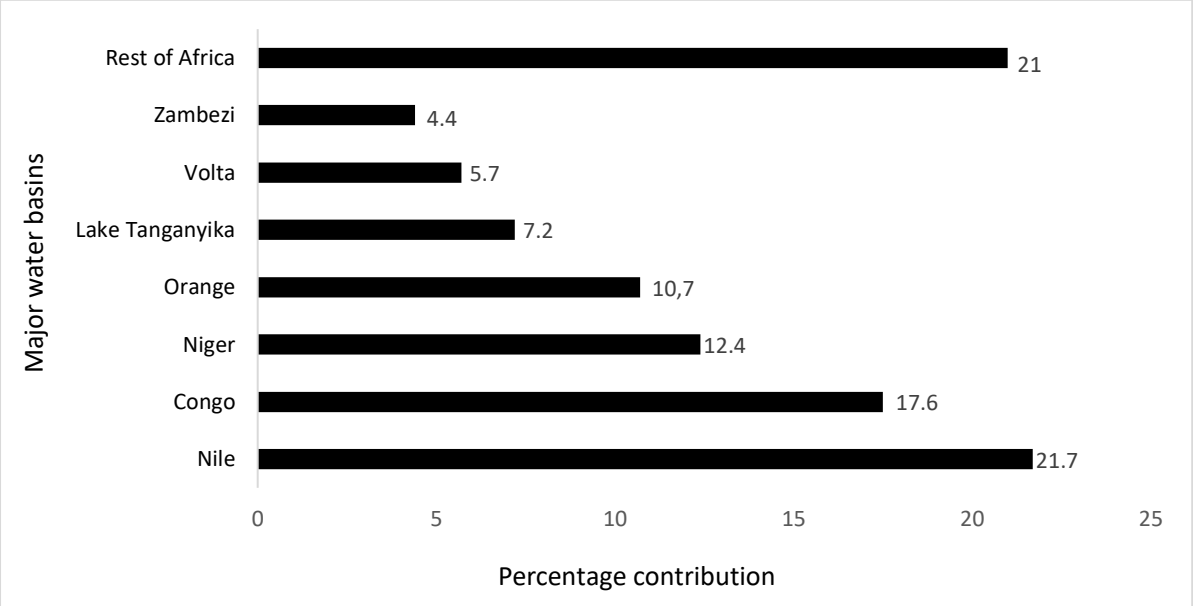


Figure 2.3: Percentage contribution of African major water basins showing published studies on freshwater snails conducted in Africa between 1757 and 2024 across African water basins.

2.4.3 Field of study focus

The majority of freshwater snail study objectives related to conservation and taxonomy (553/791, 70%), were followed by disease vector (162/791, 20.5%), with genetics/genomic/DNA barcoding/ environmental DNA receiving focus lately (41/791, 5.2%). Studies focusing on geology and palaeontology were (20/791, 2.5%), followed by climate change (12/791, 1.5%), and machine learning (3/791, 0.4%) (Figure 2.4; Supplementary information Table S2.3, Ziganira and Downs, 2024).

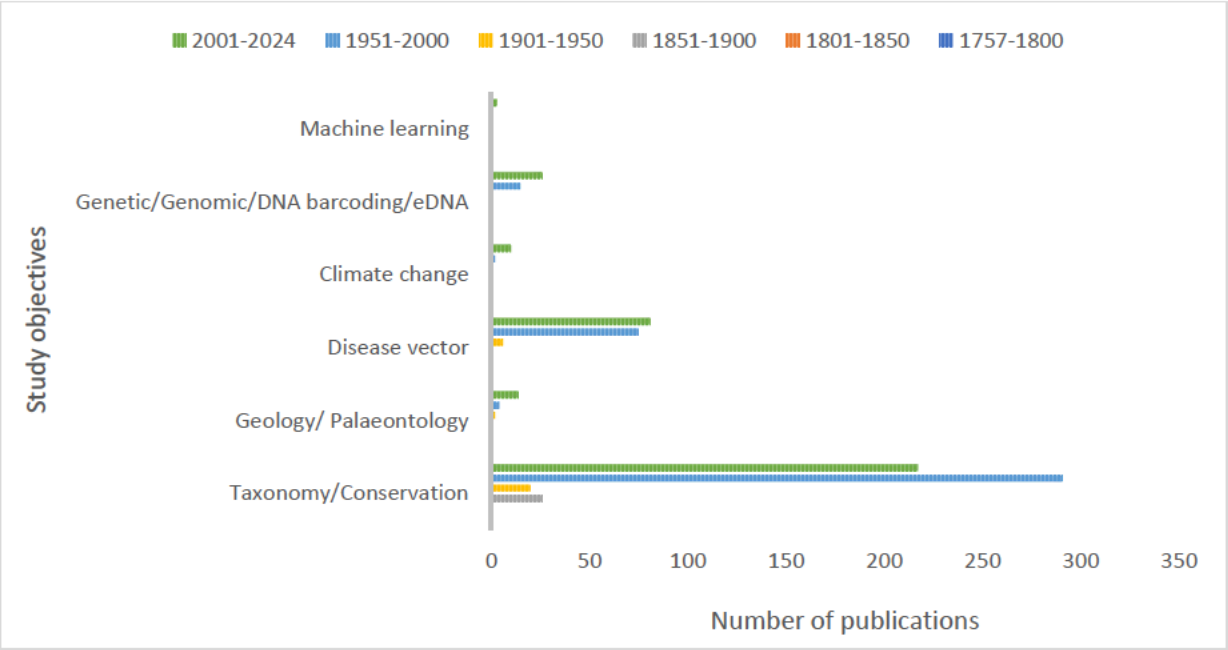


Figure 2.4: Total number of freshwater snail study objectives recorded across African water basins between 1757 and 2024.

2.4.4 Notable pioneer of the 18th century

The most notable pioneer in the study of plant and animal biodiversity in Africa in the 18th century was Michel Adanson, a French citizen from Aix-en-Provence, southern France (Carteret, 2012). At the end of 1748, Michel Adanson (1727-1806) was one of the most important naturalists of the eighteenth century. He left France for Senegal on an exploratory expedition as a botanist. He remained there for five years until 1753, moving from one trading post to another, collecting all kinds of biological specimens (plants and animals), including molluscs (Brown, 1994; Carteret, 2012; Paugy, 2010). Nearly 260 years ago (1757), the first study volume dedicated to molluscs was published, and his real contribution covered fifteen years of his work, from *Histoire naturelle du Sénégal* (published in 1757) to the *Cours d'histoire naturelle* (concerning zoology) which he taught between 1772 and 1774 (Carteret, 2012; Fischer-Piette, 1942). From freshwater snails, Adanson described shells, anatomy and habitats using a binomial nomenclature system one year before Linnaeus introduced his own

system (Brown, 1994). He was the first to describe '*Le Coret*' (*Afrogyrus coretus*, now *Hovorbis coretus*) and 'Le Bulin' (now *Bulinus senegalensis*), which became the type of the genus *Bulinus* (Brown, 1994). Later, the discovery in Egypt of the life cycle of *Schistosoma haematobium* would make *Bulinus* one of the most intensively studied snails in the world (Brown, 1994).

2.4.5 The rise of freshwater malacology in Africa in the 19th century

During the 19th century, some scientists did not share Adanson's interest in anatomy and conchology. As a result, many species were never named according to their shell differences, and important characteristics were left out (Brown, 1994). The political scramble for Africa can also be seen in the way in which authors in Britain, France, and Germany published their names for 'new shells' (Brown, 1980; 1994). Numerous species were rapidly named from shells which reached Europe in increasing numbers during the 19th century (Brown, 1980; 1994).

2.4.5.1 Southern Africa, especially South Africa

The publication of F. Krauss's "Die südafrikanischen Mollusken" in 1848, was the first major step to studying the molluscan fauna in South Africa (Kilburn, 1999). Towards the end of the 19th century, local interest increased when amateur malacologists such as W.H. Turton began collecting shells in the Eastern Cape and KwaZulu-Natal to send them overseas (Kilburn, 1999). The Deutsche Tiefsee-Expedition (1898–1899) and the Cape and Natal governments Expedition (1897-1901), led by Pieter Faure, were the first to scientifically sample molluscs in South Africa (Kilburn, 1999). Most of the South African materials were first studied by overseas malacologists in the 19th century, but that rapidly changed in the 20th century and beyond.

2.4.5.2 Central East-Africa, Lake Tanganyika

Lake Tanganyika is the second deepest lake in the world (maximum 1470 m, south basin), after Lake Baikal in Russia. Situated at an altitude of 773 m and an area of 32,900 km^2, Lake Tanganyika's varied shoreline has rocky outcrops and sandy beaches, swamps and estuaries (Brown, 1994). The lake and its surrounding rivers have attracted international expeditions and subsequent malacological descriptions since the 1850s (Smith, 1880a,b), and some unresolved controversy about the origin and evolution of the lake and its fauna are still being studied (Glaubrecht and Strong, 2004; 2007; Glaubrecht, 2008; Kring et al., 2021; Michel et al., 1992; Michel, 2000; Michel et al., 2003; West and Michel, 2000; Wilson et al., 2004).

The first scientific expeditions to study freshwater organisms in tropical Africa were sent by the Royal Society in 1858 and 1899 to Lake Tanganyika, partly to investigate the remarkable prosobranch snails (*Melania* (now *Lavigeria*) *nasa* and *Lithoglyohys* (now *Spekia*) *zonata* (Woodward, 1859)), collected by John Speke in 1858 (Brown, 1994). With a total of 60 species (Brown and Mandahl-Barth, 1987), Lake Tanganyika has been a remarkable freshwater ecosystem in which to study speciation (Krings et al., 2021). Lake Tanganyika also presents some of the most ancient scientific and non-scientific studies on freshwater snails of Africa, dating back to the 1880s (Ancey, 1906; Bourguignat, 1885, 1886, 1890; Germain, 1908; Hubendick, 1952; Hudleston, 1904; Moore, 1897, 1898a,b,c, 1899a,b, 1903; Pelseneer, 1886; Pilsbry and Bequaert, 1927; Smith, 1880a,b; 1881, 1889, 1904; Schwetz and Dartevelle, 1948; Yonge, 1938). Most of the studies of freshwater snails conducted on Lake Tanganyika covered various fields of study, including biodiversity, conservation, ecology and taxonomy (Table 2.2).

Table 2.3: Some of the most outstanding freshwater snail publications highlighting the contributions of the 18th and 19th centuries.

Author	Year	Field of study	Country/ Region
18th century			
M. Adanson	1757	Taxonomy	Senegal
19th century			
F. Krauss	1848	Taxonomy & Conservation	South Africa
G. Dunker	1853	Taxonomy & Conservation	Angola
S.P. Woodward	1859	Taxonomy & Conservation	Lake Tanganyika
E. Martens	1860	Taxonomy & Conservation	Mozambique
H. Dohrn	1864	Taxonomy & Conservation	Lake Victoria
H. Dohrn	1865	Taxonomy & Conservation	Lake Malawi
A. Morelet	1868	Taxonomy & Conservation	Angola
C.F. Jickeli	1874	Biodiversity	North-east Africa
E. Martens	1879	Taxonomy & Conservation	Mozambique
E.A. Smith	1880a,b	Taxonomy & Conservation	Lake Tanganyika
E.A. Smith	1881	Taxonomy & Conservation	Lake Tanganyika
M.J.R. Bourguignat	1885	Taxonomy & Conservation	Lake Tanganyika
M.J.R. Bourguignat	1886	Taxonomy & Conservation	Lake Tanganyika
P. Pelseneer	1886	Biodiversity	Lake Tanganyika
E.A. Smith	1889	Taxonomy & Conservation	Lake Tanganyika
M.J.R. Bourguignat	1889	Taxonomy & Conservation	North-east Africa and East Africa
M.J.R. Bourguignat	1890	Taxonomy & Conservation	Lake Tanganyika
A. d'Ailly	1896	Taxonomy & Conservation	Cameroon
E. Martens	1897	Taxonomy & Conservation	East Africa
J.E.S. Moore	1897	Biodiversity	Lake Tanganyika
J.E.S. Moore	1898a	Biodiversity	Lake Tanganyika
J.E.S. Moore	1898b	Taxonomy	Lake Tanganyika
J.E.S. Moore	1898c	Biodiversity	Lake Tanganyika
R. Sturany	1898	Taxonomy & Conservation	Southern Africa
J.E.S. Moore	1899a,b	Biodiversity	Lake Tanganyika

Our literature search in Google Scholar©, Web of Science©, Scopus© and the Biodiversity Heritage Library revealed that 26 studies were conducted between 1848 and 1899. These studies covered large regions of Africa, including southern Africa, Central Africa and North-East Africa, and the focus of these studies was on taxonomy, conservation and biodiversity (Table 2.3). Our literature search also found that many of the studies conducted in

the 19th century (15/26, 57.7%) were conducted in or around the Lake Tanganyika region. In terms of molluscs, Lake Tanganyika belongs to the East African Great Lakes and is well known for harbouring a high proportion of endemic and morphologically distinct genera and a natural laboratory to study speciation (Krings et al., 2021).

2.4.6 Modern phase: 20th century up to the end of the Second World War

The early 20th century in Africa was marked by the discovery that *Bulinus truncatus* (Audouin, 1827) and *Biomphalaria alexandrina* (Ehrenberg, 1831) are the intermediate hosts for the parasites that cause human schistosomiasis in Egypt (Brown, 1994; Leiper, 1915, 1918). This discovery led to the modern study of African freshwater snails (Brown, 1994; Table 2.4). Because of the high prevalence of tropical diseases such as malaria, health authorities on the continent were less preoccupied with human schistosomiasis. Nevertheless, two outstanding monographs were developed by amateur and professional malacologists describing the snails of the former Belgian Congo (now Democratic Republic of the Congo) (Pilsbry and Bequaert, 1927) and South Africa (Brown, 1994; Connolly, 1939). Only after the Second World War did research on human schistosomiasis increase through the support of the World Health Organisation (WHO) (Brown, 1994; Farooq, 1973). There was also an urgent need to improve freshwater snail taxonomy, and a 'Study Group' on the Identification and Classification of the Bilharzia Snail Vectors in Africa was established in Paris in 1954 (Brown, 1994). Through the financial support of the WHO and local national health authorities, African malacological research received a substantial boost, advancing the knowledge of many snail species beyond the medical and veterinary fields of study (Brown, 1994).

Table 2.4: Some of the most outstanding freshwater snail publications highlighting the contributions of the 20th century up to 1951.

Author	Year	Field of study	Country/ Region
J.E.S. Moore	1903	Biodiversity	Lake Tanganyika
E.A. Smith	1904	Taxonomy & Conservation	Lake Tanganyika
W.H. Hudleston	1904	Geology	Lake Tanganyika
C.F. Ancey	1906	Taxonomy & Conservation	Lake Tanganyika
L. Germain	1908	Taxonomy & Conservation	Central-north Africa, Lake Tanganyika
W. Kobelt	1909	Taxonomy & Conservation	North-east Africa
M. Connolly	1912	Taxonomy & Conservation	Southern Africa (first really comprehensive check-list
H.A. Pilsbry	1919	Taxonomy & Conservation	Belgian Congo (now D.R. Congo)
L. Germain	1920	Taxonomy & Conservation	East Africa
L. Germain	1923	Taxonomy & Conservation	East Africa
L. Germain	1925	Taxonomy & Conservation	Central and West Africa
M. Connolly	1925	Taxonomy & Conservation	Portuguese East Africa (now Mozambique)
H.A. Pilsbry & J. Bequaert	1927	Taxonomy & Conservation	Belgian Congo (now D.R. Congo)
M. Connolly	1930	Taxonomy & Conservation	South West Africa (now Namibia)
E. Degner	1934	Taxonomy & Conservation	West Africa
C.M. Yonge	1938	Conservation	Lake Tanganyika
M. Connolly	1939	Taxonomy & Conservation	Southern Africa
A. Mozley	1939	Ecology & Disease vector	Tanzania
J. Bequaert & W.J. Clench	1941	Taxonomy & Conservation	Belgian Congo (now D.R. Congo)
G. Bacci	1951	Taxonomy & Conservation	Abyssinia/Somalia (now Ethiopia and various states to the East)

2.4.7 Outstanding contributions of the 20th century post 1951

In the 1950s, there was a sudden increase in studying freshwater snails to primarily understand which snail species played intermediate hosts to several platyhelminth parasites of considerable significance to humans and livestock health (Brown, 1994; De Bont and De Bont Hers, 1952; Fain, 1951a,b; Gillet, 1950; LaGrange and Fain, 1952; Schwetz, 1950, 1951a,b; WHO, 1958). Over 200 million people in the world suffer from schistosomiasis, of whom about 80% live in

sub-Saharan Africa (Kokaliaris et al., 2022; WHO, 1958). Through the financial support of the WHO and local national health authorities, African malacological research received a substantial boost, which advanced the knowledge of many snail species beyond the medical or veterinary field of study (Brown, 1994). The initiative greatly boosted African freshwater malacology and left an everlasting legacy on the continent (WHO, 1958).

Human schistosomiasis (bilharzia) is the second most important tropical parasitic disease after malaria (WHO, 2016) and is ranked the most important water-borne disease (Steinmann et al., 2006). Over 700 million people in 78 countries worldwide are at risk of infection, especially in sub-Saharan Africa (WHO, 2016), where up to 90% of rural communities are affected (Bergquist et al., 2017). Schistosomiasis is also probably one of the most neglected diseases, as funding priorities were redirected to HIV/AIDS, malaria and other new viruses (Hotez et al., 2007; Utzinger et al., 2009). However, in the last decade, there has been a growing interest (King et al., 2020; Shiff, 2017; WHO, 2012), and studies on freshwater snails have remarkably advanced in all the main fields of study such as taxonomy, ecology, distribution, snail-borne parasitic infections and genetics (Brown, 1994; Khalloufi et al., 2017; Klopper et al., 2002; Miller et al., 2023; Mukaratirwa et al., 1996a,b,c; Ndassa et al., 2007a; Zein-Eddine et al., 2017). Presently, different ecological approaches, including DNA barcoding, environmental DNA and machine learning, are being used to control the distribution of intermediate host snails of schistosomiasis (Alzaylaee et al., 2020a,b; Lawton et al., 2018; Sato et al., 2018; Standley and Stothard, 2012; Tabo et al., 2022; Tabo et al., 2024; Tchakonte et al., 2023; Webster et al., 2013).

One of the most outstanding contributors in terms of African freshwater malacology during the past 70 years was David Brown, whose work covered the regions of North East Africa (Brown, 1965; Brown et al., 1984), West Africa (Brown, 1974; Brown and Kristensen, 1993; Supplementary information Table S2.1; Ziganira and Downs, 2024), southern Africa

(Brown, 1967; 1978; Brown and Kristensen, 1989; Brown et al., 1992), Lake Tanganyika (Brown and Mandahl-Barth, 1987; Supplementary information Table S2.4; Ziganira and Downs, 2024), and East Africa (Brown et al., 1981; Table 2.4). David Brown, in his *Freshwater Snails of Africa and their Medical Importance* (2 editions, 1980, revised 1994), provided an enormously valuable synthesis of a large body of work focusing on the taxonomy, biogeography, biology, ecology and, of course, parasitology of Africa's freshwater snail fauna. His stand-out contribution to African freshwater malacology has been significant in the last 70 years.

The other notable contributor to African freshwater malacology during the past 70 years was Georg Mandahl-Barth, who published extensively on African freshwater bivalves and also established the Danish Bilharziasis Laboratory (DBL), Copenhagen, in 1964 (Mandahl-Barth, 1988; Supplementary information Table S2.4; Ziganira and Downs, 2024). His work covered the regions of Central Africa (Mandahl-Barth, 1968; Mandahl-Barth et al., 1972; 1974), South East Africa (Mandahl-Barth, 1968; 1972), Lake Tanganyika (Brown and Mandahl-Barth, 1987), and East Africa (Mandahl-Barth, 1954). Other prominent role players who have contributed from a broader malacological rather than purely parasitological or medical perspective include Thomas Kristensen and Henry Madsen at the Danish Bilharziasis Laboratory (DBL), Copenhagen which has covered the regions of North East Africa (DBL, 1983; 1986; Madsen et al., 1988; Makura and Kristensen, 1991; Supplementary information Table S2.4; Ziganira and Downs, 2024), North West Africa (Kristensen, 1985), West Africa (Madsen et al., 1987), Central Africa (DBL, 1982), southern East Africa (DBL, 1977), and East Africa (DBL, 1987). Chris Wright of the Taxonomy Unit of the Natural History Museum, London (formerly the British Museum (Natural History)), researched the research regions of Central Africa (Wright, 1965) and southern Africa (Wright, 1963). Ferdinand Starmühlner of the Institut für Zoologie, Vienna, works focused on the Indian Ocean Islands (Starmühlner,

1969; 1976a,b; 1977; 1983; 2006). Dirk van Damme (University of Ghent, Belgium) has concentrated his research on Cenozoic fossils in the regions of North East Africa (Van Damme, 1984), North West Africa (Van Damme, 1984), and West Africa (Van Damme, 1984). In southern Africa, Chris Appleton was very active with his team in the Institute for Zoological Research, North West University, Potchefstroom, South Africa since the 1970's (Appleton, 1975; 1977a,b; 1984; Appleton and Stiles, 1976; Appleton and Bruton, 1979; Appleton et al., 1983; Appleton and Branch, 1989), and is still contributing to African freshwater malacology (Appleton and Miranda, 2015; Miranda et al., 2016). Christine Betterton of Bayero University in Kano, Nigeria, has extensively worked on *Bulinus* with regard to disease transmission in Nigeria, West Africa (Betterton et al., 1983; Betterton, 1984a,b; Betterton et al., 1988a,b; Ndifon et al., 1988). More recently, Ellinor Michel (Natural History Museum, London) and her colleagues (Nyanza Project, Kelly West and Jon Todd) have contributed much in relation to the Rift Valley Lakes, in particular Lake Tanganyika (Michel, 2000; Michel et al., 1992, 2003; West and Michel, 2000). The fields of biodiversity and conservation, as well as taxonomy, have received substantial attention in the last few decades (Table 2.2 and Table 2.3; Supplementary information Table S2.4; Ziganira and Downs, 2024).

2.4.8 Modern trends of the 21st century

Alongside conventional taxonomy, systematic, and biodiversity conservation studies, there has been a steady rise in the number of genetic and cytogenetic studies with phylogenetic or taxonomic applications for snail species in Africa. Since the 1970s, there has been a body of work using different, modern methods on molecular description and identification studies of *Bulinus* and *Biomphalaria* snails with regards to diseases transmission across Africa (Akinwale et al., 2011; Alharbi et al., 2022; Amarir et al., 2023; Burch et al., 1979; DeJong, 2003; Doums et al., 1996; Goll, 1981; Mimpfoundi and Greer, 1990a,b,c; Mudavanhu et al., 2024;

Mukaratirwa et al., 1996a,b,c; 2023; Njiokou et al., 1993; Pringle et al., 1971; Rollinson and Southgate, 1979; Standley et al., 2014).

2.4.8.1 African malacologists

In many countries in Africa today, there are staff trained in malacological research in universities and public health laboratories (Brown, 1994; De Kock et al., 1974; De Kock and Wolmarans, 2005a,b; 2006; 2007a,b; 2008; 2009; 2017; Ibikounlé et al., 2009; 2013; 2014a,b; Miranda and Perissinotto, 2014; Ndassa and Mimpfoundi, 2006; Wembo Ndeo et al., 2017, 2018, 2020). We can add a growing number of younger malacologists equipped with molecular skills who have already significantly contributed to our understanding of the taxonomy and phylogenetics of African freshwater molluscs, particularly gastropods. For example, Oscar Wembo Ndeo's research has focused on gastropods of Lake Tanganyika and Central Africa (Wembo Ndeo et al., 2017, 2018, 2020). Samson Mukaratirwa has focused on the control of snail disease vectors using molecular approaches, including modern tools such as environmental DNA in Zimbabwe and South Africa (Chingwena et al., 2004; Malatji et al., 2019; 2021; Mbereko et al., 2023; Mukaratirwa et al., 1996a,b,c; 2004; 2023). Aspire Mudavanhu is employing molecular approaches to investigate freshwater snail species and parasite diversity, as well as their interactions, in Zimbabwe (Mudavanhu et al., 2024; Schols et al., 2020). Others include Siméon Tchakonté, Arouna Ndassa and Remy Mimpfoundi, who have focussed on freshwater snails of the Central African region (Mimpfoundi et al., 1986; Mimpfoundi and Greer, 1990a,b,c; Ndassa and Mimpfoundi, 2006; Ndassa et al., 2007a,b; Tchakonté et al., 2023). Fred Chibwana's research has focused on the East African region (Chibwana et al., 2020; Tumwebaze et al., 2022). Maxwell Barson's research areas include taxonomy and ecology of freshwater aquatic animal parasites (Muzarabani et al., 2024; Schols et al., 2020, 2021). Moudachirou Ibikounlé has been contributing to the study of snails as

vectors of infectious diseases (Ibikounlé et al., 2009, 2013, 2014a, b). Nelson A.F. Miranda has extensively worked on invasive gastropods such as *Terebia granifera* in South Africa (Miranda et al., 2010; Miranda et al., 2011a,b; Miranda and Perissinotto, 2014). Similarly, Kenné de Kock's contribution has been on invasive freshwater snails and disease vectors (De Kock et al., 1974; 2003; 2004; De Kock and Wolmarans, 2005a,b; 2006; 2007a,b; 2008; 2009; 2017). Moses J. Chimbari's research has been on the biological control of snail vectors of schistosomiasis in Botswana and Zimbabwe (Chimbari, 2012; Chimbari et al., 1997, 2020; Chingwena et al., 2004; Mbereko et al., 2023). Our list cited above is not exhaustive, as there are many other African malacologists (professionals and students) based in Africa who are significantly contributing to the field in their respective countries and with collaborations on the continent and with overseas institutions (Supplementary information Table S2.4; Ziganira and Downs, 2024).

2.4.8.2 Collaborations with overseas malacologists

Some overseas laboratories have worked on African freshwater snails, and some African malacologists have been trained at these institutions. Kenneth A. Hayes and Robert H. Cowie have studied the evolutionary biology of apple snails (Ampullariidae), particularly in relation to their Gondwana origin (Hayes et al., 2009a,b). Randall Dejong has contributed from the molecular biology and disease vector (DeJong, 2003; DeJong et al., 2001; Morgan et al., 2002, 2003). Matthias Glaubrecht has been working on gastropods from Lake Tanganyika, West Africa, and Madagascar (Glaubrecht and Strong, 2004, 2007; Glaubrecht, 2008; Köhler and Glaubrecht, 2010; Krings et al., 2021; Wilson et al., 2004). Thomas K. Kristensen and Henry Madsen have been very active across all regions in Africa (Kristensen, 1985; Kristensen and Ogunnowo, 1987; Kristensen and Brown, 1999; Madsen, 1983, 1992; Madsen and Stauffer, 2011; Madsen et al., 1987, 1988, 2010). They have extensively collaborated with African

malacologists on a number of projects and participated in the training of many African students (Chimbari et al., 1997; Chingwena et al., 2002, 2004; Lange et al., 2013; Malatji et al., 2019; Mukaratirwa et al., 1996c; Nalugwa et al., 2011; Plam et al., 2008; Sengupta et al., 2009; Supplementary information Table S2.4; Ziganira and Downs, 2024). Ellinor Michel and her colleagues (Nyanza Project, Kelly West and Jon Todd) have contributed much about the Rift Valley Lakes, in particular, Lake Tanganyika (Michel et al., 1992, 2003; Michel, 2000; West and Michel, 2000; Supplementary information Table S2.4; Ziganira and Downs, 2024). Christian Albrecht has been very active in Central Africa and East Africa, while Roland Schultheiß, Thomas Wilke and Bert Van Bocxlaer have covered palaeontology and climate change aspects on freshwater snails in Africa (Albrecht et al., 2004; Catharina et al., 2022; Chibwana et al., 2020; Hayes et al., 2009b; Sands et al., 2022; Schultheiß et al., 2009, 2011; 2014; Tabo et al., 2022, 2024; Tumwebaze et al., 2022; Van Bocxlaer, 2005, 2020; Van Bocxlaer and Albrecht, 2015; Van Bocxlaer and Van Damme, 2009; Van Bocxlaer et al., 2008; 2011; 2012; 2015; 2020; Wembo et al., 2017; 2020; Supplementary information Table S2.4; Ziganira and Downs, 2024). Martin J. Genner and his team have worked on aspects of the evolutionary and invasive biology of gastropods of Lake Malawi (Genner and Michel, 2003; Genner et al., 2007, 2008). Tine Huyse and Ruben Schols have been working in collaboration with African researchers based in central, east and southern Africa (Brees et al., 2021; Kapour et al., 2024a,b; Maes et al., 2022; Mudavanhu et al., 2024; Muzarabani et al., 2024; Schols et al., 2020, 2021, 2023; van der Deure et al., 2024). It is also worth mentioning that this list is not exhaustive, and the degree of collaboration between these laboratories and universities in Africa and abroad has been a positive sign, indicating a mutually beneficial exchange of ideas.

2.4.8.3 Major shifts in methodology

The studies' foci on taxonomy, biodiversity and conservation, as well as disease vectors, have laid the foundation for malacology research in Africa. These interests are still growing except in the taxonomy field, which is concerning. The population of molluscan taxonomists worldwide is decreasing, and similar trends are observed in Africa (Bouchet et al., 2016). Presently, no academic programme is dedicated to training the next generation of taxonomists in Africa. With the old generation of taxonomists, either deceased or retired, capacity building still has a long way to go, as students publishing one or two papers from their dissertations is insufficient to build sustainable capacity in this field. Things could have been different if taxonomic research had received institutional support from academic institutions and funding agencies for baseline alpha taxonomy (Bouchet et al., 2016). However, genetics has been helping to close this gap. Molecular studies of African freshwater snails have been emphasised in the past years. Genetics has been used to describe attributes of a group of taxa, solve systematic or phylogenetic questions and assess the genetic variability of a species that could potentially transmit human diseases (Bouchet et al., 2016). Unfortunately, this is not a definitive solution because not all snail species have sequences in BOLD and/or GenBank (Bouchet et al., 2016). Presently, major shifts in methodology include the use of DNA barcoding on some medically important freshwater snail genera, which have revealed multiple invasion events (Lawton et al., 2018) or sub-lineages in various locations in Africa (Standley and Stothard, 2012; Webster et al., 2013). Other shifts in methodology include the use of environmental DNA (eDNA) (Alzaylaee et al., 2020a,b; Sato et al., 2018) and, most recently, machine learning approaches using artificial intelligence are being explored (Tabo et al., 2022; 2024; Tchakonte et al., 2023).

2.5 Conclusions

Our review of the literature on freshwater snails of Africa attempted to document the major progress that has shaped the malacological research on the continent. Starting in the 18th century in Senegal, overseas researchers initiated and developed African malacology. Later in the 20th century, local interest has continued to rise to this day. Taxonomy, biodiversity and conservation were important to set the foundation, and over time, disease vectors, ecology, and palaeontology were added. New aspects, such as climate change, were also investigated. The 21st century has witnessed the emergence of new methodologies, including genetics (DNA barcoding) and environmental DNA, as well as machine learning approaches. With the global decline of taxonomists, it is essential to stress that African malacology must evolve and adapt to this new technological era. New advances will depend mainly on new collections coming from little-explored areas, or armed conflict regions such as the Congo Basin, the Ethiopian Highlands and West Africa. The latest taxonomic updates, the updated International Union for Conservation of Nature (IUCN) status of important African freshwater snail species, and data availability and access would be important tools for future research. Additionally, development programmes, collaboration, and institutional support from academic institutions and funding agencies would be a big boost to the increased study of freshwater molluscs.

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Conflict of interest statement

The authors have no competing interests to declare.

Data availability statement

Data and Supplementary Information for this study are presented in the Supporting Information (https://onlinelibrary.wiley.com/doi/10.1002/ece3.71031) or Dryad (Ziganira and Downs 2024: https://doi.org/10.5061/dryad.cjsxksndq).

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CHAPTER 3

Using natural history collections to determine the relative changes in diversity and distribution of freshwater molluscs in KwaZulu-Natal, South Africa

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Running header: Using natural history collections to determine the relative changes in diversity and distribution of freshwater Mollusca

3.1 Abstract

Research using natural history collections to track anthropogenic activities has recently been on the rise. Natural history collections have been utilised beyond their traditional taxonomic and systematic roles, generating data that shape present and future research. We evaluated the value of natural history collections in answering questions about the changes in the occurrence of freshwater mollusc species in KwaZulu-Natal, South Africa, over the past 124 years. The historical records were sourced from four natural history collections databases in South Africa. Specimen records were curated and validated against two independent online platforms. The number of shells and diversity amongst collections were compared, and trends in the database were analysed. We recorded a significant decline in the number of specimens collected between 1897 and 1960, and after 1980 and 2021, respectively. The majority of freshwater mollusc specimens that were collected belonged to *Bulinus tropicus* (Krauss, 1848) (307 records), followed by *Pseudosuccinea columella* (Say, 1817) (270 records) and *Radix natalensis* (Krauss, 1848) (268 records), while 34% of specimens collected received one observation each. Three species database records exhibited positive observation trends, while two species showed negative database records trends. We also found that potentially declining species database records accounted for 52% of the total freshwater molluscs in KwaZulu-Natal. The broad-scale compositional shift of endemic species and the greater prevalence of invasive species may be exacerbated by inadequate sampling and a lack of long-term monitoring programs at selected sites. We argue that random sampling and donations are insufficient to sustain the growth of these collections. National programs, such as the River Eco-Status Monitoring Programme (REMP) and Freshwater Biodiversity Information System (FBIS), have the opportunity to identify and include new key biodiversity sites for biomonitoring of biodiversity. Thus, an increase in financial and skills investment is advocated to monitor biodiversity and the emergence of future diseases.

KEYWORDS*:* freshwater molluscs, freshwater ecosystems, natural history collections, temporal and spatial distribution

3.2 Introduction

Historically, natural history collections were made for entertainment, where collecting efforts were intimately linked to private cabinets of "curiosities", exhibiting the status of the wealthy members of society while allowing viewers to see artefacts and biota from distant places (Lintz 1991; Hooper-Greenhill 1992; Lane 1996; Hilton et al. 2021). Thereafter, during the Renaissance, the efforts to preserve natural history collections were to "teaching our youth to appreciate the wonderful works of the Creator" (Alexander 1979). Later, this education function evolved into a view of nature as an open book, where field surveys contributed to building natural history collections (Lane 1996; Hilton 2021). It was only in the 19th century that collections were used to advance ecological studies (Farrington 1915; Farber 1982; Lane 1996; Holmes et al. 2016; Watanabe 2019; Hilton 2021; Li et al. 2023). These collections and their associated data provide a foundation for present and future research addressing national and global relevance issues. Each unique specimen record contains information regarding the name of the organism and the collector(s), as well as the date and place of collection, when applicable. These attributes could make specimen records valuable for studying ecological changes over time (Shochat et al. 2006; Ward et al. 2015; Li et al. 2023; Alofs et al. 2025).

Using natural history collections to address faunal change over time is challenging, however, because of the different, often specialised collecting reasons driven by the interests of museum researchers and their institutions (Ward 2012; de Siracusa et al. 2020). As a result, certain taxa are omitted during collecting trips instead of collecting all species present, and new localities are preferred instead of sampling the same localities over time (Ward 2012; de Siracusa et al. 2020). Freshwater ecosystems and their associated riparian habitats are amongst

the most biologically diverse on Earth, and have inestimable economic, health, cultural, scientific and educational values (Wantzen et al. 2016; Albert et al. 2021; Vári et al. 2022), and the impact of human activities on lakes, rivers, streams, wetlands, and groundwater has accelerated changes in freshwater ecosystems over time (Böhm et al. 2020; Lopes-Lima et al. 2021).

These activities significantly reduce biodiversity and deprive present and future generations of access to resources (Wantzen et al. 2016; Rodell et al. 2018; Vári et al. 2022). Globally, freshwater biodiversity is declining in major river basins (Turak et al. 2017; Böhm et al. 2020; Lopes-Lima et al. 2021; Ziganira and Downs, 2025). As a whole, South Africa is not exempt from this trend, the rivers of KwaZulu-Natal are being impacted by various anthropogenic activities that threaten their sustainability (Agboola et al. 2020; Evans et al. 2022; Burnett et al. 2025), the leading causes of natural land cover loss and the ultimate decline in environmental functionality and connectivity in KwaZulu-Natal (Alexander et al. 2021).

While the importance of natural history collections for research is generally appreciated (Shultz et al. 2021), the use of a freshwater mollusc collection to analyse changes in diversity and distribution in South Africa, particularly in KwaZulu-Natal, is lacking. We hypothesised that there would be differences in both space and time, as well as in the number of records provided by natural history collections and online records. To reconstruct long-term changes in freshwater mollusc communities in KwaZulu-Natal, we compiled a database of records from the Albany Museum in Makanda (AMM), East London Museum in East London (ELM), KwaZulu-Natal Museum in Pietermaritzburg (KZNM) and the National Freshwater Snail Collection (NFSC) of South Africa in Potchefstroom, and validate the results by comparison with online data repositories Freshwater Biodiversity Information System (FBIS) and the Global Biodiversity Information Facility (GBIF) relative trends.

3.3 Methods

3.3.1 Database preparation

Our data were drawn from the Mollusca collection of the KwaZulu-Natal Museum (KZNM) in Pietermaritzburg, KwaZulu-Natal, South Africa. This collection is relatively old, and consists predominantly of dry shells, with the oldest dated 1897. This collection is ranked among the top 15 largest in the world, and the largest in both Africa and the Indian Ocean rim (Kilburn and Herbert 1994; Ziganira 2018; Cole 2021). We also relied on previously digitised and geocoded collection records of the National Freshwater Snail Collection (NFSC), South Africa, housed at North-West University in Potchefstroom, East London Museum in East London, Eastern Cape Province (ELM), and Albany Museum in Makanda, Eastern Cape Province (AMM), from their KwaZulu-Natal collections. Despite several emails to Iziko South African Museum in Cape Town (SAMC), our data requests to include their freshwater mollusc data in our study were not responded to.

3.3.2 Study location and species

The province of KwaZulu-Natal is situated in the coastal region of eastern South Africa between latitudes 27° and 31°. Bounded by the Drakensberg escarpment to the west and the Indian Ocean to the east, the ecological conditions at the northern and southern boundaries are similar to those in neighbouring Mozambique and the Eastern Cape Province, respectively (Brown 1967). There are ca. 69 species of freshwater Mollusca inhabiting the KwaZulu-Natal (Brown 1967, 1994). For our study, we selected freshwater mollusc species whose historical distribution overlapped with the present extent of KwaZulu-Natal using QGIS version 3.8.15 (Figure 3.1). Desirable candidate species records needed to have a taxon's full name (Genus and species), locality description, collection date and geographical location coordinates. We

filtered records based on the presence or absence of collection dates and coordinates, and used these for further analyses.

3.3.3 Data curation

We filtered our database records of freshwater Mollusca belonging to KwaZulu-Natal out of the four natural history collections. Although our database includes multiple sources of specimen acquisition, we focused on taxa for which specimens were identified to species level (Ewers-Saucedo et al. 2021; Li et al. 2023). This way, we minimised the problem of misidentifications. The database was refined and organised in Microsoft Excel® version 2013. To validate taxon identification, we relied on the dedication of data providers because digitised specimens required data entry from physical specimens and checked species identification if validation suggested discrepancies (Ewers-Saucedo et al. 2021). We attempted to provide geographic location coordinates for each record that lacked these coordinates but had a locality description. Records without geographical location coordinates were geocoded using GEOLocate Web Application tool (https://www.geo-locate.org/; Ziganira 2018). The NFSC data were geocoded using the Natural Science Collections Facility (NSCF) Georeferencer tool and standardised protocols from the Georeferencer tool (Engelbrecht 2021). Molluscs with no locality information or ambiguous distribution description were excluded. Several natural history records had outdated taxon names. We validated species names for all records using the 'MolluscaBase' (https://www.molluscabase.org/) to avoid discrepancies during data analyses.

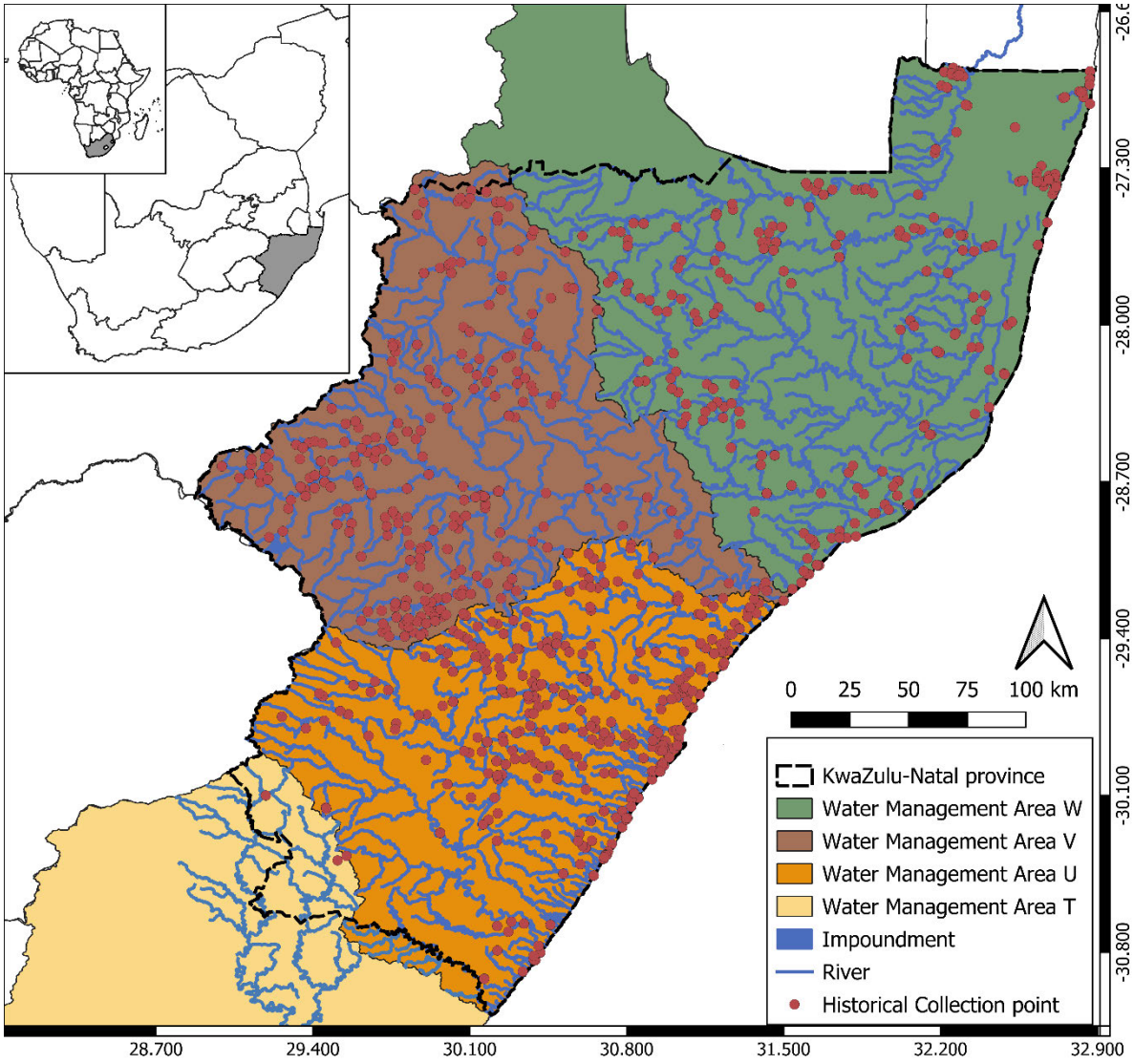


Figure 3.1: Map of KwaZulu-Natal, South Africa, showing spatial distribution of the investigated collection records.

3.3.4 Temporal and spatial analyses

We refined the data by excluding specimen records that lacked a collection date or locality information. This limited our study to specimens collected between 1897 and 2021. For temporal analyses, we used the collection date for each specimen to rank records obtained each year between 1897 and 2021, examining the trends in specimen records collection over time. To better understand long-term collection trends, we calculated the total number of records

based on a 10-year interval, as annual fluctuations can be challenging to interpret (Li et al. 2023). This allowed us to determine the number of species recorded sequentially through time (Muratov 2010; Table 3.1) between 1897 and 2021.

For spatial analyses, all records, regardless of whether they had geographical location coordinates, were used, regardless of the collection year. Map layers were created in QGIS (version 3.8.15), from selected records with geographical location coordinates. We explored the spatio-temporal trends of records by examining specimen distribution and density across 10-year periods, 1897-1906, 1907-1916, 1917-1926, 1927-1936, 1937-1946, 1947-1956, 1957-1966, 1967-1976, 1977-1986, 1987-1996, 1997-2006, 2007-2016, 2017-2021 (Table 3.1).

3.3.5 Database validation

To validate our data, we compared the species record numbers and distribution in our collection database with the species list in the Freshwater Biodiversity Information System (FBIS) for KwaZulu-Natal (FBIS 2022). The FBIS is a powerful, open-access platform for hosting, sharing, and analysing freshwater biodiversity data for South Africa (Dallas and Shelton 2024). These data records are harvested from the Global Biodiversity Information Facility (GBIF), peer-reviewed scientific papers, published reports, university theses, and unpublished reports (Dallas and Shelton 2024). Also, for all species records present in both the investigated database and the FBIS, we compared the number of species records between 1897 and 2021 over 10-year intervals.

3.3.6 Records of potentially declining species

A potentially declining species' database records approach allowed us to compare the distribution and frequency of each species' database records between historical and present dates (Appendix Table S3.1). Each species' database record was compared against the 10-year

interval to simplify collection periods. Potentially declining species are those that should have been collected more frequently in the past than in present times (Ewers-Saucedo et al. 2021). Furthermore, this mapping allowed us to validate our findings by comparing the species we identified as potentially declining with those listed as endangered in the Red List (https://www.iucnredlist.org/, Appendix Table S3.1), and their status was further analysed.

3.3.7 Relative records trends

We calculated the changes in the relative number of database records over time to estimate changes in occurrence and distribution. This approach is implemented in GBIF's 'relative observation trends' tool, which we adopted for our investigated data. We used the genus as the higher taxonomic unit to include all available records in our database, and tested for significant linear regression trends over time. Significant record trends were considered when the relative number of records changed significantly with regard to genus. Also, species with no geocode data in GBIF, or if existing data did not represent South Africa or cover KwaZulu-Natal, were excluded. These criteria also helped us identify which freshwater mollusc records from South Africa, particularly those from KwaZulu-Natal, are not yet geocoded or represented on GBIF (Appendix Table S3.1).

3.3.8 Introduced, non-invasive, invasive and endemic species

We also re-evaluated the status of freshwater molluscs in KwaZulu-Natal (Appleton 2003). The status of each species was examined and compared over time to determine whether species were endemic, invasive, non-invasive, or introduced (Appleton and Miranda 2015). We used both the dates of the first collection and the localities where alien species were found, and compared trends over time and whether the status has been reported in the province. We filtered

endemic species from the data, noting their collection dates and localities to determine if there was any correlation with invasive species presence.

3.3.9 Statistical analyses

We collated all these data and mainly used descriptive statistics to show trends. We also used One-Way Analysis of Variance (ANOVA), linear regression, and percentages generated using Microsoft Excel© 2013 to illustrate trends.

3.4 Results

3.4.1 Data curation

Initially, the freshwater Mollusca database of the KwaZulu-Natal Museum contained 957 records. We removed records that lacked locality information or contained ambiguous data. After filtering these, we found 607 records from KwaZulu-Natal. Specimen records with collection dates were 356 (59%), while those without dates were 251 (41%). Of the 607 records, many (n = 346; 57%) were not geocoded but contained a locality description. We matched these localities with those in the database that have geographical coordinates. Identical localities of 20 records were identified and matched. We geocoded the remaining 326 localities using the GEOLocate online portal (https://www.geo-locate.org/; Ziganira 2018).

We also received 1588 freshwater mollusc records for KwaZulu-Natal from the National Freshwater Snail Collection (NFSC), South Africa. Of these, 1260 records met our criteria and had dates of collection, locality and coordinates. From the East London Museum (ELM), we received 244 South African records, of which only five records of KwaZulu-Natal met our criteria. Similarly, 732 records were received from Albany Museum in Makhanda (AMM), of which 263 records met our criteria. We subsequently merged the four databases from these four institutions, and a total of 1884 records were selected and used in our analyses

(Table 3.1). Furthermore, all records received with coordinates were used for spatial visualisation (Figure 3.1).

3.4.2 Temporal and spatial analyses

The large-scale specimen collection and preservation for the 67 freshwater mollusc species appear to have been initiated between 1967 and 1976 (1047/1884, 56%). The lowest specimen collection and preservation appear to be between 1927 and 1946 (7/1884, 0.4%) (Table 3.1). The number of KwaZulu-Natal freshwater mollusc species found and deposited in the natural history collections reached a maximum between 2007 and 2016, while the number of families remained 16 between 1967 and 2021. After 1967 and 2016, no new family or new species were added to the collection (Table 3.1). The growth of the specimen's collection, the number of species collected and their associated families displayed an increasing trend from 1897 to 2007. Between 2007 and 2021, no new species or families were discovered through new samplings, maintaining the total of 67 species and 16 families, respectively (Table 3.1).

Overall, between 1897 and 2021, a total of 1,884 specimen records were deposited into the four collections, including collecting dates, coordinates, and locality information. *Bulinus tropicus* (Krauss 1848) recorded the highest (307/1884, 16%), followed by *Pseudosuccinea columella* (Say 1817) (270/1884, 14%), and *Radix natalensis* (Krauss 1848) (268/1884, 14%). A large proportion of the 67 freshwater mollusc species (14/67, 21%) received one record each (Table 3.1).

Table 3.1: Total number of collection and preservation records of freshwater mollusc species and families in the Albany Museum (AMM), East London Museum (ELM), KwaZulu-Natal Museum (KZNM), and the National Freshwater Snail Collection (NFSC), South Africa, collected between 1897 and 2021. In total, 1884 database records were collected from 16 families and 69 species. Number refers to the number of specimens.

Family	Taxa	1897-1906	1907-1916	1917-1926	1927-1936	1937-1946	1947-1956	1957-1966	1967-1976	1977-1986	1987-1996	1997-2006	2007-2016	2017-2021	Total	%
Planorbidae	*Afrogyrorbis natalensis*	1		6				13	14	1					35	1.86
Viviparidae	*Bellamya capillata*	1		2					3	1	1	3	2		13	0.69
Planorbidae	*Biomphalaria pfeifferi*	2	1	5				23	50	5	2	1			89	4.72
Mytilidae	*Brachidontes virgiliae*						1	1	3	1	3		1		10	0.53
Bulinidae	*Bulinus africanus*				2			15	1	1	1	2			22	1.17
Bulinidae	*Bulinus forskalii*	2	2	4				7	142	4	2	14			177	9.39
Bulinidae	*Bulinus globosus*	2						3	1	1	1	4			12	0.64
Bulinidae	*Bulinus natalensis*							5	42	4	1				52	2.76
Bulinidae	*Bulinus reticulatus*								1						1	0.05
Bulinidae	*Bulinus tropicus*			15				20	225	8	12	26		1	307	16.30
Burnupiidae	*Burnupia brunnea*								1						1	0.05
Burnupiidae	*Burnupia caffra*			4				1	18						23	1.22
Burnupiidae	*Burnupia capensis*						3	1	32						36	1.91
Burnupiidae	*Burnupia capensis natalensis*							1	7						8	0.42
Burnupiidae	*Burnupia farquhari*		1												1	0.05
Burnupiidae	*Burnupia gordonensis*		4	6					1	1					12	0.64
Burnupiidae	*Burnupia mooiensis*[*]						1								1	0.05
Burnupiidae	*Burnupia nana*		1	1				2							4	0.21

Burnupiidae	*Burnupia ponsonbyi*		1		1			2	1					5	0.27
Burnupiidae	*Burnupia stenochorias*								2	1	3			6	0.32
Burnupiidae	*Burnupia transvaalensis*							3			6			9	0.48
Iridinidae	*Chambardia wahlbergi*			1	1			1	1	1	3	3	1	12	0.64
Thiaridae	*Cleopatra ferruginea*							9				1		10	0.53
Unionidae	*Coelatura mossambicensis*								1					1	0.05
Cyrenidae	*Corbicula africana*			1				5	3	4	5		1	19	1.01
Cyrenidae	*Corbicula astartina*											1		1	0.05
Cyrenidae	*Corbicula fluminalis*									1		8	2	11	0.58
Sphaeriidae	*Euglesa costulosa*								10					10	0.53
Sphaeriidae	*Euglesa langleyana*							2	5					7	0.37
Sphaeriidae	*Euglesa ovampica*[*]								1					1	0.05
Sphaeriidae	*Euglesa viridaria*								6					6	0.32
Sphaeriidae	*Eupera ferruginea*			2										2	0.11
Lymnaeidae	*Galba truncatula*					1			7					8	0.42
Planorbidae	*Gyraulus andrussovi*		1	2										3	0.16
Planorbidae	*Gyraulus chinensis*												1	1	0.05
Planorbidae	*Gyraulus connollyi*							7	33	3		2		45	2.39
Planorbidae	*Gyraulus costulatus*		7	6				30	77	3	5	7		135	7.17
Planorbidae	*Hovorbis coretus*								1			1		2	0.11
Ampullariidae	*Lanistes ovum*							2		1	1	4	3	11	0.58
Planorbidae	*Lentorbis carringtoni*								1					1	0.05
Thiaridae	*Melanoides tuberculata*	4		6		2		8	9	3	6	37	2	77	4.09
Neritidae	*Neritina pulligera*							1		3		2		6	0.32
Planorbidae	*Pettancylus burnupi*		1	1					4					6	0.32
Planorbidae	*Pettancylus cawstoni*								1					1	0.05
Planorbidae	*Pettancylus connollyi*			4					1					5	0.27
Planorbidae	*Pettancylus fontinalis*			1										1	0.05
Planorbidae	*Pettancylus natalensis*			1										1	0.05

Physidae	*Physella acuta*						1	1	9	3	5	25			44	2.34
Planorbidae	*Planorbella duryi*											3			3	0.16
Ampullariidae	*Pomacea bridgesii*										2				2	0.11
Lymnaeidae	*Pseudosuccinea columella*						1	47	151	5	7	59			270	14.33
Lymnaeidae	*Radix natalensis*	1	1			1		39	171	7	6	41	1		268	14.23
Lymnaeidae	*Radix rubiginosa*												1		1	0.05
Planorbidae	*Segmentorbis angustus*								2						2	0.11
Planorbidae	*Segmentorbis kanisaensis*			2				1				1			4	0.21
Planorbidae	*Segmentorbis planodiscus*			1						1					2	0.11
Neritidae	*Septaria porcellana borbonica*														0	0.00
Neritidae	*Septaria tessellaria*												1		1	0.05
Sphaeriidae	*Sphaerium capense*							1	4			1			6	0.32
Sphaeriidae	*Sphaerium incomitatum*								2						2	0.11
Physidae	*Stenophysa marmorata*										4	5			9	0.48
Thiaridae	*Tarebia granifera*										5	4	6		15	0.80
Thiaridae	*Thiara amarula*			1	2			2			2	1			8	0.42
Tomichiidae	*Tomichia natalensis*								1						1	0.05
Tomichiidae	*Tomichia tristis*								1	2					3	0.16
Tomichiidae	*Tomichia ventricosa*						1	1							2	0.11
Unionidae	*Unio caffer*		5				6	3	1	1	8	1			25	1.33
Neritidae	*Vittina gagates*			3											3	0.16
Neritidae	*Vittina natalensis*								1						1	0.05
16 Families	69 species	13	25	75	6	1	17	258	1047	66	95	258	22	1	1884	100

Burnupia mooiensis and *Euglesa ovampica* were two species additions from the FBIS database, totalling our records to 69 species.

3.4.3 Database validation

When comparing the four natural history collections (AMM, ELM, KZNM, NFSC) with the Freshwater Biodiversity Information System (FBIS) for KwaZulu-Natal, the number of species and records did not match as expected (Figure 3.2). The FBIS database added two species to our list, namely *Burnupia mooiensis* (B. Walker, 1912) and *Euglesa ovampica* (Ancey, 1890), bringing the total to 69 freshwater molluscs. The ELM had the fewest freshwater mollusc species and records, while KZNM had the most species and NFSC had the most records (Figure 3.2). Our analysis showed no significant differences among the five groups ($p > 0.05$). The relatively low numbers of molluscan species and records in the FBIS database may be because many of the KZNM and NFSC collection records have not yet been shared either with GBIF or directly with FBIS.

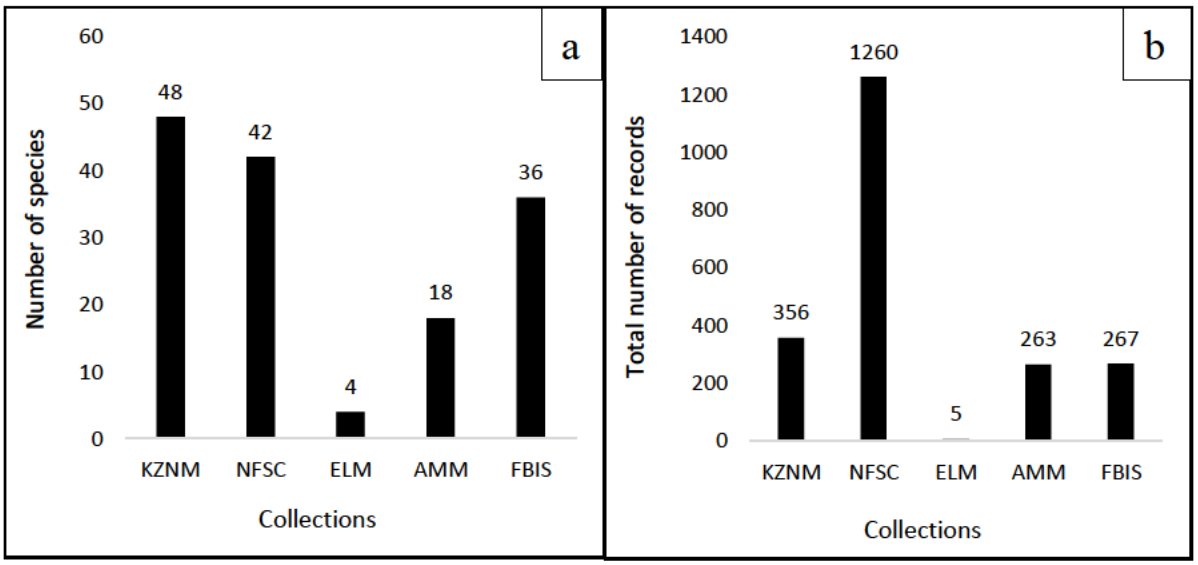


Figure 3.2: Number of (a) species and (b) number of records in the databases of the Albany Museum in Makanda (AMM), East London Museum (ELM), KwaZulu-Natal Museum (KZNM), National Freshwater Snail Collection (NFSC), South Africa and the Freshwater Biodiversity Information System (FBIS) for KwaZulu-Natal.

Specimens were unevenly collected and preserved at the KwaZulu-Natal Museum, both in terms of space and time. The oldest record, belonging to *Biophalaria pfeifferi* (Krauss 1848) (Planorbidae), was collected near Umbogintwini in 1897 by H.C. Burnup and donated to the museum in July 1926 (catalogue number: NMSA-Mol 003700). Few new specimens were collected, donated, purchased or deposited in the Mollusca collection of the KwaZulu-Natal Museum between 1917 and the 1960s, but these records provide temporal continuity in the data. From the 1950s to 2006, extensive freshwater mollusc samplings were observed in KwaZulu-Natal and across South Africa. Most of the sampling surveys were conducted by the National Freshwater Snail Collection team between the 1960s and 1980s, accounting for 67% of the specimen deposition used in this study (Figure 3.3; Appendix Table S3.1). Specimens were unevenly collected and stored both in time and space, showing positive efforts in recent years in the FBIS database for KwaZulu-Natal (Figure 3.3).

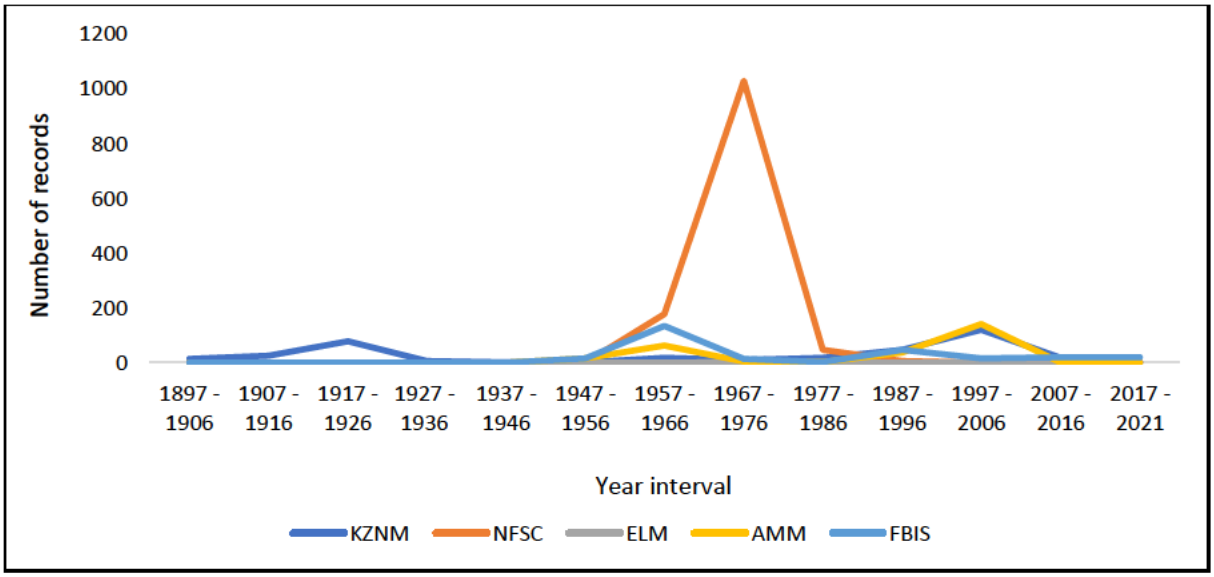


Figure 3.3: Number of freshwater mollusc database records over time in the Albany Museum in Makanda (AMM), East London Museum (ELM), KwaZulu-Natal Museum (KZNM), National Freshwater Snail Collection (NFSC), South Africa and the Freshwater Biodiversity Information System (FBIS) for KwaZulu-Natal. The year indicates the collection date.

3.4.4 Records of potentially declining species

We further analysed our data of the 67 freshwater mollusc species and noticed that 35 species (52%) were deposited less frequently than most records. These 35 species were considered 'potentially declining' among all the species investigated (Appendix Table S3.1). In our long list of species identified as potentially declining, only *Tomichia tristis* (Morelet 1889) (Tomichiidae) and *Tomichia natalensis* (Connolly 1939) (Tomichiidae) are considered Critically Endangered (CR) by the International Union for Conservation of Nature (IUCN) Red List Categories and Criteria (https://www.iucnredlist.org). Nevertheless, their IUCN status is presently unknown. Curiously, we also found that five species considered 'declining' (5/35, 14%): *Burnupia farquhari* (B. Walker 1912) (Burnupiidae), *Eupera ferruginea* (Krauss 1848) (Sphaeriidae), *Pettancylus fontinalis* (B. Walker 1912) (Planorbidae), *Pettancylus natalensis* (B. Walker 1924) (Planorbidae) and *Vittina gagates* (Lamarck 1822) (Neritidae), were deposited at one event in the early 1900s (1907-1926). Their relative number of observations declined over time, and after 1926, they were never deposited in a natural history collection. We also identified four 'declining' species as Data Deficient by the IUCN Red List Categories and Criteria, except *Eupera ferruginea* (Krauss 1848) (Sphaeriidae), which is considered Least Concern (LC) (Appendix Table S3.1, Ziganira et al. 2026). The proportion of all the 'potentially declining' species lots deposited between 1957 and 2006 was 46% (16/35), with many of them being endemic species collected or deposited only at one event.

The GBIF's relative observation trends tool yielded similar results for only one species (1/35, 3%), namely *Bulinus africanus* (Krauss 1848) (Bulinidae), and its relative number of observations declined over time. 'Stable' status in the proportion of GBIF observations confirmed our findings, except for *Vittina natalensis* (Reeve 1855) (Neritidae), which has only one deposition record (Appendix Table S3.1, Ziganira et al. 2026).

3.4.5 Relative records trends

Relative record trends were negative, positive or stable for 11 species. *Bulinus africanus* was the only species with negative GBIF observation trends; its IUCN Red List status is ‘Least Concern’, and its status is presently unknown. Three species had positive trends, and seven had stable trends. Contrary to our inferences, three species showed positive GBIF observation trends, with *Bulinus tropicus* (Krauss 1848) having the highest number of specimen records in our data and being the most frequently sampled species (Table 3.1; Figure 3.4c). The three species were considered Least Concern, *Melanoides tuberculata* (O. F. Müller 1774) had 'unknown' status in the IUCN Red List, while *Bulinus tropicus* (Krauss 1848) had stable status. Only *Tarebia granifera* (Lamarck 1816) was considered increasing by both the IUCN status and using the GBIF relative records tool (Figure 3.4).

Of the 35 freshwater mollusc species in KwaZulu-Natal, South Africa, identified as potentially declining, 31 species (89%) had neither geocoded data records nor South African data records on the GBIF relative observations tool between 1900 and 2021. Most of these species had few occurrences and deposition records in the investigated database (Appendix Table S3.1).

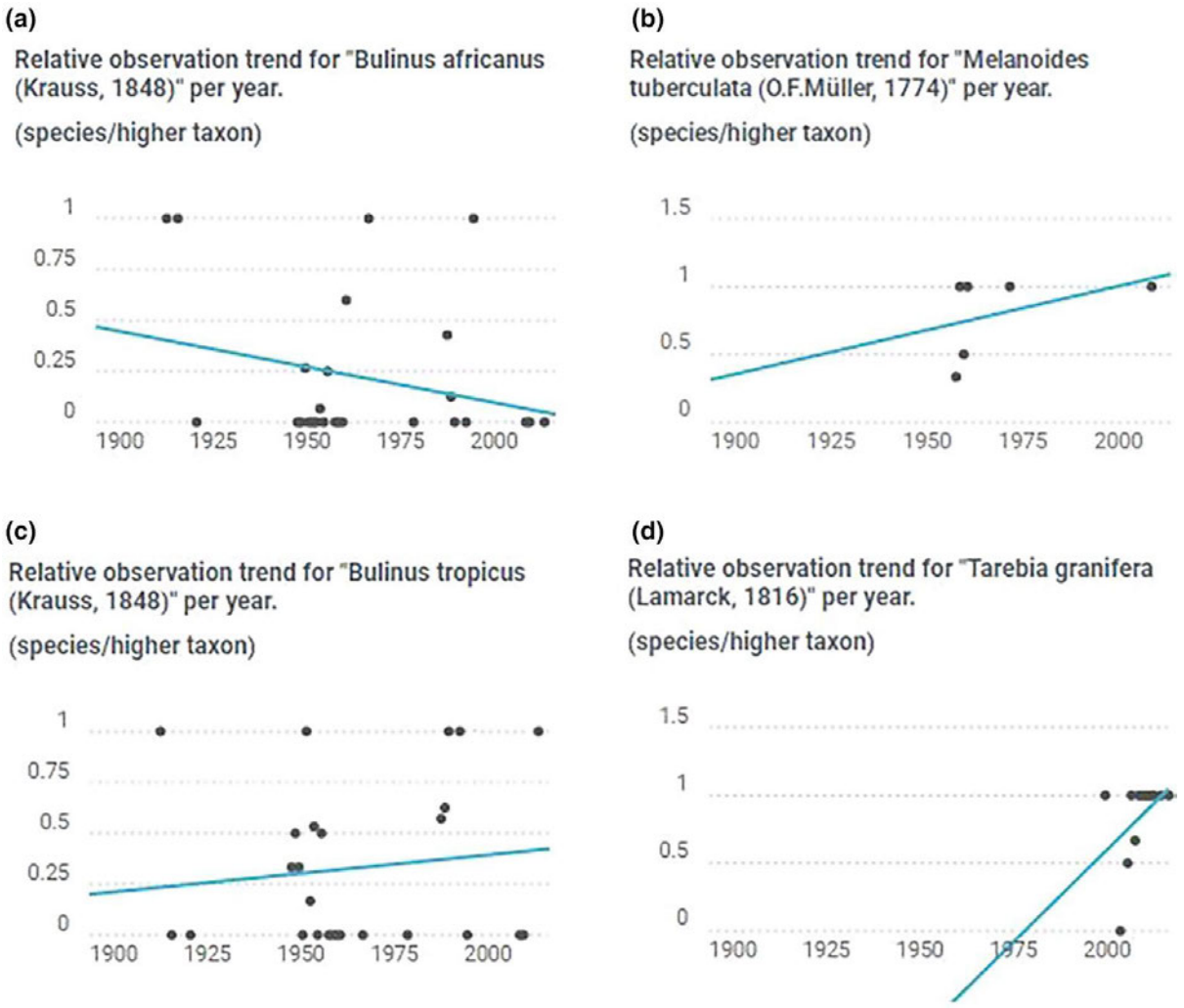


Figure 3.4: Regression slopes of freshwater mollusc species in KwaZulu-Natal, South Africa, that were significantly declining or increasing using the GBIF relative observations tool between 1900 and 2021, namely (a) *Bulinus africanus* (Krauss 1848), (b) *Melanoides tuberculata* (O.F. Muller 1774), (c) *Bulinus tropicus* (Krauss 1848), and (d) *Tarebia granifera* (Lamarck 1816).

3.4.6 Indigenous and endemic species

The South African freshwater mollusc endemicity is low and difficult to assess accurately because of discrepancies among some speciose genera (Herbert 1998; Appleton 2002). As expected, our record database showed a high number of endemic species. Besides *Ferrissia* (B. Walker 1903), now *Pettancylus* (Planorbidae), most of the freshwater molluscs native to

KwaZulu-Natal were represented in our database (Table 3.2). The IUCN Red List Categories and Criteria for most were listed as Data Deficient, and Critically Endangered for only *Tomichia natalensis* and *Tomichia tristis* (Appendix Table S3.1).

Table 3.2: The total number of endemic freshwater mollusc species and family records occurring in KwaZulu-Natal.

Family	Taxa	Author	References
Planorbidae	*Ancylus sp.*	(O.F. Müller 1773)	Appleton, 1996; Brown, 1967; 1994; Herbert, 1998
Burnupiidae	*Burnupia brunnea*	(B. Walker 1924)	Appleton, 1996; Brown, 1967; 1994; Herbert, 1998
Burnupiidae	*Burnupia caffra*	(Krauss 1848)	Appleton, 1996; Brown, 1967; 1994; Herbert, 1998
Burnupiidae	*Burnupia capensis*	(B. Walker 1912)	Appleton, 1996; Brown, 1967; 1994; Herbert, 1998
Burnupiidae	*Burnupia capensis natalensis*	(B. Walker 1924)	Appleton, 1996; Brown, 1967; 1994; Herbert, 1998
Burnupiidae	*Burnupia farquhari*	(B. Walker 1912)	Appleton, 1996; Brown, 1967; 1994; Herbert, 1998
Burnupiidae	*Burnupia gordonensis*	(Melvill and Ponsonby 1903)	Appleton, 1996; Brown, 1967; 1994; Herbert, 1998
Burnupiidae	*Burnupia nana*	(B. Walker 1912)	Appleton, 1996; Brown, 1967; 1994; Herbert, 1998
Burnupiidae	*Burnupia ponsonbyi*	(B. Walker 1924)	Appleton, 1996; Brown, 1967; 1994; Herbert, 1998
Burnupiidae	*Burnupia stenochorias*	(Melvill and Ponsonby 1903)	Appleton, 1996; Brown, 1967; 1994; Herbert, 1998
Burnupiidae	*Burnupia transvaalensis*	(Craven 1881)	Appleton, 1996; Brown, 1967; 1994; Herbert, 1998
Planorbidae	*Gyraulus connollyi*	(D.S. Brown and Van Eeden 1969)	Appleton, 1996; Brown, 1967; 1994; Herbert, 1998
Sphaeriidae	*Pisidium sp.*	(C. Pfeiffer 1821)	Appleton, 1996; Brown, 1967; 1994; Herbert, 1998
Planorbidae	*Segmentorbis angustus*	(Jickeli 1874)	Appleton, 1996; Brown, 1967; 1994; Herbert, 1998
Planorbidae	*Segmentorbis kanisaensis*	(Preston 1914)	Appleton, 1996; Brown, 1967; 1994; Herbert, 1998
Planorbidae	*Segmentorbis planodiscus*	(Melvill and Ponsonby 1897)	Appleton, 1996; Brown, 1967; 1994; Herbert, 1998
Tomichiidae	*Tomichia natalensis*	(Connolly 1939)	Appleton, 1996; Brown, 1967; 1994; Herbert, 1998
Tomichiidae	*Tomichia tristis*	(Morelet 1889)	Appleton, 1996; Brown, 1967; 1994; Herbert, 1998
Tomichiidae	*Tomichia ventricosa*	(Reeve 1842)	Appleton, 1996; Brown, 1967; 1994; Herbert, 1999
Unionidae	*Unio caffer*	(Krauss 1848)	Appleton, 1996; Brown, 1967; 1994; Herbert, 1998

Table 3.3: Updated list of introduced and invasive freshwater gastropod species found in KwaZulu-Natal, with their status in South Africa, year of first collection, earliest publication source, region of origin and year of deposition in the natural history collection.

Taxa	Status in South Africa	Year of first collection	Earliest published source	Region of origin	Year of deposition
Physella acuta	Invasive	1956	Van Bruggen (1966)	North and South America	1968 - 2021
Stenophysa marmorata	Invasive	1986	Appleton et al. (1989)	South America and some Caribbean Islands. First collected in Durban in 1986	1987 - 2006
Radix rubiginosa	Introduced, status unknown	2004	Appleton and Miranda (2015)	Southeast Asia	2007 - 2016
Gyraulus chinensis	Introduced, potentially invasive	2006	Appleton and Miranda (2015)	Southeast Asia	2007 - 2016
Pomacea diffusa	Introduced, not invasive	1980s	Appleton (2003) as *P. bridgesii*	South America	1996
Melanoides tuberculata	Indigenous but may be replaced by an invasive morph from Asia (Genner et al. 2004) or a hybrid	no data	Appleton and Miranda (2015)	Southeast Asia and northern Australia	1957 - 2021
Tarebia granifera	Invasive	1999	Appleton and Nadasan (2002)	Southeast Asia	1997 - 2021
Pseudosuccinea columella	Invasive	1942	Barnard (1948)	North America	1960 - 2006
Glyptophysa gibbosa	Unknown	1944	Barnard (1948) as Lenameria disar	Australia	Not in our database
Biomphalaria angulosa	Unknown	1957	Mandahl-Barth (1957)	East Africa	Not in our database
Planorbella spp.	Non-invasive	1960s	Van Bruggen (1974)	North America	Not in our database

Planorbella duryi	Non-invasive	1966	Brown (1967)	North America	1997 - 2006
Biomphalaria glabrata	Introduced	1969	Bruton & Merron (1985) as *Biomphalaria* spp.; Joubert et al. (1986) as *Biomphalaria cf. glabrata*	South America	Not in our database
Marisa cornuarietis	Non-invasive	1986	Van Aardt and De Kock (1991)	South America	Not in our database
Pomacea lineata	Non-invasive	no data	Appleton (2003)	South America	Not in our database

3.4.7 Introduced and non-invasive species

In South Africa, research on introduced freshwater molluscs has focused on the biology of species that have become invasive or shown potential to become invasive in the future (Appleton 2003; Weyl et al. 2020). Four freshwater mollusc species are presently considered introduced in KwaZulu-Natal (Appleton 2003; Appleton and Miranda 2015; Table 3.3). In our database, three introduced species were recorded, including *Radix rubiginosa* (Micholin 1831) (Lymnaeidae), *Gyraulus chinensis* (Dunker 1848) (Planorbidae), and *Pomacea brigessii* (Reeve 1856) (Ampullariidae) (Table 3.3). Interestingly, *R. rubiginosa* and *G. chinensis* were both collected in 2013 by Miranda in the Amatikulu River after they were introduced into South Africa in 2004 and 2006, respectively (Appleton and Miranda 2015). Four introduced species were confirmed non-invasive, and three of them did not occur in our database, including *Planorbella* (Haldeman 1843) species, *Marisa cornuarietis* (Linnaeus 1758) (Ampullariidae), and *Pomacea linnaei* (R.A. Philippi 1852) (Ampullariidae). Only *Planorbella duryi* (Wetherby 1879) (Planorbidae) is non-invasive in KwaZulu-Natal, and its records occurred in our database between 1997 and 2006 (Appleton 2003; Appleton and Miranda 2015; Table 3.3). Similarly, *Pomacea bridgesii* (Reeve 1856) (Ampullariidae) is originally from South America. Our data showed that this species was reported to be distributed on the south coast of KwaZulu-Natal in 1996. This species has not been reported in new localities, confirming its 'non-invasive' status in the province (Appleton 2003).

3.4.8 Invasive species

We identified 15 species, representing 22% of all investigated species, as non-native to South Africa or specifically KwaZulu-Natal (Appleton and Miranda 2015; Table 3.3). Of those, four species are known invasive species that were introduced into KwaZulu-Natal by people coming

from different parts of the world, including Asia, Australia, East Africa, and North, Central and South America (Appleton and Miranda 2015; Lawton et al. 2018). Of the four invasive species, only *Stenophysa marmorata* (Guilding 1828) (Physidae) had no data available using the GBIF observation trends tool, and its IUCN status is 'Least Concern', assessed in 2011. The IUCN status of the three invasive species, i.e., *Physella acuta*, *Pseudosuccinea columella*, and *Tarebia granifera* is 'Increasing' but 'Least Concern' according to the latest assessments of 2016, 2012, and 2010, respectively.

3.5 Discussion

Building on previous work (e.g., Sonamzi et al. 2019), our research demonstrated that evaluating the status and distribution of freshwater molluscs provides a valuable opportunity to utilise natural history collections and their associated data. By analysing the freshwater mollusc specimens deposited in the collection between 1897 and 2021, we discovered a significant inconsistency in the specimen samplings for the 69 freshwater mollusc species. A large proportion of specimen records prior to the 1950s lacked general information, including the year of collection and, in some cases, the collection location. However, relatively few specimen records lacked this information from 1950 onwards. Other studies using natural history collections have reported similar results. Ziganira (2018) reported that 80% of specimen records in the bivalve collection of the KwaZulu-Natal Museum were not geocoded. A study of mammal collections across museums in the United States of America (USA) found that 6% of 1.6 million specimens lacked a collection date, and 34% lacked geocodes (Malaney and Cook 2018). In our study, a few records were not geocoded, yet these data were still useful in our analysis.

Specimen deposition began in 1897, with a 7% increase between then and 1926. However, it then steeply declined by 99% in the 1930s, reaching its peak in the 1950s. This sharp increase corresponded with the establishment of the KwaZulu-Natal Museum in 1904, and specimens were acquired through donations, purchases, and field collections. The greatest increase in specimens occurred during the 1960s and 1970s, peaking at 77% of the total of 1,884 specimens (Table 3.1), before declining thereafter. Many specimens collected during this period were deposited at the National Freshwater Snail Collection of South Africa (NFSC) in Potchefstroom. A national survey of the freshwater Mollusca in South Africa was conducted between 1960 and 1980 by the Bilharzia Research Group of the Council for Scientific and Industrial Research, which was housed at North-West University, Potchefstroom, at the time (Brown 1967; Hadfield 2020). Some studies have shown similar trends. An analysis of 18 years since the establishment of the Mammal Collection at the Federal University of Espirito Santo (UFES-MAM) in Brazil found that specimen deposition into the collection increased when funds were available and decreased as funds were depleted, as well as being affected by strategic changes in policies (Bissoli-Silva et al. 2021). However, this study established that studies using natural history collections can provide a complete picture when all relevant collections are included (Sonamzi et al. 2019).

Additionally, the results of our study showed that the growth of the KwaZulu-Natal freshwater mollusc specimens for the 69 species and 16 families was optimal in 2007, and no new species have been collected since (Table 3.1). Spatially, few collection points were apparent outside the borders of KwaZulu-Natal, and were excluded through our curation and validation criteria. These points were geocoded only to refine the map references because locality descriptions of a river or a farm name were at a 1:50,000 map reference attached to them. These errors are common during the georeferencing protocol. Proper inspection and quality control are

essential to prevent such errors, and every record should be thoroughly double-checked. Interestingly, only one mollusc species *Septaria porcellana borbonica* (Bory de Saint-Vincent 1804), with only a few records in the KwaZulu-Natal Museum's database, had no collection dates. Yet, it was still important to add this species to our comprehensive list (Table 3.1).

We anticipated that FBIS would provide more data records than the four natural history collections investigated in this study. However, many species records collected before the 1940s, were not captured on the FBIS or GBIF. This lack of records in FBIS is because most of these records have not yet been uploaded to GBIF. Additionally, recent data deposition efforts, aimed at adding freshwater mollusc data to the FBIS data repository, are not yet complete (FBIS 2022). This suggests that incorporating the historical records compiled in this study would provide a more comprehensive picture of mollusc distribution and conservation in freshwater ecosystems throughout KwaZulu-Natal as well as South Africa as a whole. Nevertheless, duplicate information existed in specimen collections and deposition in the four natural history collections and FBIS databases between 1960 and 1980. We assume that FBIS benefited from the national freshwater survey conducted from 1960 to 1980, as specimen records were donated, in addition to receiving digitised records collected in peer-reviewed publications, published reports from the bilharzia project collection effort, and donations or university theses (Dallas and Shelton 2024). Two unique records from the FBIS database, *Burnupia mooiensis* and *Euglesa ovampica,* completed our list to 69 freshwater mollusc species known in KwaZulu-Natal.

The fact that several declining species identified in this study have not been recorded frequently in recent studies and ongoing surveys by FBIS, stresses the importance of continuing large-scale samplings and the deposition of specimens into natural history collections (Brown 1967; De Kock et al. 2004; De Kock and Wolmarans, 2005a, 2005b, 2005c, 2006a, 2006b, 2009;

Le Roux 2023). A study utilising natural history collections demonstrated that evolutionary processes revealed a decline in the population of 38 Central American amphibian species over time because of fungal infection (Holmes et al. 2016). We identified 16 declining species considered 'Data deficient' or 'No data', whose IUCN status was unknown. Additionally, *T. natalensis, T. tristis* and *T. ventricosa* were identified as declining species and are considered 'critically endangered', while *T. ventricosa* is considered ‘Endangered’ in South Africa by the IUCN Red List Category assessment of 2007. The present IUCN status of *T. natalensis, T. tristis* and *T. ventricosa* in South Africa is largely unknown (Appendix Table S1, Ziganira and Downs 2025). Similarly, a recent study on 242 epibenthic invertebrate species from the North and Baltic Seas, collected over the last 200 years, identified 18 species as declining and considered 'Endangered' or 'Extinct' by the German Red List (Ewers-Saucedo 2021). Their data, which utilises IUCN Red List categories and criteria for 1,428 freshwater molluscs, randomly indicates that one-third of the species are threatened with extinction (Böhm et al. 2020).

Our study assigned 20 freshwater mollusc species as endemic to KwaZulu-Natal. These species were represented by seven taxa from five families. Ten *Burnupia* species represented 50% of the endemic species, while three *Segmentorbis* species (*S. angustus, S. kanisaensis, S. planodiscus*) (15%) and three *Tomichia* species (*T. natalensis, T. tristis and T. ventricosa*) (15%) were also present. Except for *Segmentorbis* species (*S. angustus, S. kanisaensis, S. planodiscus*), which are presently considered as Least Concern by the IUCN Red List, *T. natalensis* and *T. tristis* are considered Critically Endangered by the IUCN Red List, while *T. ventricosa* is Endangered; their IUCN status is unknown, and their records were not available on GBIF observation trends. Much of the information on South African freshwater mollusc species is not available in GBIF trends, and their IUCN Red List status is unknown. Herbert (1998) suggested that further study for

both *Burnupia* species and *Pettancylus* species in relation to the possible existence of narrow-range endemics is urgently needed to understand the mollusc genetic variation among populations and taxa (Brown 1994; de Kock and Wolmarans 2017). Out of the 20 freshwater molluscs identified as endemic in our database, only three species are presently considered endemic gastropod taxa, including *G. connollyi* (Brown and van Eeden 1969), *Tomichia* species and possibly *S. planodiscus* (Melvill and Ponsonby 1897; Herbert 1998).

3.6 Limitations of collection data used

Museum collections provide a foundation for present and future research addressing national and global relevance issues. In consequence, any attempt to identify data that address changes in biodiversity and distribution of taxon-specific collections through voucher specimens is potentially compromised by uneven sampling in both space and time (Ewers-Saucedo et al. 2021). In our investigated database, temporally uneven sampling efforts were observed for the past 126 years, resulting in some species only occurring once. Although these species were referred to as records of potentially declining, inferences based on the presence–absence data could at times be erroneous because of limited sampling effort. In this study, catalogued museum specimens were used, with the assumption that they had been catalogued following a standardised protocol. In addition, when requesting the data, access to the specimens was limited; instead, metadata assigned to the specimens could be used. To avoid false inferences, we firstly excluded 'generic' genera and only used records with full taxonomic names at the species level. Secondly, given an understanding of South African freshwater biodiversity, our study region was chosen because of high freshwater mollusc species diversity in the province of KwaZulu-Natal in comparison to other provinces, both from an ecological or taxonomic perspective. Finally, MolluscaBase was used for all taxonomic

verification. We were aware of other limitations of historical data, which constrained the study's focus to an ecological perspective. The fact that these 126 years of records were collected by various people for various reasons and different research questions (if collected for research purposes), a two-year sampling could only be supplementary for future studies. Despite this, the historical data were summarised into known locality data to inform which species were reported in the province, where and when they were collected, how many specimens were collected, and where they are presently kept.

3.7 Conclusions

Our study reports a decline in freshwater Mollusca specimen collection and deposition, possibly because of decreased financial investment in natural history fieldwork and a decline in taxonomic capacity. We also report that potentially declining species accounted for 52% of the total freshwater mollusc diversity in KwaZulu-Natal, which is a concerning finding. Further constraints and limitations on regular sampling could severely impede future research, management, and conservation plans, as random sampling and donations alone are insufficient. This emphasises the importance of the invaluable efforts of the FBIS and the need for substantial financial support locally and nationally. Future collections should focus on new sites that have not been previously sampled, allowing for a better understanding of the population dynamics of certain taxa. Our study also highlighted another problem: recent studies on freshwater molluscs in KwaZulu-Natal have not donated voucher specimens and their data to the natural history collections. We therefore advocate that public engagement and raising awareness about the existence of these collections should be considered, so that collaboration between the general public and research institutions can increase. In addition, increasing financial and skills investment in natural history collections would facilitate wider geographical and temporal sampling, taxonomic updates, as well as data

mobilisation and sharing. This is crucial for national programs, such as the River Eco-Status Monitoring Programme (REMP) and the Freshwater Biodiversity Information System (FBIS), which aim to identify and include new key biodiversity sites for biomonitoring biodiversity and emerging diseases of medicinal importance.

3.8 Acknowledgements

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Conflicts of interest

The authors declare that they have no conflicts of interest.

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3.10 Appendix

Appendix Table S3.1. Combined total number of collection and preservation records of freshwater mollusc species and families in the Albany Museum (AMM), East London Museum (ELM), KwaZulu-Natal Museum (KZNM) and the National Freshwater Snail Collection (NFSC), South Africa, collected between 1897 and 2021. Number refers to the number of specimens.

Family	**Taxa**	**1897 - 1906**	**1907 - 1916**	**1917 - 1926**	**1927 - 1936**	**1937 - 1946**	**1947 - 1956**	**1957 - 1966**	**1967 - 1976**	**1977 - 1986**	**1987 - 1996**	**1997 - 2006**	**2007 - 2016**	**2017 - 2021**	**Total**	**%**	**Status**	**IUCN Red List Category**	**IUCN status**	**GBIF Relative observation trends**
Planorbidae	*Afrogyrorbis natalensis*	1		6				13	14	1					35	1.86	Potentially declining	Least Concern (LC), Date assessed 2006	Unknown	Stable
Viviparidae	*Bellamya capillata*	1		2					3	1	1	3	2		13	0.69		Least Concern (LC), Date assessed 2017	Stable	No South African data records available
Planorbidae	*Biomphalaria pfeifferi*	2	1	5				23	50	5	2	1			89	4.74		Least Concern (LC), Date assessed 2016	Increasing	No South African data records available
Mytilidae	*Brachidontes virgiliae*						1	1	3	1	3		1		10	0.53		No data	Unknown	No geocoded data available
Bulinidae	*Bulinus africanus*				2			15	1	1	1	2			22	1.17	Potentially declining	Least Concern (LC), Date assessed 2006	Unknown	Decreasing, Potentially declining
Bulinidae	*Bulinus forskalii*	2	2	4				7	142	4	2	14			177	9.42		Least Concern (LC), Date assessed 2006	Stable	No South African data records available
Bulinidae	*Bulinus globosus*	2						3	1	1	1	4			12	0.64		Least Concern (LC), Date assessed 2017	Stable	No South African data records available
Bulinidae	*Bulinus natalensis*							5	42	4	1				52	2.77		Least Concern	Stable	No geocoded

																		(LC), Date assessed 2017		data available
Bulinidae	*Bulinus reticulatus*								1						1	0.05	Potentially declining	Least Concern (LC), Date assessed 2016	Unknown	No geocoded data available
Bulinidae	*Bulinus tropicus*			15				20	225	8	12	26		1	307	16.34		Least Concern (LC), Date assessed 2017	Stable	Increasing
Burnupiidae	*Burnupia brunnea*								1						1	0.05	Potentially declining	Data Deficient (DD), Date assessed 2007	Unknown	No geocoded data available
Burnupiidae	*Burnupia caffra*			4				1	18						23	1.22	Potentially declining	Data Deficient (DD), Date assessed 2006	Unknown	No geocoded data available
Burnupiidae	*Burnupia capensis*						3	1	32						36	1.92	Potentially declining	Data Deficient (DD), Date assessed 2007	Unknown	No geocoded data available
Burnupiidae	*Burnupia capensis natalensis*							1	7						8	0.43	Potentially declining	Data Deficient (DD), Date assessed 2007	Unknown	No geocoded data available
Burnupiidae	*Burnupia farquhari*		1												1	0.05	Potentially declining	Data Deficient (DD), Date assessed 2007	Unknown	No geocoded data available
Burnupiidae	*Burnupia gordonensis*		4	6					1	1					12	0.64	Potentially declining	Data Deficient (DD), Date assessed 2007	Unknown	No geocoded data available
Burnupiidae	*Burnupia nana*		1	1				2							4	0.21	Potentially declining	Data Deficient (DD), Date assessed 2007	Unknown	No geocoded data available
Burnupiidae	*Burnupia ponsonbyi*		1		1			2	1						5	0.27	Potentially declining	Data Deficient (DD), Date assessed 2007	Unknown	No geocoded data available

Burnupiidae	*Burnupia stenochorias*								2	1	3				6	0.32	Potentially declining	Data Deficient (DD), Date assessed 2007	Unknown	No geocoded data available
Burnupiidae	*Burnupia transvaalensis*							3			6				9	0.48	Potentially declining	Data Deficient (DD), Date assessed 2007	Unknown	No geocoded data available
Iridinidae	*Chambardia wahlbergi*			1	1			1	1	1	3	3	1		12	0.64		Least Concern (LC), Date assessed 2018	Stable	No geocoded data available
Thiaridae	*Cleopatra ferruginea*							9				1			10	0.53		Least Concern (LC), Date assessed 2020	Unknown	No South African data records available
Unionidae	*Coelatura mossambicensis*								1						1	0.05	Potentially declining	Least Concern (LC), Date assessed 2006	Unknown	No geocoded data available
Cyrenidae	*Corbicula africana*			1				5	3	4	5		1		19	1.01		Least Concern (LC), Date assessed 2018	Stable	Stable
Cyrenidae	*Corbicula astartina*											1			1	0.05	Potentially declining	Least Concern (LC), Date assessed 2006	Unknown	No geocoded data available
Cyrenidae	*Corbicula fluminalis*									1		8	2		11	0.59		Least Concern (LC), Date assessed 2016	Increasing	No South African data records available
Sphaeriidae	*Euglesa costulosa*								10						10	0.53	Potentially declining	No data	Unknown	No geocoded data available
Sphaeriidae	*Euglesa langleyana*							2	5						7	0.37	Potentially declining	No data	Unknown	No geocoded data available
Sphaeriidae	*Euglesa viridaria*								6						6	0.32	Potentially declining	No data	Unknown	No geocoded data available

Sphaeriidae	*Eupera ferruginea*			2										2	0.11	Potentially declining	Least Concern (LC), Date assessed 2018	Unknown	No South African data records available
Lymnaeidae	*Galba truncatula*						1		7					8	0.43	Potentially declining	Least Concern (LC), Date assessed 2013	Unknown	No South African data records available
Planorbidae	*Gyraulus andrussovi*		1	2										3	0.16	Potentially declining	No data	Unknown	No geocoded data available
Planorbidae	*Gyraulus chinensis*												1	1	0.05	Invasive	Least Concern (LC), Date assessed 2010	Increasing	No South African data records available
Planorbidae	*Gyraulus connollyi*							7	33	3		2		45	2.39		Least Concern (LC), Date assessed 2007	Unknown	No geocoded data available
Planorbidae	*Gyraulus costulatus*		7	6				30	77	3	5	7		135	7.18	Invasive	Least Concern (LC), Date assessed 2017	Unknown	No geocoded data available
Planorbidae	*Hovorbis coretus*								1			1		2	0.11		Least Concern (LC), Date assessed 2017	Unknown	No geocoded data available
Ampullariidae	*Lanistes ovum*							2		1	1	4	3	11	0.59		Least Concern (LC), Date assessed 2017	Unknown	No South African data records available
Planorbidae	*Lentorbis carringtoni*								1					1	0.05	Potentially declining	Least Concern (LC), Date assessed 2009	Unknown	No geocoded data available
Thiaridae	*Melanoides tuberculata*	4		6			2	8	9	3	6	37	2	77	4.10		Least Concern (LC), Date assessed 2017	Unknown	Increasing
Neritidae	*Neritina pulligera*							1		3		2		6	0.32		Least Concern (LC), Date	Unknown	No South African data

																		assessed 2016		records available
Planorbidae	*Pettancylus burnupi*		1	1					4						6	0.32	Potentially declining	Data Deficient (DD), Date assessed 2009	Unknown	No geocoded data available
Planorbidae	*Pettancylus cawstoni*								1						1	0.05	Potentially declining	Data Deficient (DD), Date assessed 2009	Unknown	No geocoded data available
Planorbidae	*Pettancylus connollyi*			4					1						5	0.27	Potentially declining	Data Deficient (DD), Date assessed 2009	Unknown	No geocoded data available
Planorbidae	*Pettancylus fontinalis*			1											1	0.05	Potentially declining	Data Deficient (DD), Date assessed 2009	Unknown	No geocoded data available
Planorbidae	*Pettancylus natalensis*			1											1	0.05	Potentially declining	Data Deficient (DD), Date assessed 2007	Unknown	No geocoded data available
Physidae	*Physella acuta*						1	1	9	3	5	25			44	2.34	Invasive	Least Concern (LC), Date assessed 2016	Increasing	Stable
Planorbidae	*Planorbella duryi*											3			3	0.16		Data Deficient (DD)	Unknown	No South African data records available
Ampullariidae	*Pomacea bridgesii*										2				2	0.11		Least Concern (LC), Date assessed 2011	Unknown	No geocoded data available
Lymnaeidae	*Pseudosuccinea columella*						1	47	151	5	7	59			270	14.37		Least Concern (LC), Date assessed 2012	Increasing	Stable
Lymnaeidae	*Radix natalensis*	1	1			1		39	171	7	6	41	1		268	14.26		Least Concern (LC), Date assessed 2017	Stable	Stable

Lymnaeidae	*Radix rubiginosa*												1		1	0.05	Introduced, status unknown	No data	Unknown	No geocoded data available
Planorbidae	*Segmentorbis angustus*								2						2	0.11	Potentially declining	Least Concern (LC), Date assessed 2017	Unknown	No geocoded data available
Planorbidae	*Segmentorbis kanisaensis*			2				1				1			4	0.21		Least Concern (LC), Date assessed 2017	Unknown	No geocoded data available
Planorbidae	*Segmentorbis planodiscus*			1						1					2	0.11	Potentially declining	Least Concern (LC), Date assessed 2009	Unknown	No geocoded data available
Neritidae	*Septaria porcellana borbonica*														0	0.00	No collection date	No data	Unknown	No geocoded data available
Neritidae	*Septaria tessellaria*												1		1	0.05		Least Concern (LC), Date assessed 2010	Unknown	No geocoded data available
Sphaeriidae	*Sphaerium capense*							1	4			1			6	0.32		Least Concern (LC), Date assessed 2016	Stable	No geocoded data available
Sphaeriidae	*Sphaerium incomitatum*								2						2	0.11	Potentially declining	Least Concern (LC), Date assessed 2009	Unknown	No geocoded data available
Physidae	*Stenophysa marmorata*										4	5			9	0.48	Invasive	Least Concern (LC), Date assessed 2011	Unknown	No South African data records available
Thiaridae	*Tarebia granifera*										5	4	6		15	0.80	Invasive	Least Concern (LC), Date assessed 2010	Increasing	Increasing
Thiaridae	*Thiara amarula*			1	2			2			2	1			8	0.43		Least Concern (LC), Date assessed 2016	Unknown	No South African data records available

Tomichiidae	*Tomichia natalensis*								1						1	0.05	Potentially declining	Critically Endangered (CR), Date assessed 2007	Unknown	No geocoded data available
Tomichiidae	*Tomichia tristis*								1	2					3	0.16	Potentially declining	Critically Endangered (CR), Date assessed 2007	Unknown	No geocoded data available
Tomichiidae	*Tomichia ventricosa*						1	1							2	0.11	Potentially declining	Endangered (EN), Date assessed 2007	Unknown	No geocoded data available
Unionidae	*Unio caffer*		5				6	3	1	1	8	1			25	1.33		Least Concern (LC), Date assessed 2007	Unknown	Stable
Neritidae	*Vittina gagates*			3											3	0.16	Potentially declining	Least Concern (LC), Date assessed 2016	Unknown	No geocoded data available
Neritidae	*Vittina natalensis*								1						1	0.05	Potentially declining	No data	Unknown	Stable

CHAPTER 4

A comparison of molluscan species diversity, composition and distribution across freshwater ecosystems in KwaZulu-Natal, South Africa

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Running header: Molluscan species diversity across freshwater ecosystems in KwaZulu-Natal

4.1 Abstract

Globally, freshwater ecosystems are under threat, and their biodiversity is declining. In our study, we assessed the present composition and distribution of freshwater malacofauna in the major freshwater ecosystems of KwaZulu-Natal, South Africa, in relation to water quality and whether these patterns had changed over time. We conducted our study at 52 selected sites as part of the River Eco-Status Monitoring Program (REMP) in the three 'U', 'V', and 'W' water management areas of KwaZulu-Natal. Our surveys were conducted between February 2024 and September 2025, and each site was visited four times. Semi-quantitative samplings were conducted using the kick-stir-sweep method, as well as hand-picking, in three distinct biotopes: stone, vegetation, and gravel, sand, and mud. Water quality variables (pH, water temperature, dissolved oxygen, total dissolved solids, electrical conductivity and salinity were recorded *in situ* at each sampling site. Collected freshwater molluscs were sorted and identified to the species level. Additionally, historical records were sourced and used in our analyses. These records were mapped to the nearest 10 km radius, using their locality descriptions and coordinates, to match the 52 REMP sites in KwaZulu-Natal. The site localities surveyed in the present study overlapped with some of the historical records and spanned the three Water management areas. We found 24 mollusc species belonging to 12 families (four Bivalvia and eight Gastropoda) across the freshwater ecosystems of KwaZulu-Natal, which was lower than historically (69 species) but higher than historical taxa (13 species) mapped at the REMP sites. The majority of the species were found in the 'U' water management area (22/24, 92%), followed by 'W' water management area (11/24, 46%) and 'V' water management area (8/24, 33%). Our results revealed that the availability of vegetation biotope and the total dissolved solids (TDS), significantly influenced mollusc species diversity, distribution, and composition. A high proportion of sites lacked molluscs, indicating that

freshwater mollusc species richness and composition may be influenced by natural and anthropogenic disturbances, sampling effort, and site characteristics. Anthropogenic sewage discharge favoured the proliferation of select tolerant freshwater mollusc species, while less tolerant taxa were negatively affected, leading to degradation of critical ecosystem processes and river health. Anthropogenic factors, competition, predation, and tolerance to urban pollution significantly impacted the diversity, abundance, and composition of molluscs. We advocate for the inclusion of more mollusc families in REMP, the identification and integration of new sites into REMP surveys, data sharing, and improved management of freshwater ecosystems in KwaZulu-Natal, to enhance the sustainability and health of these systems, benefiting both conservation and the communities that depend on them.

KEYWORDS: anthropogenic factors, biotopes**,** freshwater mollusc species diversity, freshwater ecosystems, historical records, pollution, water quality variables

4.2 Introduction

Freshwater ecosystems are among the most biologically diverse on Earth and have inestimable economic, health, cultural, scientific, and educational values (Wantzen et al. 2016; Böhm et al. 2020; Albert et al. 2021; Vári et al. 2022). However, freshwater ecosystems are under threat, and their biodiversity is declining, especially in major global river basins (Vörösmarty et al. 2010; Turak et al. 2017; Böhm et al. 2020; Lopes-Lima et al. 2021). Freshwater molluscs are poorly documented, extremely threatened, and have the highest number of recorded extinctions of any major taxonomic group (Vaughn and Taylor 1999; Lydeard et al. 2004; Lopes-Lima et al. 2021). The decline in freshwater molluscs often goes unnoticed because of poor documentation and

monitoring, as only a fraction of molluscan species (< 2%) have had their conservation status accurately assessed (Lydeard et al. 2004; Reckendorfer et al. 2006; Kemp et al. 2016).

There are ca. 69 species of freshwater Mollusca distributed in the KwaZulu-Natal, South Africa (Appleton 1996; Brown 1967, 1994; Ziganira et al. 2026). It has been reported that freshwater molluscs' distribution is influenced by the availability of suitable aquatic biotopes and depends on water quality (De Kock and Wolmarans 1998; Dallas 2007; Zeybek et al. 2012). The relationships amongst freshwater molluscs and biotopes such as marginal and aquatic vegetation and sediment are well documented (Brown 1978, 1994; Dallas 2007; Odume et al. 2015; Kemp et al. 2016). These biotopes are constantly under threat from anthropogenic activities (Vaughn and Taylor 1999; De Klerk et al. 2012; DWA 2012; Kemp et al. 2016). Nearly 71% of freshwater ecosystems in South Africa are considered endangered or critically endangered because of anthropogenic activities (Nel et al. 2004; Kemp et al. 2016). Recent reports indicate that rivers in KwaZulu-Natal are being affected by various anthropogenic activities that threaten their sustainability (Agboola et al., 2020; Evans et al., 2022; Burnett et al., 2025).

The province of KwaZulu-Natal is the only region in South Africa that can be described as not being water-scarce under present or possible future climatic conditions (Rivers-Moore et al., 2007), and is therefore the best place to study freshwater molluscs (Brown, 1967, 1994). Freshwater mollusc surveys in South Africa and the KwaZulu-Natal in particular are well documented, and supported by 124 years of historical collection data (Connolly 1939; Mandahl-Barth 1958, 1960; Kuiper 1964, 1966; Van Eeden and Brown 1966; Brown 1967, 1994; Appleton 1996; Herbert 1998; Ziganira et al. 2026). However, recent and ongoing surveys in the province have recorded fewer freshwater mollusc species than previously documented (Brown 1967, 1994; Appleton 1996; FBIS, 2022; Nwoko et al. 2022; Ziganira et al. 2026), suggesting a decline of

mollusc diversity in KwaZulu-Natal. Additionally, ever since the River Eco-Status Monitoring Programme (REMP) was established in the last decade, aquatic macroinvertebrates, including 11 mollusc families, have been used for biomonitoring of freshwater ecosystems in South Africa (DWS, 2016). Yet, historical records have reported 16 mollusc families (Ziganira et al. 2026), and no higher resolution data have been used to assess mollusc diversity at REMP sites in KwaZulu-Natal. Hence, updated information on the distribution of freshwater molluscs across major freshwater ecosystems of KwaZulu-Natal is needed for conservation decision-making. The aim of our study was to assess the composition and distribution of freshwater malacofauna in major freshwater ecosystems of KwaZulu-Natal in relation to water quality and to determine whether these patterns had changed over time. We predicted a decline in the number of mollusc species present and a contraction in their distribution ranges.

4.3 Methods

4.3.1 Study area

The province of KwaZulu-Natal is situated in the coastal region of eastern South Africa between latitudes 27° and 31°. Bounded by the Drakensberg escarpment in the west and the Indian Ocean in the east, the ecological conditions at the northern and southern boundaries are similar to those in neighbouring Mozambique and the Eastern Cape Province, respectively (Brown 1967; 1994; Ziganira et al. 2026). For this study, we selected sites from the River Eco-Status Monitoring Programme (REMP) in 16 major rivers in KwaZulu-Natal, spanning three water management areas (Evans et al., 2022). The three water management areas were (1) from the Mvoti River catchment south to the Mzimkulu River catchment is managed under the water management area ‘U’ and making up southern KwaZulu-Natal, (2) the Thukela River catchment is managed as the water

management area ‘V, and (3) from the Amatigulu River catchment north to the Usuthu River catchment, making up northern KwaZulu-Natal, is managed as the water management area ‘W’ (Evans et al. 2022; Figure 4.1).

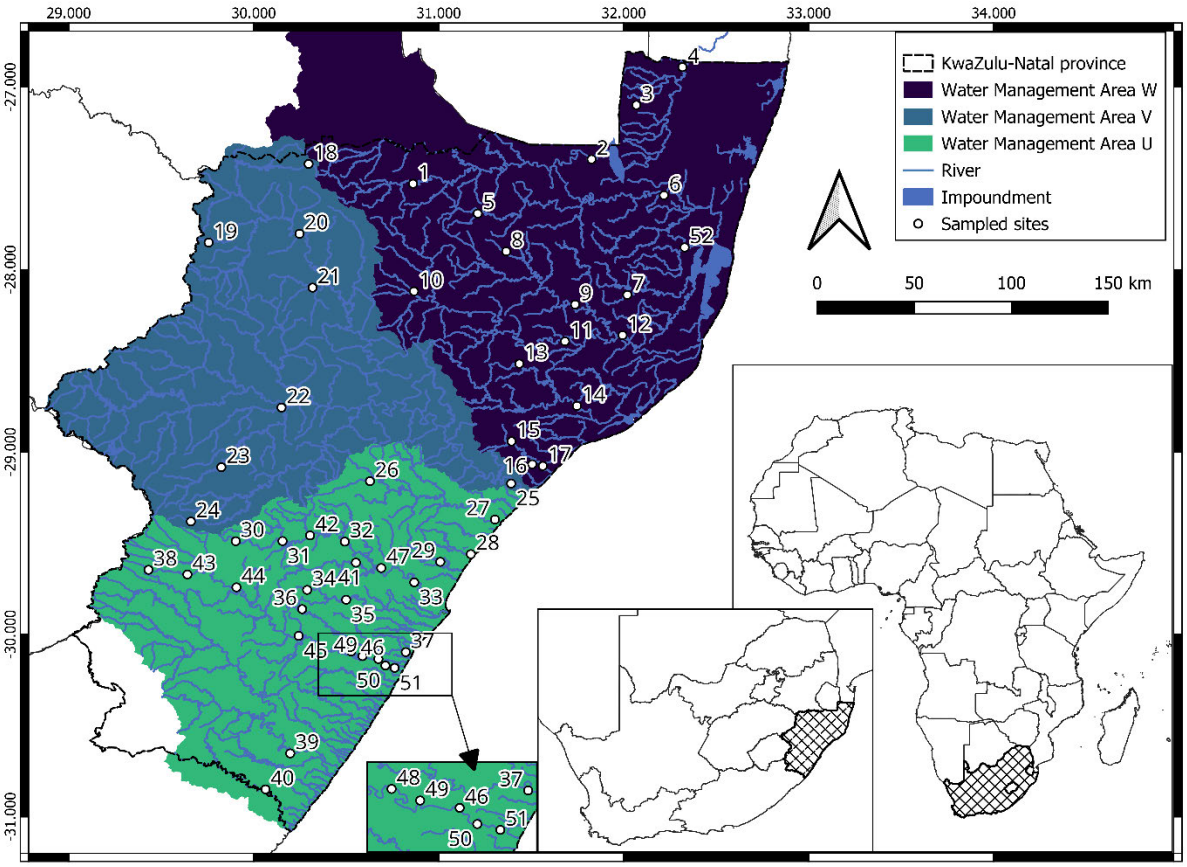


Figure 4.1: Spatial representation of the 52 REMP sites scattered across the three water management areas of KwaZulu-Natal. The 52 REMP sites were surveyed four times between February 2024 and September 2025.

4.3.2 Surveyed sites

We conducted surveys of 52 REMP sites across freshwater ecosystems of KwaZulu-Natal between February 2024 and September 2025. The 52 surveyed sites covered major localities in the three

water management areas of KwaZulu-Natal (Figure 4.1, Supplementary information Table S4.1). High flow season was sampled when river base flows were higher than in the low flow season's base flow. Molluscs were sampled in summer and autumn (high flow season) and in winter and spring (low flow season). Each of the 52 sites was visited four times. At each site, three distinct biotopes —stone, vegetation, and gravel, sand, and mud (GSM) —were sampled using a standard net with a mesh size of approximately 500 μm and a 300 mm x 300 mm opening. The 52 surveyed sites represented altitudinal and latitudinal variation, as well as a wide range of biotopes, within KwaZulu-Natal.

4.3.3 Molluscs sampling

We collected freshwater mollusc specimens using the kick-stir-sweep method as outlined in the South African Scoring System 5 (SASS5) (Dickens and Graham 2002), and active searching through hand-picking during each sampling event. At each site, ~15 min were spent sampling all the biotopes, and we attempted to exhaustively sample each site through hand collection. Contents of the net were then transferred to a circular tray (60 cm diameter), which was filled with water from the habitat. Most of the debris was carefully removed by hand and scrutinised for specimens that might still be attached. Collected samples from each biotope were fixed in a jar of 80% ethanol and later identified to the species level at the KwaZulu-Natal Museum in Pietermaritzburg, South Africa, under a stereomicroscope. The identification keys developed by Brown (1994) and Appleton (2002) were used to identify molluscs morphologically to the species level.

4.3.4 Water quality variables

We recorded water quality variables (pH, water temperature, dissolved oxygen, total dissolved solids, electrical conductivity and salinity) *in situ* at each sampling site using a calibrated Eutech PCD 650 multimeter (EUTECH Instruments Ltd, Singapore) and a clarity tube (Kilroy and Biggs 2002). We also recorded species richness, a count of different species per site, noting the relative number of individual shells collected for each species.

4.3.5 Historical data

We sourced historical data on freshwater molluscs from the study by Ziganira et al. (2026) (Chapter 3), and used them in our analyses. These records, dated between 1897 and 2021, were randomly collected across the three water management areas of KwaZulu-Natal. Additionally, historical mollusc taxa were mapped to the nearest 10 km radius using GEOLocate Web Application tool (https://www.geo-locate.org/) based on their locality descriptions and coordinates, to match the 52 REMP sites in KwaZulu-Natal (Table 4.4). The 52 REMP sites surveyed in the present study overlapped with some of the historical records.

4.3.6 Statistical analyses

We performed a redundancy analysis (RDA) using RStudio version 1.4.1717. The RDA is a linear response model relating species to their measured environmental variables (Van den Brink et al. 2003), allowing direct interpretation of mollusc community composition with respect to these variables. An ANOVA test was run in R to assess significant differences and select the best-fit model. The RDA result was plotted on an ordination diagram, which reflects similarities and dissimilarities between mollusc assemblages and measured variables at sampling sites.

4.4 Results

A total of 24 freshwater mollusc species were recorded from freshwater ecosystems in the three water management areas of KwaZulu-Natal between February 2024 and September 2025 (Figures 4.2 and 4.3; Tables 4.1, 4.2 and 4.3), compared with 69 species historically recorded. Furthermore, seasonal differences in freshwater mollusc diversity and abundance were observed between high- and low-flow seasons (Figure 4.4). Higher diversity and abundance were observed during the high-flow season (Figure 4.4). The water management area 'U' had the highest mollusc species diversity (species richness = 22) (Table 4.1). Sites 33 and 51 had the highest species diversity in the water management area 'U', while the highest total number of species per survey per site was found at site 51 (species richness = 13) (Table 4.1). Species richness in water management area 'V' was between two and four species, and 'W' between one and six species (Tables 4.2 and 4.3).

The most common and abundant mollusc species were *Tarebia granifera* (Lamarck, 1816), *Corbicula fluminalis* (O. F. Müller, 1774), and *Melanoides tuberculata* (O. F. Müller, 1774) (Tables 4.1, 4.2 and 4.3). These species are considered tolerant taxa. A total of 1371 individuals were recorded in this study, of which 577 (42%) were *Tarebia granifera* (Figure 4.5). While low species richness was recorded at several sites, many sites had no molluscs. The proportion of sites with no records of molluscs was unequally distributed within the three water management areas, with 'U' (4/25, 16%), 'V' (2/9, 22%), while 'W' recorded the highest (10/18, 56%) (Tables 4.1, 4.2 and 4.3). Compared with historical records, 45 species were not recovered in this study. While 24 species were collected in this study, historical records mapped at the 52 REMP sites indicated 13 species, with high or low diversity recorded at some sites (Table 4.4).

Water temperature, pH, and electrical conductivity did not vary significantly among sites in the three water management areas of KwaZulu-Natal between February 2024 and September 2025; however, temperature fluctuations were observed across seasons (Tables 4.1, 4.2 and 4.3). Water quality variables did not vary considerably across sites; however, seasonal fluctuations were observed, with a higher diversity and number of shells collected during high-flow seasons.

Multivariate analyses carried out by Redundancy Analysis (RDA) on the three water management areas, 'U', 'V' and 'W' revealed that the availability of vegetation biotope and the total dissolved solids (TDS), significantly influenced mollusc species diversity, distribution, and composition ($p < 0.05$, Figure 4.3). In addition, there were associations among taxa, sites, and water quality variables, allowing certain species to thrive in those environments (Figure 4.3; Table 4.1). Regarding the position, most species were located at the centre of the RDA biplot, suggesting tolerance to measured environmental variables except *T. granifera, P. acuta, C. africana* and *C. fluminalis* (Figures 4.3).

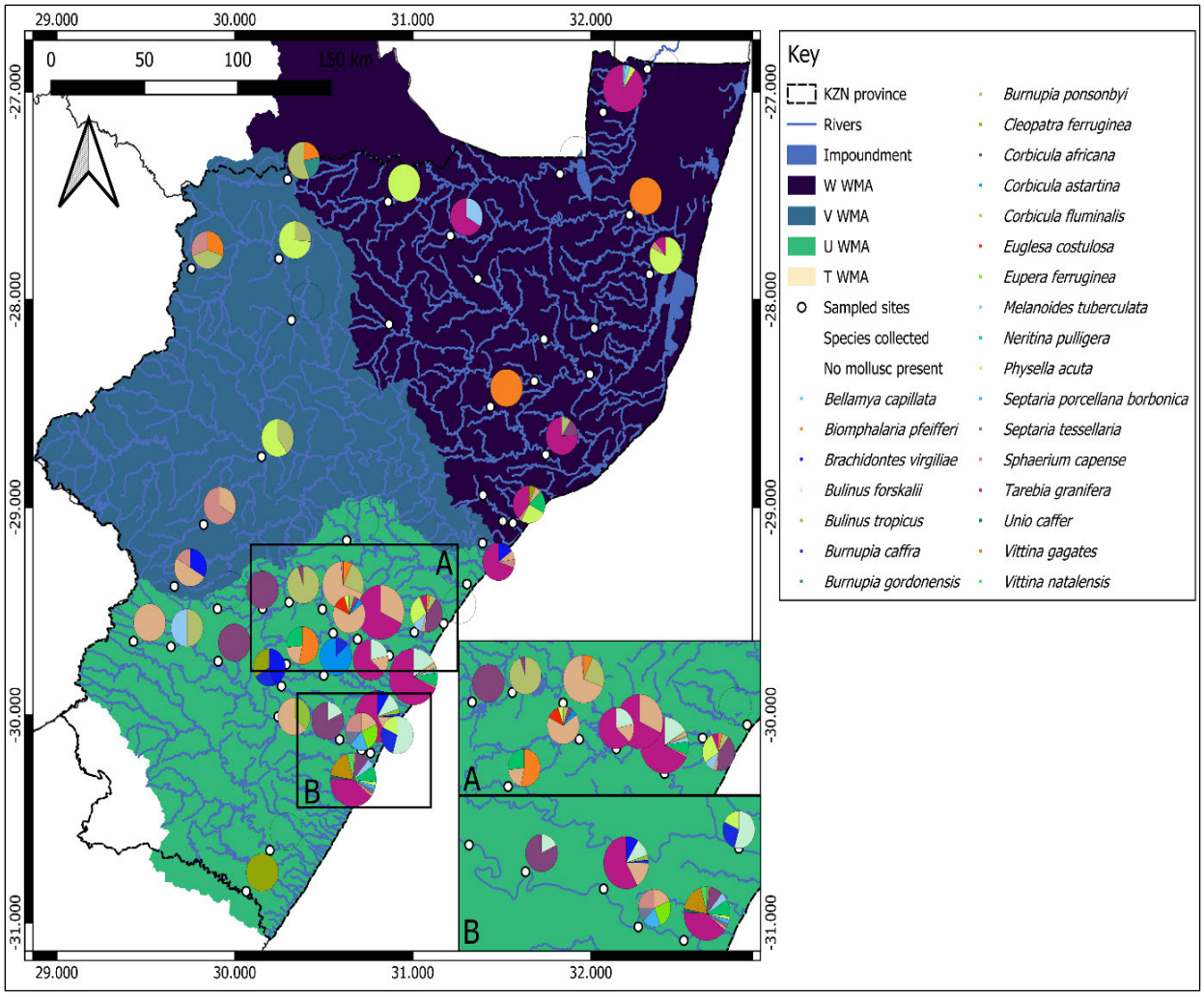


Figure 4.2: The percentage of total freshwater mollusc richness and relative number of collected individuals per site sampled during the present study in KwaZulu-Natal. The highest species richness was found in the 'U' and the lowest in the 'V' water management area. Sites without a pie-chart had no molluscs collected.

Table 4.1: Freshwater mollusc species richness and number of collected individuals found between sites 27 and 51, in the 'U' water management area in the present study, between February 2024 and September 2025. No molluscs were found on sites 27, 28, 30 and 39. Water quality variables expressed as mean values. (Note: TDS – total dissolved solids, DO- dissolved oxygen).

Taxa	Sites																					Number of collected individuals
	29	31	32	33	34	35	36	37	38	40	41	42	43	44	45	46	47	48	49	50	51	
Biomphalaria pfeifferi (Krauss, 1848)	1		8		8																	17
Brachidontes virgiliae (Barnard, 1964)							4									12						16
Bulinus forskalii (Ehrenberg, 1831)				25				6								15		18	4			68
Bulinus tropicus (Krauss, 1848)															6	4						10
Burnupia caffra (Krauss, 1848)						3	2	3							3							11
Burnupia ponsonbyi (B. Walker, 1924)	2		26	1							2	18	2								2	53
Cleopatra ferruginea (I. Lea & H. C. Lea, 1851)							3			2												5
Corbicula africana (Krauss, 1848)	12	2									2	1		14					18		14	63
Corbicula astartina (E. von Martens, 1860)						19					2											21
Corbicula fluminalis (O. F. Müller, 1774)	1		76	4	3				35		26				10	22	46	12		3		238
Euglesa costulosa (Connolly, 1931)											5											5
Eupera ferruginea (Krauss, 1848)				1																	4	5
Melanoides tuberculata (O. F. Müller, 1774)	3			4									2								7	16
Neritina pulligera (Linnaeus, 1767)				12	4																14	30
Physella acuta (Draparnaud, 1805)	8							2			2										3	15
Septaria porcellana borbonica (Bory de Saint-Vincent, 1804)																				3	4	7
Septaria tessellaria (Lamarck, 1816)																				2	3	5
Sphaerium capense (Krauss, 1848)			2	2		4	3	2		1		2								4	3	23
Tarebia granifera (Lamarck, 1816)	2			105												78	98	52			56	391
Unio caffer (Krauss, 1848)																					3	3
Vittina gagates (Lamarck, 1822)																					25	25

Vittina natalensis (Reeve, 1855)																					6	6
Specie richness	7	1	4	8	3	3	4	4	1	2	6	3	2	1	3	5	2	3	2	4	13	**1033**
Temperature (˚C)	20.5	14.5	27.5	16.8	14	18.1	13.8	20.9	15.5	11.8	14	18	14.7	15.2	17.7	17.9	20.2	21.2	24.6	24.6	25.7	
pH	5.35	5.2	7.52	6.53	7.24	7.37	7.32	6.22	8.60	4.96	8	8.51	6.46	8.93	7.54	8.29	8.51	7.81	7.50	7.50	6.20	
Conductivity (µS/cm)	199.8	60.0	33.8	150.0	86.1	98.4	91.1	270	327	215	257	120	122.0	102.1	11.14	330	51.0	272	281	281	284	
TDS (mg/L)	100.0	30.0	256	195	43.1	99	46.1	401	164.3	107.3	128	59.9	61.2	51.0	16.64	165.2	191.5	135.8	139.9	139.9	141.8	
Salinity (‰)	0.10	0.02	0.02	0.04	0.04	0.09	0.04	2.45	0.14	0.01	0.11	0.06	0.05	0.04	0.02	0.15	0.18	0.13	0.13	0.13	0.13	
DO (mg/L)	9.84	9.46	9.08	9.66	9.53	8.16	8.34	5.07	8.72	9.31	10.45	8.91	9.82	9.32	9.60	9.90	9.92	10.31	9.94	9.94	10.30	

Table 4.2: Freshwater mollusc species richness and number of collected individuals found between sites 18 and 26, in the 'V' water management area in the present study between February 2024 and September 2025. No molluscs were found on sites 21 and 26. Water quality variables expressed as mean values. (Note: TDS – total dissolved solids, DO- dissolved oxygen).

Taxa	Sites									Number of collected individuals
	18	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	
*Biomphalaria pfeifferi (*Krauss, 1848)	2	3								5
*Brachidontes virgiliae (*Barnard, 1964)							4	8		12
*Burnupia ponsonbyi (*B. Walker, 1924)	5	4	4		4					17
*Burnupia gordonensis (*Melvill & Ponsonby, 1903)	2									2
*Corbicula fluminalis (*O. F. Müller, 1774)						3	6	4		13
*Physella acuta (*Draparnaud, 1805)			11		6					17
*Sphaerium capense (*Krauss, 1848)		3				6	2	4		15
*Tarebia granifera (*Lamarck, 1816)								37		37
Specie richness	3	3	2	0	2	2	3	4	0	118
Water temperature (˚C)	11.5	19.3	15.8	25.4	18.8	16.1	10.6	18.1	13.8	
pH	8.16	6.85	7.40	8.38	6.50	6.49	6.82	8.24	7.24	
Conductivity (µS/cm)	121.6	119	688	790	137.38	94.4	55.1	286	134.4	
TDS (mg/L)	60.4	61.3	344	396	69.3	47.3	27.6	143.2	672	
Salinity (%)	0.05	0.04	0.31	0.44	0.07	0.04	0.02	0.14	0.65	
DO (mg/L)	10.26	9.53	7.66	9.25	9.88	9.34	9.60	10.60	5.66	

Table 4.3: Freshwater mollusc species richness and number of collected individuals found between sites 1 and 17, in the 'W' water management area in the present study between February 2024 and September 2025. No molluscs were found on sites 2, 4, 7, 8, 9, 10, 11, 12, 15 and 16. Site 52 belonged in this area, and water quality variables expressed as mean values. (Note: TDS – total dissolved solids, DO- dissolved oxygen).

Taxa	Sites																		Number of collected individuals
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**52**	
*Bellamya capillata (*Frauenfeld, 1865)			2																2
*Biomphalaria pfeifferi (*Krauss, 1848)						3							3						6
*Burnupia ponsonbyi (*B. Walker, 1924)														3					3
*Cleopatra ferruginea (*I. Lea & H. C. Lea, 1851)																	2		2
*Corbicula africana (*Krauss, 1848)														5					5
*Corbicula fluminalis (*O. F. Müller, 1774)																	2		2
*Melanoides tuberculata (*O. F. Müller, 1774)			4		6														10
*Neritina pulligera (*Linnaeus, 1767)																	6		6
*Physella acuta (*Draparnaud, 1805)	6		5														8	14	33
*Sphaerium capense (*Krauss, 1848)																	1	1	2
*Tarebia granifera (*Lamarck, 1816)			98		12									25			12	2	149
Specie richness	1	0	4	0	2	1	0	0	0	0	0	0	1	3	0	0	6	3	**220**
Temperature (˚C)	18.5	25	28	11.5	21.0	27.5	25.4	21.1	23.6	13.8	27.6	23	18.3	17.9	22.2	13.8	17.8	25.4	
pH	7	7.68	6.90	8.16	7.41	7.52	8.38	7.39	6.46	7.24	7.78	7.79	7.77	7.70	6.84	7.24	7.90	8.38	
Conductivity (µS/cm)	127.9	685	233	121.6	612	33.8	790	136.9	377	134.4	514	565	369	323	182	134.4	633	793	
TDS (mg/L)	63.7	338	618	60.4	304	256	396	68.4	198.1	672	257	282	184.4	161.0	91.1	672	324	396	
Salinity (‰)	0.06	0.37	0.72	0.05	0.31	0.02	0.44	0.07	0.21	0.65	0.30	0.30	0.17	0.15	0.09	0.65	0.30	0.44	
DO (mg/L)	9.01	11.16	11.14	10.26	7.56	9.08	9.25	9.64	9.59	5.66	8.09	9.89	8.45	9.79	8.95	5.66	7.97	9.25	

Table 4.4: Occurrence of freshwater mollusc taxa collected at the 52 REMP sites during this study (2024 – 2025) compared with historical mollusc taxa (1897 – 2021) mapped to the nearest 10 km radius, using GEOLocate Web Application tool (https://www.geo-locate.org/), based on their locality descriptions and coordinates, to match the REMP sites in KwaZulu-Natal.

Site no.	WMA	Tributary and main stem	Latitude	Longitude	Taxa	
					Historical (1897-2023)	**Present study (2024 - 2025)**
1	W	Bivane River	-27,52937	30,86144		*Physella acuta*
2	W	Phongolo River	-27,39519	31,82661	*Bellamya capillata* *Biomphalaria pfeifferi* *Bulinus forskalii* *Bulinus globosus* *Bulinus tropicus* *Burnupia caffra* *Chambardia wahlbergi* *Corbicula africana* *Gyraulus costulatus* *Melanoides tuberculata* *Pseudosuccinea columella* *Radix natalensis* *Vittina natalensis*	*Bellamya capillata* *Melanoides tuberculata* *Physella acuta* *Tarebia granifera*
3	W	Ngwavuma River	-27,09789	32,06888	*Afrogyrorbis natalensis* *Bulinus forskalii* *Bulinus natalensis* *Coelatura mossambicensis* *Gyraulus costulatus*	*Bellamya capillata* *Physella acuta* *Tarebia granifera*
4	W	Phongolo River	-26,89004	32,31803	*Bellamya capillata* *Biomphalaria pfeifferi* *Bulinus forskalii* *Bulinus globosus* *Bulinus tropicus*	

					Burnupia caffra *Chambardia wahlbergi* *Corbicula africana* *Gyraulus costulatus* *Melanoides tuberculata* *Pseudosuccinea columella* *Radix natalensis* *Vittina natalensis*	
5	W	Mkuze	-27,69256	31,21129	*Bellamya capillata* *Corbicula africana*	*Melanoides tuberculata* *Tarebia granifera*
6	W	Mkuze	-27,59227	32,21795	*Bellamya capillata* *Corbicula africana*	*Sphaerium capense* *Tarebia granifera*
7	W	Hluhluwe	-28,13856	32,01995	*Corbicula astartina* *Physella acuta*	
8	W	Sikwebezi, Black Mfolozi, Mfolozi	-27,90033	31,36522		
9	W	Black Mfolozi, Mfolozi	-28,19122	31,73751		
10	W	Mvunyana, White Mfolozi, Mfolozi	-28,11899	30,86683		
11	W	White Mfolozi, Mfolozi	-28,39348	31,68303		
12	W	Mfolozi	-28,35960	31,99434	*Biomphalaria pfeifferi* *Bulinus forskalii* *Bulinus natalensis* *Bulinus tropicus* *Burnupia capensis natalensis* *Corbicula africana* *Melanoides tuberculata* *Radix natalensis*	
13	W	Mfule, Mhlathuze	-28,51589	31,43614	*Corbicula fluminalis*	*Biomphalaria pfeifferi*
14	W	Mhlathuze	-28,74695	31,74745	*Corbicula fluminalis*	*Burnupia ponsonbyi* *Corbicula africana* *Tarebia granifera*
15	W	Nwaku, Matikulu	-28,94142	31,39416		
16	W	Vutha, Matikulu	-29,06709	31,50588		

					Thiara amarula	*Cleopatra ferruginea* *Corbicula fluminalis*
17	W	Matikulu	-29,07655	31,56309		*Neritina pulligera* *Physella acuta* *Sphaerium capense* *Tarebia granifera*
18	V	Slang, Buffalo, Thukela	-27,42067	30,29681	*Burnupia capensis* *Unio caffer*	*Biomphalaria pfeifferi* *Burnupia gordonensis*
19	V	Ncandu, Buffalo, Thukela	-27,85144	29,75663		*Biomphalaria pfeifferi* *Burnupia ponsonbyi* *Sphaerium capense*
20	V	Buffalo, Thukela	-27,80344	30,24793	*Bulinus tropicus* *Radix natalensis*	*Burnupia ponsonbyi* *Physella acuta*
21	V	Mzinyashana, Buffalo, Thukela	-28,09882	30,31853	*Corbicula astartina*	
22	V	Thukela	-28,75633	30,15038	*Bulinus tropicus* *Burnupia gordonensis* *Gyraulus costulatus* *Melanoides tuberculata* *Physella acuta* *Pseudosuccinea columella* *Unio caffer*	*Burnupia ponsonbyi* *Corbicula fluminalis* *Physella acuta*
23	V	Bushmans, Thukela	-29,08337	29,82504	*Gyraulus costulatus* *Melanoides tuberculata* *Physella acuta* *Pseudosuccinea columella* *Radix natalensis* *Tomichia ventricosa* *Unio caffer*	*Corbicula fluminalis* *Sphaerium capense*
24	V	Mfulankomo, Mooi, Thukela	-29,38081	29,66052	*Bulinus tropicus* *Physella acuta* *Radix natalensis* *Tomichia ventricosa*	*Brachidontes virgiliae* *Corbicula fluminalis* *Sphaerium capense*

25	V	Thukela	-29,17262	31,39192	*Burnupia capensis* *Burnupia farquhari* *Physella acuta* *Unio caffer*	*Brachidontes virgiliae* *Corbicula fluminalis* *Sphaerium capense* *Tarebia granifera*
26	U	Mvoti	-29,15986	30,62869	*Biomphalaria pfeifferi* *Bulinus forskalii* *Bulinus tropicus* *Burnupia caffra* *Burnupia caffra* *Burnupia capensis* *Cleopatra ferruginea* *Euglesa costulosa* *Euglesa langleyana* *Gyraulus connollyi* *Gyraulus costulatus* *Physella acuta* *Pseudosuccinea columella* *Radix natalensis* *Unio caffer*	
27	U	Mvoti	-29,37000	31,30434		
28	U	Tongati	-29,55991	31,17409	*Bulinus tropicus* *Burnupia transvaalensis* *Pseudosuccinea columella*	
29	U	Mdloti	-29,60208	31,00902		*Biomphalaria pfeifferi* *Burnupia ponsonbyi* *Corbicula fluminalis* *Melanoides tuberculata* *Physella acuta* *Sphaerium capense* *Tarebia granifera*
30	U	Umgeni	-29,48881	29,90304		
31	U	Umgeni, Midmar Dam	-29,48813	30,15600	*Euglesa costulosa*	*Corbicula africana*

32	U	Umgeni, Fountain Hill estate	-29,49125	30,49263		*Biomphalaria pfeifferi* *Burnupia ponsonbyi* *Corbicula fluminalis* *Sphaerium capense*
33	U	Umgeni, Mzinyathi	-29,71452	30,86806		*Bulinus forskalii* *Burnupia ponsonbyi* *Corbicula fluminalis* *Eupera ferruginea* *Melanoides tuberculata* *Neritina pulligera* *Sphaerium capense* *Tarebia granifera*
34	U	Mlazi	-29,75600	30,28900		*Biomphalaria pfeifferi* *Corbicula fluminalis* *Neritina pulligera*
35	U	Mlazi	-29,80972	30,50000		*Burnupia caffra* *Corbicula astartina* *Sphaerium capense*
36	U	Lovu	-29,86145	30,26196	*Afrogyrorbis natalensis* *Biomphalaria pfeifferi* *Bulinus africanus* *Bulinus natalensis* *Euglesa langleyana* *Gyraulus connollyi* *Gyraulus costulatus* *Pseudosuccinea columella* *Radix natalensis*	*Brachidontes virgiliae* *Burnupia caffra* *Cleopatra ferruginea* *Sphaerium capense*
37	U	Lovu	-30,09689	30,82220	*Afrogyrorbis natalensis*	*Bulinus forskalii* *Burnupia caffra* *Physella acuta* *Sphaerium capense*
38	U	Mkhomazana, Mkomazi	-29,64577	29,43134	*Bulinus tropicus*	*Corbicula fluminalis*

					Pseudosuccinea columella	
39	T	Mzimkhulu	-30,65224	30,19769		
40	T	Mtamvuna	-30,84924	30,06400		*Cleopatra ferruginea* *Sphaerium capense*
41	U	Msunduzi, Umgeni, Nkanyezini	-29,60655	30,55259		*Burnupia ponsonbyi* *Corbicula africana* *Corbicula astartina* *Corbicula fluminalis* *Euglesa costulosa* *Physella acuta*
42	U	Umgeni, Hilton college NR	-29,46352	30,29355		*Burnupia ponsonbyi* *Corbicula africana* *Sphaerium capense*
43	U	Mkomazi, Ad-hoc site 5	-29,67111	29,64172	*Pseudosuccinea columella*	*Burnupia ponsonbyi* *Melanoides tuberculata*
44	U	Mkomazi, Ad-hoc site 4	-29,74174	29,90672	*Pseudosuccinea columella*	*Corbicula africana*
45	U	Mkomazi, Ad-hoc site 2	-30,00797	30,24332		*Burnupia caffra* *Corbicula fluminalis* *Bulinus tropicus*
46	U	Mkomazi, Ingulube bush camp Weir 3	-30,13493	30,67410		*Brachidontes virgiliae* *Bulinus tropicus* *Corbicula fluminalis* *Melanoides tuberculata* *Tarebia granifera*
47	U	Gcumisa, Mlahlanja, Umgeni River	-29,63601	30,68950	*Gyraulus costulatus*	*Corbicula fluminalis* *Tarebia granifera*
48	U	Ad hoc Site 1	-29,63601	30,68950		*Bulinus forskalii* *Corbicula fluminalis* *Tarebia granifera*
49	U	Weir 4 Mkomazi	-30,11880	30,58855	*Physella acuta*	*Bulinus forskalii* *Corbicula africana*
50	U	LMB WSS	-30,17047	30,71209		*Corbicula fluminalis*

						Septaria porcellana borbonica *Septaria tessellaria* *Sphaerium capense*
51	U	Weir 1 Sappi, Craigieburn, Mkomazi	-30,18329	30,76199	*Bulinus africanus* *Tomichia tristis*	*Burnupia ponsonbyi* *Corbicula africana* *Eupera ferruginea* *Melanoides tuberculata* *Neritina pulligera* *Physella acuta* *Septaria porcellana borbonica* *Septaria tessellaria* *Sphaerium capense* *Tarebia granifera* *Unio caffer* *Vittina gagates* *Vittina natalensis*
52	W	Wild tomorrow, Msinene site	-27,87825	32,33004	*Bulinus natalensis* *Chambardia wahlbergi* *Corbicula africana* *Melanoides tuberculata* *Radix natalensis* *Tarebia granifera*	*Physella acuta* *Sphaerium capense* *Tarebia granifera*
					Total: 13 species	Total: 24 species

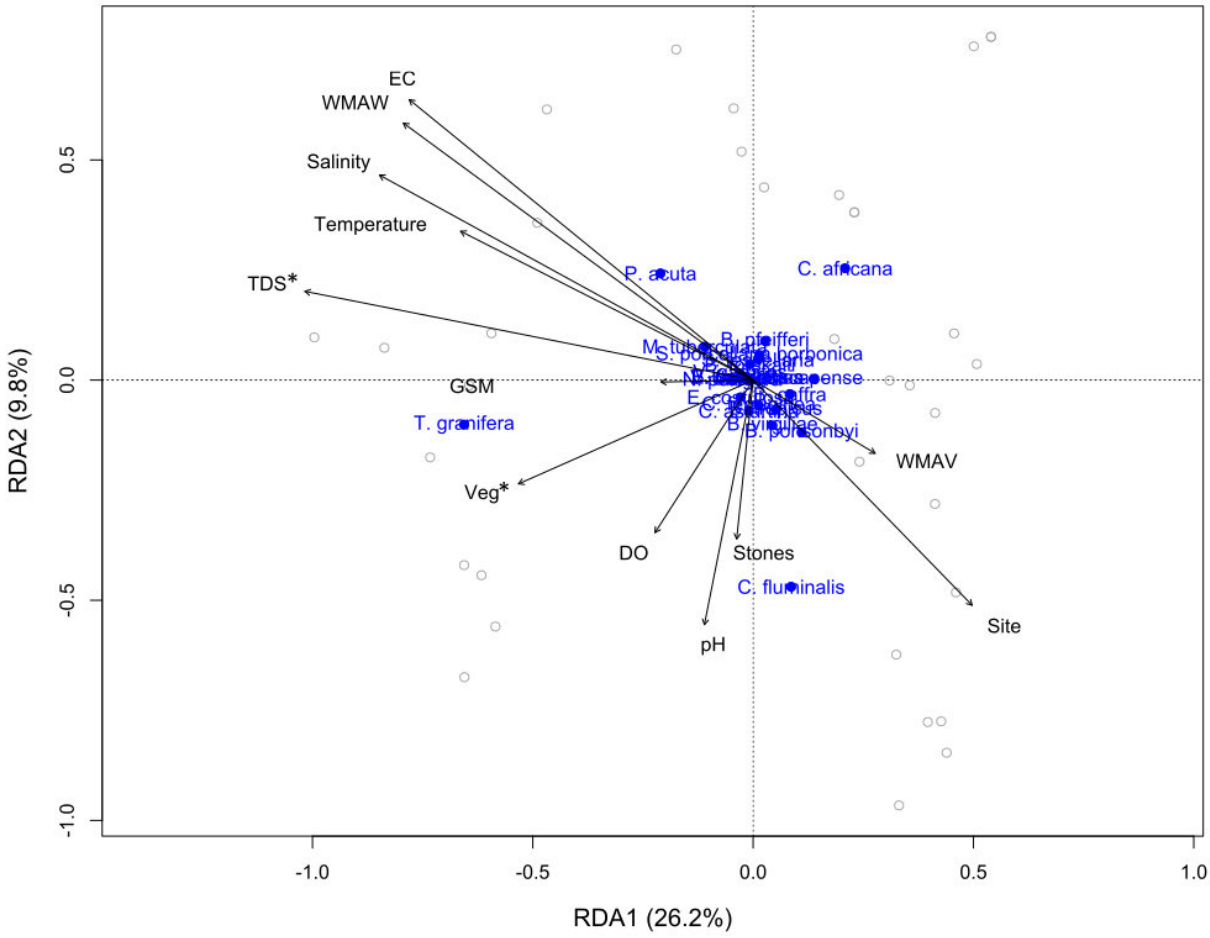


Figure 4.3: Redundancy analysis (RDA) biplot showing dissimilarity based on mollusc communities (taxa in blue, see Tables 4.1, 4.2 and 4.2 for species full names) and sampling sites in the three water management areas (WMAs), and associated biotopes, and water quality variables. The direction of the arrows indicates which biotope and water quality variables were important for the taxa collected at those sites. (Note: biotopes —stone, vegetation (VEG), and gravel, sand, and mud (GSM); water variables —pH, water temperature, dissolved oxygen (DO), total dissolved solids (TDS), electrical conductivity (EC) and salinity. 26.2% of the variability is displayed on axis 1, and 9.8% of the variability is displayed on axis 2).

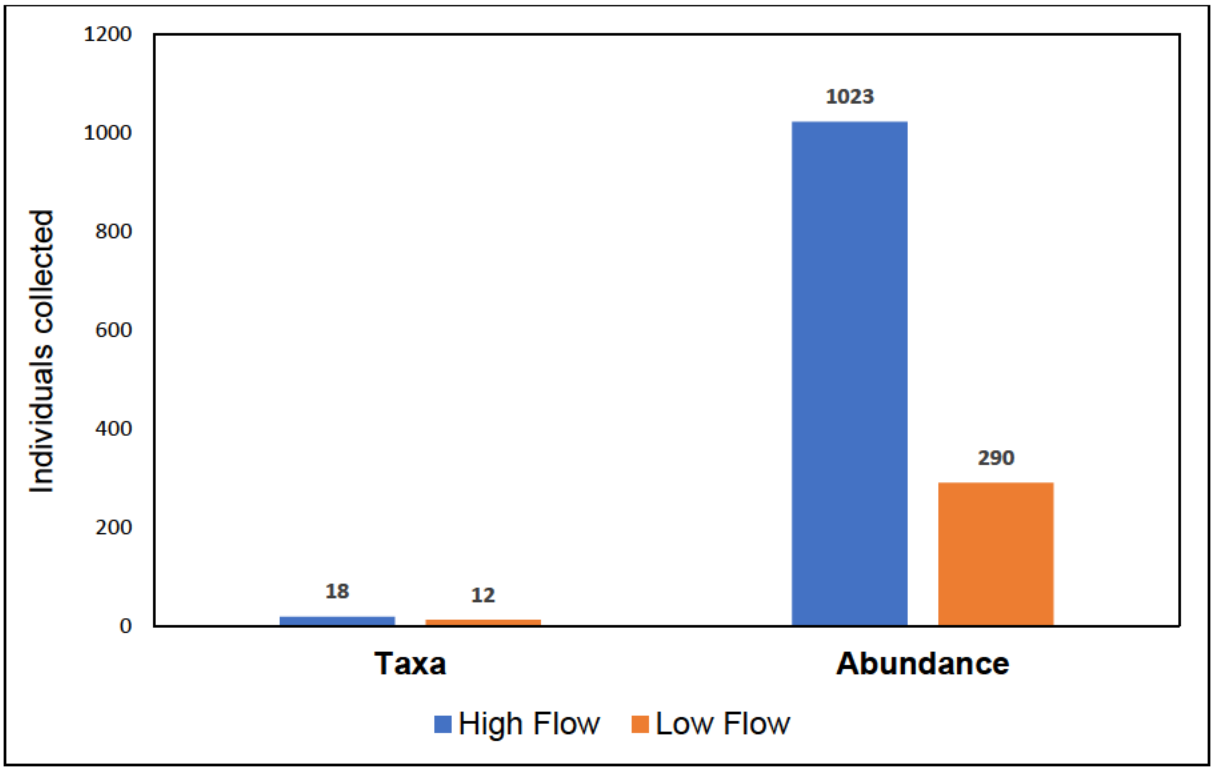


Figure 4.4: Seasonal differences between high and low flow seasons in freshwater mollusc diversity and abundance in KwaZulu-Natal.



Figure 4.5: Photograph of the lower Umgeni River, Mzinyathi, REMP site number 33, showing biotope availability and pools infestation by *Tarebia granifera*. (Photograph© Matabaro Ziganira, taken on 26 March 2024).

4.5 Discussion

Examining the data from our study, it is clear that more freshwater molluscs were recorded historically than are present at the sampling sites today. Our surveys recorded 24 out of 69 known species, suggesting that freshwater ecosystems in KwaZulu-Natal have potentially lost nearly 65% (45/69) of their mollusc species. These observations are supported by the ongoing surveys across the KwaZulu-Natal conducted by the Freshwater Biodiversity Information System (FBIS), which has recorded only 19 freshwater mollusc species between 2022 and 2025 (FBIS 2022), while other surveys on 127 sites only recovered eight freshwater mollusc species between 2020 and 2021 (Nwoko et al. 2022). Of the 24 species collected during this study, 22 were collected in the 'U' water management area, except *Bellamya capillata* (Frauenfeld 1865), which was only recorded in 'W' and *Burnupia gordonensis* (Melvill & Ponsonby, 1903) recorded only in the 'V', while their range covers the whole province (Brown 1994). As expected, these changes were not consistent across the three water management areas of KwaZulu-Natal. In the 'U', the number of species decreased from 55 species to 22 species, while in the 'V', 30 species to eight species, and 41 species to 11 in the 'W'. Another inconsistency was that 'V' had fewer sites than 'U' and 'W', which might have contributed to lower species diversity and fewer collected individuals in this region. Interestingly, while all sampled sites in the 'V' had freshwater molluscs, out of 18 sites in the 'W', 10 sites (55%) had no molluscs.

Compared with historical records mapped at the 52 REMP sites, this study collected 24 species, more than the 13 species mapped at the historical REMP sites, and observed high or low diversity at certain sites. For instance, 15 freshwater molluscs were historically collected at REMP site number 26 at Mvoti River in the 'U', while no molluscs were recorded on this site during this study. One possible reason is that this site is surrounded by agricultural farms and an industrial

processing plant (pers. obs.), which may not have been present in the 1960s and 1980s when most of the recorded molluscs were collected. Hence, we suspect that chemical pollution may be the leading cause of diversity loss at this site. Additionally, this study notes that increased mollusc diversity at some REMP sites, compared with mapped historical records, indicates that identifying and including new sites in the REMP could enhance our understanding of the present status of freshwater ecosystems in KwaZulu-Natal and, by extension, in South Africa as a whole. This is important because historical records of the vast majority of freshwater molluscs were collected in the 1960s and 1980s, primarily along the east coast of KwaZulu-Natal, regions that have experienced rapid industrialisation. Many of these historically sampled coastal sites are presently not included in the REMP surveys.

Corbicula fluminalis (O. F. Müller 1774) and *Tarebia granifera* (Lamarck 1816) were the most abundant species recorded in the three water management areas of KwaZulu-Natal between February 2024 and September 2025. A total of 1371 individuals were collected in this study, of which 42% were *Tarebia granifera*. Similarly, the occurrence range of *P. acuta* and *T. granifera* was recorded at multiple sites during this study. This suggests that these two invasive species may have a high tolerance to a wide range of water temperatures, conductivity, and pH, and that this tolerance could be exacerbated by climate change (Chitramvong et al. 1981; Appleton and Miranda 2015). Compared with historical records (Ziganira et al., 2026), a large number of endemic and indigenous species were not recorded in the three water management areas of KwaZulu-Natal between February 2024 and September 2025, confirming the possible negative impact of alien species on local biota. These endemic species are considered less tolerant taxa. Both *T. granifera* and *P. acuta* have greater reproductive capacities than indigenous species and can spread widely into natural ecosystems (Brackenbury and Appleton 1991; Brown 1994; Appleton 1996; Herbert

1998). Many studies have concluded that alien freshwater molluscs, such as *T. granifera,* can displace native species (Miranda and Perissinotto 2014; Perissinotto et al. 2014; Nwoko et al. 2022). However, it remains unknown to what extent alien freshwater molluscs out-compete with and/or displace indigenous species (Herbert 1998).

4.5.1 Effect of biotopes

Our results revealed that the availability of vegetation biotope and the total dissolved solids (TDS), significantly influenced mollusc species diversity, distribution, and composition in the three WMAs of KwaZulu-Natal between February 2024 and September 2025. The TDS and vegetation biotope were the most important driving factors for all mollusc species' community and composition, except for *T. granifera, P. acuta, C. africana*, and *C. fluminalis*. The highest species richness (species richness = 13) was recorded at REMP site 51 (Mkomazi River, upstream Sappi Plant), and on REMP site 33 (species richness = 8) in the 'U' water management area (Tables 4.1, 4.2, and 4.3). Species richness at these two sites highlighted the importance of biotope availability that supported high species diversity (Dallas 2007). We observed that sites 33 and 51 of the 'U', had a combination of biotopes that were favourable to molluscs. These sites were characterised by rocky pools, runs, riffles, and muddy and sandy vegetation, as well as abundant marginal and aquatic vegetation, and stones in and out of the current (pers. obs.). Our findings were consistent with those of Min et al. (2022), who observed that the abundance and occurrence of molluscs were affected by the presence of predators and competitors, macrophyte cover, chlorophyll a, substrate type, river depth, and water velocity. High freshwater mollusc diversity has also been associated with riverbed substrate heterogeneity, which improves nutrient flow, thereby increasing mollusc diversity and abundance (Vinson and Hawkins 1998). Similarly, our surveys found that a stand-

alone biotope, such as stone and sand, recorded the lowest diversity. This is because sand can be easily disturbed by water currents, potentially creating unstable conditions in freshwater ecosystems (Verdonschot 2001; Min et al. 2022). While stone requires specialist taxa such as *Burnupia* species, we observed that sites with slow-moving or stagnant water favoured high mollusc diversity and abundance (pers. obs.). This observation was similar to Maes et al. (2021), who noted that fast-moving water disturbed mollusc breeding habitats and flushed away food sources.

In the water management 'W', 10 sites (2, 4, 7, 8, 9, 10, 11, 12, 15, and 16) recorded no molluscs, while low diversity was observed at multiple sites. Although suitable biotopes were present in some sites, other sites had either less water available or freshwater ecosystems had completely dried up because of disturbances associated with anthropogenic activities or the impact of climate change. Our study found that the association between site and biotope availability was the most significant factor influencing the distribution and abundance of freshwater molluscs. We noticed that many sites in the 'W' were surrounded by agricultural fields, while others suffered gross disturbance and transformation of aquatic biotopes because of cleared riparian vegetation and grazing cattle from rural settlements. These observations were supported by Agboola et al. (2020a), who found that many rivers in northern KwaZulu-Natal had limited biotope availability, riverbank modification, and prevailing drought. Hence, they suggested that the combination of these factors contributed to lower macroinvertebrate diversity (Agboola et al. 2020a). Other threats to freshwater biodiversity include anthropogenic activities such as damming, sedimentation, mining, sewage, and chemical pollution, as well as natural disasters like flooding (Böhm et al. 2020; Lopes-Lima et al. 2021). Over the last decade, flooding of freshwater ecosystems in

KwaZulu-Natal has increased, causing not only disturbance to molluscs but also to the overall ecosystem health (Agboola et al. 2020b).

4.5.2 Water quality variables

Our results showed that most measured water quality variables did not significantly influence mollusc species diversity, composition, and distribution, except TDS. However, seasonal fluctuations were observed, with high diversity and abundance of molluscs collected during high-flow seasons in the three water management areas of KwaZulu-Natal between February 2024 and September 2025 (Figure 4.4). While the high flow season (rainy season) was characterised by higher river base flow, rather than flooding, this could be detrimental to molluscs. The low-flow season (dry season) was characterised by cold water, lower river base levels, and sometimes dry river beds at some sites, which we believed contributed to lower diversity at those sites (pers. obs.).

We argued that the combination of factors, including habitat characteristics, the tolerance of certain species to organic pollution, competition, and predation, potentially affected species diversity, distribution, and the number of shells collected or observed at some sites. For instance, at the 'U' two sites (33 and 51), located near rural community settlements, a surprisingly high species diversity was observed compared with other sites. Site 51 was located on the Mkomazi River, while site 33 was located on the Mdloti River. Min et al. (2022) found that habitat characteristics and the presence of predators and competitors were the primary variables determining the abundance and distribution of snail intermediate hosts of parasites. Similarly, a study by Pinto et al. (2013) revealed that untreated sewage discharge led to algal blooms and the proliferation of aquatic macrophytes in the Pampulha Reservoir in Brazil, thereby contributing to the establishment of high snail densities in the water body.

Although high diversity was observed at organic-polluted sites (33 and 51), sites rich in vegetation, biotope, sensitive freshwater molluscs, and endemic species were less frequently detected in the three water management areas of KwaZulu-Natal between February 2024 and September 2025. Therefore, endemic freshwater mollusc species might have been displaced, lost, or possibly declining. Studies on freshwater taxa, such as stoneflies (Plecoptera) and blue-winged olive mayflies (*Baetis* spp.), have revealed that abundance is higher in the absence of treated sewage discharge, indicating greater tolerance to urban pollution (Everall et al. 2018; Johns and Benning 2021). Our study aligns with other studies showing that the loss of some freshwater mollusc species is a consequence of wastewater pollution, which alters or degrades critical ecosystem processes (Burdon et al. 2020; Jackson et al. 2020; Albini et al. 2023). Compared with historical data, only *B. ponsonbyi*, an endemic species, and the invasive species *M. tuberculata* and *P. acuta* showed high tolerance to most water quality variables.

While low mollusc diversity (24 species) was recorded in the present study compared with the 69 species historically recorded, a total of 19 and eight species were recorded in new studies and the ongoing surveys by the FBIS over the past five years (FBIS 2022; Nwoko et al. 2022). One possible reason is that the historical data were collected by multiple individuals over several decades and spanned a broader range of geographic locations. However, we also believe that low diversity may potentially be attributed to river disconnection resulting from anthropogenic activities in KwaZulu-Natal. Alexander et al. (2021) found that human activities, such as agriculture and urban development, were identified as the leading causes of natural land cover loss and the ultimate decline in environmental functionality and connectivity in KwaZulu-Natal. Additionally, the low mollusc diversity in the province could also be attributed to chemical pollution, inadequate sampling, and a lack of a long-term monitoring program at selected sites

over the last decade. Many REMP surveys in KwaZulu-Natal have utilised fish and macroinvertebrates to contribute to national efforts to monitor and provide management tools for freshwater ecosystems in South Africa (DWS 2016; Agboola 2020a,b; Evans et al. 2022; Burnett et al. 2025). Thus, our presence or absence data may not directly suggest possible extinction or species decline because a large portion of mollusc families have been left out of REMP, long-term monitoring of the same sites focusing on molluscs has not been done over the last decade, and mollusc records data from REMP sites have not been donated to museums. Therefore, this study is the first of its kind to use high-resolution imaging microscopic identification in assessing molluscs collected at the REMP sites in KwaZulu-Natal. Although ongoing samplings by the FBIS team have been closing this gap, we believe that inadequate sampling and the lack of long-term follow-up monitoring at the exact same sites may not provide a comprehensive representation of species diversity and composition in the province. However, this study clearly supports the national mandate to monitor the ecological status of freshwater ecosystems in South Africa (DWS 2016).

4.5.3 Limitations of our approach

With the understanding that freshwater molluscs were historically collected in the field using various methodologies that maximised active search, including hand-picking, this study used active search by hand-picking for 1 hour and SASS 5. Because of the transdisciplinary nature of the methodologies used to collect the historical data, our approach entails notable but acceptable trade-offs. In this study, without SASS 5, no mollusc collections would have been made in the field, although we did not compare the efficacy of the two methods (SASS 5 vs active search). We consider this a poor practice, given the national effort invested in sampling for ecological status,

notwithstanding the limitations of SASS 5 as mentioned. We acknowledge that the SASS 5 methodologies were not ideal for sampling freshwater molluscs. However, as previously stated, it is a method for sampling macroinvertebrates as a whole, including molluscs. Since biotopes are directly linked to flow type (see the Hjulström curve), whether instream or marginal vegetation, they are a major contributor to freshwater macroinvertebrate diversity and are independent of substrate type. Our approach aimed to obtain a representative sample of the available habitat, defined into biotopes per the SASS 5 protocol, in addition to an active search of 1 hour.

4.6 Conclusions

Freshwater ecosystems are constantly exposed to multiple interacting stressors that might lead to high or low diversity (Albini et al. 2023). The relatively low freshwater mollusc diversity recorded at the 52 REMP sites throughout this study, as well as recent studies and ongoing surveys, suggests that either the present state of freshwater ecosystems in KwaZulu-Natal is unsuitable for the persistence of many mollusc species, or SASS 5 methodologies were not ideal for mollusc sampling. A high number of sites with no molluscs indicated that freshwater mollusc species richness and composition may be affected by both natural and anthropogenic disturbances, such as droughts, flooding, river disconnection and chemical pollution (Agboola et al. 2020a). Anthropogenic sewage discharge favoured the proliferation of select tolerant freshwater mollusc species, while less tolerant taxa were negatively affected, leading to degradation of critical ecosystem processes and river health. We believe that FBIS and REMP have the opportunity to identify and include new key biodiversity sites for monitoring and conservation. This is important for tracking land-use activities and climate change, which seem detrimental to freshwater ecosystems, particularly in KwaZulu-Natal. More freshwater mollusc families should be included

in SASS 5 to better represent this group. Data mobilisation and sharing are essential for the effective management of freshwater ecosystems in KwaZulu-Natal and South Africa, enabling improvements in the sustainability and health of these systems, which in turn benefit both conservation and the communities that depend on them.

4.7 Acknowledgements

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Conflicts of Interest

The authors declare no conflicts of interest.

Ethical and permit approval

We had animal ethics approval from the University of KwaZulu-Natal Animal Ethics Committee (permit: AREC/00005460/2023(00029716)) and a permit from Ezemvelo KZN Wildlife.

Data availability

Data will be made available on request

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4.9 Supplementary information

Supplementary information Table S4.1: The 52 REMP sites and associated water management areas (WMAs) and freshwater ecosystems of KwaZulu-Natal surveyed in this study between February 2024 and September 2025.

Site No:	WMA	River	Latitude	Longitude
1	W	Bivane, Phongolo	-27.52937	30.86144
2	W	Phongolo	-27.39519	31.82661
3	W	Ngwavuma, Phongolo	-27.09789	32.06888
4	W	Phongolo	-26.89004	32.31803
5	W	Mkuze	-27.69256	31.21129
6	W	Mkuze	-27.59227	32.21795
7	W	Hluhluwe, Mkuze	-28.13856	32.01995
8	W	Sikwebezi, Black Mfolozi, Mfolozi	-27.90033	31.36522
9	W	Black Mfolozi, Mfolozi	-28.19122	31.73751
10	W	Mvunyana, White Mfolozi, Mfolozi	-28.11899	30.86683
11	W	White Mfolozi, Mfolozi	-28.39348	31.68303
12	W	Mfolozi	-28.35960	31.99434
13	W	Mfule, Mhlathuze	-28.51589	31.43614
14	W	Mhlathuze	-28.74695	31.74745
15	W	Nwaku, Matikulu	-28.94142	31.39416
16	W	Vutha, Matikulu	-29.06709	31.50588
17	W	Matikulu	-29.07655	31.56309
18	V	Slang, Buffalo, Thukela	-27.42067	30.29681
19	V	Ncandu, Buffalo, Thukela	-27.85144	29.75663
20	V	Buffalo, Thukela	-27.80344	30.24793
21	V	Mzinyashana, Buffalo, Thukela	-28.09882	30.31853
22	V	Thukela	-28.75633	30.15038
23	V	Bushmans, Thukela	-29.08337	29.82504
24	V	Mfulankomo, Mooi, Thukela	-29.38081	29.66052
25	V	Thukela	-29.17262	31.39192
26	U	Mvoti	-29.15986	30.62869
27	U	Mvoti	-29.37000	31.30434
28	U	Tongati	-29.55991	31.17409
29	U	Mdloti	-29.60208	31.00902
30	U	Umgeni	-29.48881	29.90304
31	U	Umgeni, Midmar Dam	-29.48813	30.15600
32	U	Umgeni, Fountain Hill Estate	-29.49125	30.49263
33	U	Umgeni, Mzinyathi	-29.71452	30.86806
34	U	Mlazi	-29.75600	30.28900

35	U	Mlazi	-29.80972	30.50000
36	U	Lovu	-29.86145	30.26196
37	U	Lovu	-30.09689	30.82220
38	U	Mkhomazana, Mkomazi	-29.64577	29.43134
39	T	Mzimkhulu	-30.65224	30.19769
40	T	Mtamvuna	-30.84924	30.06400
41	U	Msunduzi, Umgeni, Nkanyezini	-29.60655	30.55259
42	U	Umgeni, Hilton College NR	-29.46352	30.29355
43	U	Mkomazi, Ad-hoc site 5	-29.67111	29.64172
44	U	Mkomazi, Ad-hoc site 4	-29.74174	29.90672
45	U	Mkomaz, Ad-hoc site 2	-30.00797	30.24332
46	U	Mkomazi, Ingulube bush camp Weir 3	-30.13493	30.67410
47	U	Gcumisa, Mlahlanja, Umgeni	-29.63601	30.68950
48	U	Ad hoc Site 1	-29.63601	30.68950
49	U	Weir 4 Mkomazi	-30.11880	30.58855
50	U	LMB WSS	-30.17047	30.71209
51	U	Weir 1 Sappi, Craigieburn	-30.18329	30.76199
52	W	Wild tomorrow, Msinene	-27.87825	32.33004

CHAPTER 5

Updated checklist of freshwater molluscs to assess species diversity and distribution in freshwater ecosystems of KwaZulu-Natal, South Africa

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Running header: Updated checklist of freshwater molluscs of KwaZulu-Natal, South Africa

5.1 Abstract

It has been more than 20 years since the last checklist on freshwater molluscs of KwaZulu-Natal was compiled. Since then, there have been rapid changes in ecosystems as well as in mollusc systematics, and a complete checklist of freshwater malacofauna is presently lacking. Here, we present a checklist of 69 freshwater mollusc species (55 gastropods and 14 bivalves) belonging to 16 families (11 gastropods and five bivalves) in KwaZulu-Natal, South Africa. The list includes historical records, online sources, and our latest research sampling, which collected data on only 24 species. Family Planorbidae amongst the gastropods was the most diverse (17 species), while Sphaeriidae was the most diverse within the bivalves (seven species). Of the three water management areas (WMAs) in the province, U, V, W, 'U' harboured the most diverse mollusc community, with a total of 54 species (43 gastropods and 11 bivalves). The gastropods *Tomichia natalensis* (Connolly, 1939) and *Tomichia tristis* (Morelet, 1889) are listed as Critically Endangered (CR), and *Tomichia ventricosa* (Reeve, 1842) Endangered (EN) on the International Union for Conservation of Nature (IUCN) Red List; while the vast majority of freshwater molluscs are listed as either Least Concern (LC) or Data Deficient (DD). In comparison with the previous published freshwater mollusc checklist for the province, a total of 21 species were added in this study: *Euglesa costulosa* (Connolly, 1931), *Euglesa langleyana* (Melvill and Ponsoby, 1891), *Euglesa ovampica* (Ancey, 1890), *Euglesa viridaria* (Kuiper, 1956), *Tomichia natalensis* (Connolly, 1939), *Tomichia tristis* (Morelet, 1889), *Tomichia ventricosa* (Reeve, 1842) and *Gyraulus chinensis* (Dunker, 1848), *Stenophysa marmorata* (Guilding, 1828), *Tarebia granifera* (Lamarck, 1816), and eleven *Burnupia* species. Twenty-four freshwater molluscs recovered in recent surveys suggest a possible decline in mollusc freshwater species diversity, given the lack of

a long-term monitoring program, as well as global and regional trends in anthropogenic activities, invasive species, and climate change in the province of KwaZulu-Natal.

Keywords: checklist, freshwater molluscs, historical records, molluscs sampling

5.2 Introduction

Biodiversity in freshwater ecosystems accounts for approximately 10% of the global species richness and provides invaluable ecosystem services that sustain human health, nutrition, and freshwater supply (Darwall et al., 2018; Neubauer et al., 2021; Ziganira and Downs, 2025). Freshwater molluscs of Africa are approximately 75% gastropods and 25% bivalves, and are less diverse than those of Europe and North America (Bogan 2008; Seddon et al. 2011; Ziganira and Downs 2025). Globally, freshwater molluscs are under threat, and species diversity is declining because of anthropogenic activities (Darwall et al. 2018; Neubauer et al. 2021). According to the IUCN Red List of Threatened Species, nearly 25% of freshwater gastropods and 10% of freshwater bivalves are extinct (http://www.iucnredlist.org/; Marković et al. 2021). As a result, many freshwater molluscs are listed for conservation at national, regional, and global levels (Herbert 1998; Marković et al. 2021).

South Africa's biodiversity exhibits high levels of endemism (Herbert 1998). Within South Africa, the Maputaland–Pondoland–Albany (MPA) region on the eastern coast has been identified as a biodiversity hotspot and centre for endemism for Mollusca (Hart et al. 2014; Perera et al. 2021; Chapter 3). With its diverse geology and climate, the province of KwaZulu-Natal harbours a high diversity of freshwater mollusc species, including endemic taxa (Brown 1967, 1994; Herbert 1998; Chapter 3). The previous checklist of freshwater molluscs of KwaZulu-Natal included ca. 60 species (Brown 1967, 1980, 1994; Mandahl-Barth 1988; Appleton 1996), but the list was not exhaustive, as some species mentioned by Ziganira et al. (2026, see Chapter 3), were omitted.

According to Ziganira et al. (2026, see Chapter 3), 69 freshwater mollusc species were historically found in KwaZulu-Natal, and their data and specimens are deposited in museum collections across South Africa. However, Ziganira et al. (2026) only provided the species list and its historical occurrences, without adding other information such as type localities, habitat preferences, and present distribution.

Recent surveys across 52 REMP sites in KwaZulu-Natal confirmed the validity of historical data, suggesting the presence of one invasive species, *Tarebia granifera* (Lamarck, 1816), which was not accounted for in the previous checklist (Appleton 1996; Chapter 4). It has been more than 20 years since the checklist on freshwater molluscs of KwaZulu-Natal was compiled (Brown 1967; 1994; Appleton 1996). Since then, there have been rapid changes in the freshwater ecosystems of KwaZulu-Natal, and a revised checklist of freshwater malacofauna is presently lacking. Presently, the sustainability of freshwater ecosystems and all living organisms inhabiting them is under severe anthropogenic pressure in this province (Agboola et al. 2020b; Evans et al. 2022; Burnett et al. 2025). Thus, the need to protect freshwater ecosystems is prominent. Our study aimed to present an up-to-date checklist of freshwater molluscs recorded in KwaZulu-Natal. Our goal was to compile a reviewed checklist of all freshwater gastropod and bivalve species to assess changes in faunal composition that have occurred, and to provide information to enhance the conservation of these species. We predicted that historical data would present more records than the present study, and a high abundance of molluscs would be found in areas with a high number of sites. Additionally, we predicted that endemic species would be less abundant, while invasive species would be the most prevalent at sampled sites.

5.3 Methods

5.3.1 Historical records

Historical records of freshwater molluscs of KwaZulu-Natal were sourced from a recent comprehensive study by Ziganira et al. (2026, see Chapter 3), which analysed 124 years (1897 to 2021) of mollusc sampling in the province. These historical data were drawn from the Mollusca collections of the Albany Museum in Makanda (AMM), Eastern Cape Province, East London Museum (ELM), East London, Eastern Cape, KwaZulu-Natal Museum (KZNM), Pietermaritzburg, KwaZulu-Natal, the National Freshwater Snail Collection of South Africa (NFSC) and Freshwater Biodiversity Information System (FBIS) for KwaZulu-Natal (FBIS, 2022). The FBIS sourced data from the Global Biodiversity Information Facility (GBIF), peer-reviewed scientific papers, published reports, university theses, and unpublished reports (Dallas and Shelton 2024).

5.3.2 Mollusc sampling

We surveyed freshwater ecosystems in KwaZulu-Natal between February 2024 and September 2025. Samples were collected from 52 River Eco-Status Monitoring Programme (REMP) sites across the three water management areas (WMAs) of KwaZulu-Natal (Figure 5.1). Molluscs were sampled in summer and autumn (high-flow season) and in winter and spring (low-flow season) of 2024 and 2025. We visited each of the 52 sites four times. Mollusc specimens were collected using the kick-stir-sweep methodology as outlined by the South African Scoring System 5 (SASS5) (Dickens and Graham 2002); and hand picking during each sampling event. All the collected mollusc specimens were identified to species level based on shell characteristics by referring to the identification key developed by Brown (1994), and Appleton and Miranda (2015).

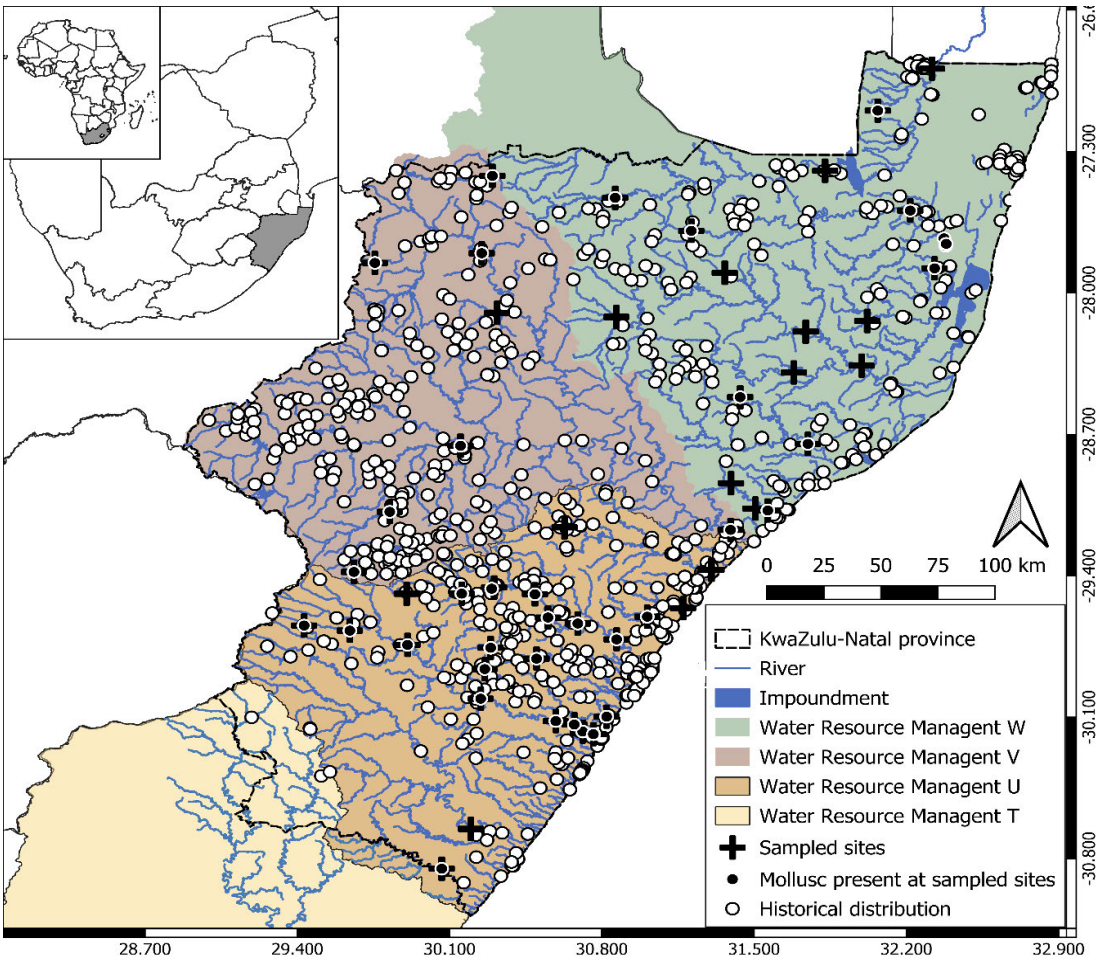


Figure 5.1: Freshwater mollusc spatial distribution showing historical sites and the 52 REMP sampled sites in the present study, with focus on the presence of molluscs.

5.3.3 Compilation of an annotated checklist

In this study, we used freshly collected mollusc specimens, historical records and records from FBIS to compile an up-to-date species checklist. We organised the checklist according to higher taxonomic levels (phylum, class, subclass, order, superfamily, family, subfamily, genus, and species). We grouped the family in alphabetic order, and species names were validated using the

'MolluscaBase' (https://www.molluscabase.org/). We deposited voucher specimens at the KwaZulu-Natal Museum (KZNM) in Pietermaritzburg.

5.4 Results

Sixty-nine freshwater mollusc species have been recorded in KwaZulu-Natal, but among these, only 24 species were recorded during our recent field study (Table 5.1). In the 'U' water management area, 22 species were sampled compared with 54 historical records, followed by eight species in the 'V' compared with 30 historical records, and 11 species in the 'W' compared with 41 historical records (Table 5.1). Overall, 45 freshwater mollusc species were not recovered in our recent field surveys of 2024 and 2025. *Bellamya capillata* (Frauenfeld, 1865) was the only species found in the 'W' water management area, while *Biomphalaria pfeifferi* (Krauss, 1848), *Burnupia Ponsonbyi* (B. Walker, 1924), *Corbicula fluminalis* (O. F. Müller, 1774), *Physella acuta* (Draparnaud, 1805), *Sphaerium capense* (Krauss, 1848), and *Tarebia granifera* (Lamarck, 1816) were sampled across the three water management areas (Table 5.1).

Family Planorbidae, amongst the gastropods, was the most diverse (17 species), while Sphaeriidae was the most diverse within the bivalves (seven species) (Figure 5.2). The 'U' Water Management Area harboured the most diverse mollusc community, with a historical total record of 54 species (43 gastropods and 11 bivalves). The gastropods *Tomichia natalensis* (Connolly, 1939) and *Tomichia tristis* (Morelet, 1889) are listed as Critically Endangered (CR), and *Tomichia ventricosa* (Reeve, 1842) is Endangered (EN) on the IUCN Red List; while the vast majority of freshwater molluscs are listed either Least Concern (LC) or Data Deficient (DD).

In comparison with the previous freshwater mollusc checklist by Appleton (1996), a total of 21 species were added in this study: *Euglesa costulosa* (Connolly, 1931), *Euglesa langleyana*

(Melvill and Ponsoby, 1891), *Euglesa ovampica* (Ancey, 1890), *Euglesa viridaria* (Kuiper, 1956), *Tomichia natalensis* (Connolly, 1939), *Tomichia tristis* (Morelet, 1889), *Tomichia ventricosa* (Reeve, 1842) and *Gyraulus chinensis* (Dunker, 1848), *Stenophysa marmorata* (Guilding, 1828), *Tarebia granifera* (Lamarck, 1816), and eleven *Burnupia* species.

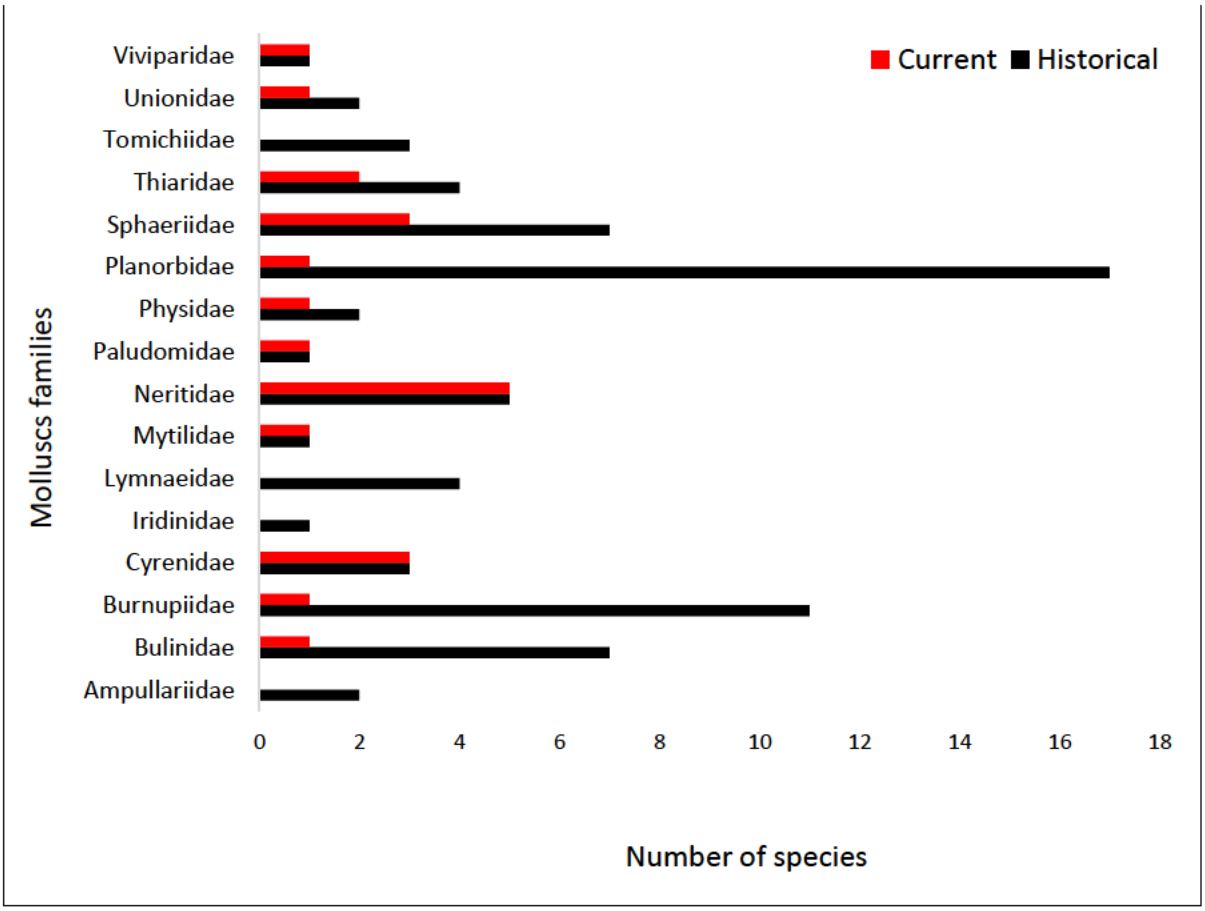


Figure 5.2: Species richness shown per freshwater mollusc family between historical data (1897 – 2021) and present data (2024 - 2025) collected across the three water management areas of KwaZulu-Natal, South Africa. In total, 16 families representing 69 species were recorded historically, while 11 families representing 24 species were recorded in the recent field study.

Table 5.1: Occurrence of freshwater mollusc species in the three water management areas (WMA) of KwaZulu-Natal between Historical records (1897 - 2021) and this study (2024 - 2025). Historical points were estimated within the radius of sampling sites of the present study within each of the three WMAs using GEOLocate Web Application tool (https://www.geo-locate.org/), based on their locality descriptions and coordinates (see also Chapter 4).

Family	Taxa	Water management areas of KwaZulu-Natal					
		1897 - 2021			2024 - 2025		
		U	V	W	U	V	W
Planorbidae	*Afrogyrorbis natalensis* (Krauss, 1848)	x	x	x			
Viviparidae	*Bellamya capillata* (Frauenfeld, 1865)			x			x
Planorbidae	*Biomphalaria pfeifferi* (Krauss, 1848)	x	x	x	x	x	x
Mytilidae	*Brachidontes virgiliae* (Barnard, 1964)	x		x	x	x	
Bulinidae	*Bulinus africanus* (Krauss, 1848)	x	x	x			
Bulinidae	*Bulinus forskalii* (Ehrenberg, 1831)	x	x	x	x		
Bulinidae	*Bulinus globosus* (Morelet, 1866)	x		x			
Bulinidae	*Bulinus natalensis* (Kuster, 1841)	x		x			
Bulinidae	*Bulinus reticulatus* (Mandahl-Barth, 1954)		x				
Bulinidae	*Bulinus tropicus* (Krauss, 1848)	x	x	x	x		
Burnupiidae	*Burnupia brunnea* (B. Walker, 1924)	x					
Burnupiidae	*Burnupia caffra* (Krauss, 1848)	x	x	x	x		
Burnupiidae	*Burnupia capensis* (B. Walker, 1912)	x	x	x			
Burnupiidae	*Burnupia capensis natalensis* (B. Walker, 1924)	x					
Burnupiidae	*Burnupia farquhari* (B. Walker, 1912)	x	x				
Burnupiidae	*Burnupia gordonensis* (Melvill & Ponsonby, 1903)	x	x			x	
Burnupiidae	*Burnupia mooiensis* (B. Walker, 1912)	x	x				
Burnupiidae	*Burnupia nana* (B. Walker, 1912)	x		x			
Burnupiidae	*Burnupia ponsonbyi* (B. Walker, 1924)	x	x		x	x	x

Burnupiidae	*Burnupia stenochorias* (Melvill & Ponsonby, 1903)		x				
Burnupiidae	*Burnupia transvaalensis* (Craven, 1881)	x					
Iridinidae	*Chambardia wahlbergi* (Krauss, 1848)	x		x			
Paludomidae	*Cleopatra ferruginea* (I. Lea & H. C. Lea, 1851)			x	x		x
Unionidae	*Coelatura mossambicensis* (E. von Martens, 1860)			x			
Cyrenidae	*Corbicula africana* (Krauss, 1848)	x		x	x		x
Cyrenidae	*Corbicula astartina* (E. von Martens, 1860)			x	x		
Cyrenidae	*Corbicula fluminalis* (O. F. Müller, 1774)	x	x	x	x	x	x
Sphaeriidae	*Euglesa costulosa* (Connolly, 1931)	x	x		x		
Sphaeriidae	*Euglesa langleyana* (Melvill & Ponsoby, 1891)	x	x				
Sphaeriidae	*Euglesa ovampica* (Ancey, 1890)	x					
Sphaeriidae	*Euglesa viridaria* (Kuiper, 1956)	x	x				
Sphaeriidae	*Eupera ferruginea* (Krauss, 1848)	x			x		
Lymnaeidae	*Galba truncatula* (O. F. Müller, 1774)	x	x				
Planorbidae	*Gyraulus andrussovi* (A. A. Ali-Zade & Kabakova, 1969)	x					
Planorbidae	*Gyraulus chinensis* (Dunker, 1848)			x			
Planorbidae	*Gyraulus connollyi* (D. S. Brown & Van Eeden, 1969)	x	x	x			
Planorbidae	*Gyraulus costulatus* (Krauss, 1848)	x	x	x			
Planorbidae	*Hovorbis coretus* (Blainville, 1826)	x	x				
Ampullariidae	*Lanistes ovum* (Troschel, 1845)			x			
Planorbidae	*Lentorbis carringtoni* (Azevedo, de Medeiros & M. C. Faro, 1961)	x					
Thiaridae	*Melanoides tuberculata* (O. F. Müller, 1774)	x		x	x		x
Neritidae	*Neritina pulligera* (Linnaeus, 1767)	x		x	x		x
Planorbidae	*Pettancylus burnupi* (B. Walker, 1912)		x	x			
Planorbidae	*Pettancylus cawstoni* (B. Walker, 1924)	x					
Planorbidae	*Pettancylus connollyi* (B. Walker, 1912)	x		x			
Planorbidae	*Pettancylus fontinalis* (B. Walker, 1912)	x					
Planorbidae	*Pettancylus natalensis* (B. Walker, 1924)	x					
Physidae	*Physella acuta* (Draparnaud, 1805)	x	x	x	x	x	x
Planorbidae	*Planorbella duryi* (W. B. Marshall, 1926)	x					

Ampullariidae	*Pomacea bridgesii* (Reeve, 1856)	x					
Lymnaeidae	*Pseudosuccinea columella* (Say, 1817)	x	x	x			
Lymnaeidae	*Radix natalensis* (Krauss, 1848)	x	x	x			
Lymnaeidae	*Radix rubiginosa* (Michelin, 1831)			x			
Planorbidae	*Segmentorbis angustus* (Jickeli, 1874)	x		x			
Planorbidae	*Segmentorbis kanisaensis* (Preston, 1914)	x		x			
Planorbidae	*Segmentorbis planodiscus* (Melvill & Ponsonby, 1897)	x	x				
Neritidae	*Septaria porcellana borbonica* (Bory de Saint-Vincent, 1804)			x	x		
Neritidae	*Septaria tessellaria* (Lamarck, 1816)			x	x		
Sphaeriidae	*Sphaerium capense* (Krauss, 1848)			x	x	x	x
Sphaeriidae	*Sphaerium incomitatum* (Kuiper, 1966)	x	x	x			
Physidae	*Stenophysa marmorata* (Guilding, 1828)	x		x			
Thiaridae	*Tarebia granifera* (Lamarck, 1816)	x		x	x	x	x
Thiaridae	*Thiara amarula* (Linnaeus, 1758)	x		x			
Tomichiidae	*Tomichia natalensis* (Connolly, 1939)		x				
Tomichiidae	*Tomichia tristis* (Morelet, 1889)	x					
Tomichiidae	*Tomichia ventricosa* (Reeve, 1842)	x	x				
Unionidae	*Unio caffer* (Krauss, 1848)	x	x	x	x		
Neritidae	*Vittina gagates* (Lamarck, 1822)	x			x		
Neritidae	*Vittina natalensis* (Reeve, 1855)			x	x		
16 Families	69 species	54	30	41	22	8	11
Proportion (%)		78.2%	43.4%	59.4%	91.7%	33.3%	45.8%
Species richness		69 species			24 species		

5.5 Annotated checklist

The presented taxa list and corresponding check references are based on historical records of freshwater molluscs in KwaZulu-Natal and include data from our most recent surveys. A total of 69 valid freshwater mollusc species of KwaZulu-Natal (55 gastropods and 14 bivalves) belonging to 16 families (11 gastropods and five bivalves) are presented here.

Phylum Mollusca

Class Gastropoda (Cuvier, 1795)

Subclass Caenogastropoda L. R. Cox, 1960

Order Architaenioglossa Haller, 1892

Superfamily Ampullarioidea Gray, 1824

Family Ampullariidae J. E. Gray, 1824

Subfamily Ampullariinae J. E. Gray, 1824

Genus *Lanistes* Montfort, 1810

1. *Lanistes ovum* (Troschel, 1845)

Type locality: Zambezi River, Tete, Mozambique (Troschel 1845). This freshwater mollusc prefers a habitat of standing and slowly flowing waters, with muddy bottoms and vegetation (Mandahl-Barth et al. 1974), seasonal pans (Appleton 1977), rainpools (Betterton 1984), and fishponds (Fashuyi 1990). *Lanistes ovum* is widely distributed in southern Africa, including Congo and Kenya, and from the Okavango River system to the Pongolo River in KwaZulu-Natal (Brown 1967, 1994; Appleton 1996; Mahulu et al. 2021; Rapalai 2024). Our historical data revealed nine records collected in the Ndumo Nature Reserve, located in northern KwaZulu-Natal

(Supplementary information Figure S5.1). However, our recent surveys in 2024 and 2025 did not collect this freshwater mollusc (Chapter 4). IUCN Red List Category: Least Concern (LC). Year assessed: 2017.

Subfamily Pomaceinae Starobogatov, 1983

Genus *Pomacea* Perry, 1810

2. *Pomacea bridgesii* (Reeve, 1856)

Type locality: central South America (Reeve 1856). *Pomacea bridgesii* is commonly sold by aquarium dealers in South Africa and is bred commercially within the country (Appleton 2003). KwaZulu-Natal, *P. bridgessii* was collected in an impoundment on the Kloof River in Westville, Durban (Appleton 2003). Our historical data showed two records collected in 1996 on the Uvongo, Doolings Fish Farm and in Shelly Beach, KwaZulu-Natal (Supplementary information Figure S5.2). However, our recent surveys in 2024 and 2025 did not collect this species in the region (Chapter 4). IUCN Red List Category: Least Concern (LC). Year Assessed: 2011.

Order Caenogastropoda *incertae sedis* (temporary name)

Superfamily Cerithioidea J. Fleming, 1822

Family Paludomidae Stoliczka, 1868

Subfamily Cleopatrinae Pilsbry and Bequaert, 1927

Genus *Cleopatra* Troschel, 1857

3. *Cleopatra ferruginea* (I. Lea and H. C. Lea, 1851)

Type locality: Zanzibar, Tanzania (Lea and Lea 1851). *Cleopatra ferruginea* inhabits ponds, streams, swamps, and ditches. Muddy residual pools of seasonal streams and rocks in permanent

rivers have been reported (Brown 1994). The distribution of this mollusc is found in Eastern Kenya, Tanzania, Mozambique, as well as in Mpumalanga and KwaZulu-Natal, South Africa (Brown 1967). In KwaZulu-Natal, *C. ferruginea* was reported in the Zululand area around Lake St. Lucia, Manuan Creek, and Tete Pan (Connolly 1939; Brown 1967). Our historical data showed three records of *C. ferruginea* collected in the Ndumo Nature Reserve, Nyamithi Pan. Our recent surveys, conducted in 2024 and 2025, collected molluscs at three sites: the Umtamvuna River, Matigulu River, and Mlazi River (Supplementary information Figure S5.3). IUCN Red List Category: Least Concern (LC), Year Assessed: 2020.

Family Thiaridae Gill, 1871 (1823)

Subfamily Thiarinae Gill, 1871 (1823)

Genus *Melanoides* Olivier, 1804

4. *Melanoides tuberculata* (O. F. Müller, 1774)

Type locality: Coromandel Coast, south-eastern India (Müller 1774). *Melanoides tuberculata* inhabits various permanent waterbodies, including rivers, lakes and human-made habitats (Ndifon and Ukoli 1989; Brown 1994). The mollusc is widely distributed in the Indo-Pacific region, the Arabian Peninsula, sub-Saharan Africa and the Caribbean Islands, where it is considered introduced (Pointier 1989; Brown 1994; Genner et al. 2004; Van Bocxlaer et al. 2015). In South Africa, the mollusc was reported in the Eastern Cape, Mpumalanga and KwaZulu-Natal (Brown 1967). In KwaZulu-Natal, *M. tuberculate* was collected along the coastal areas between the Umzimai River and north of Port Shepstone, and more inland around the Riet River, Pongola (Brown 1967). Our historical data showed 39 records scattered across the ‘U’ and ‘W’ Water Management Areas of KwaZulu-Natal. Our recent surveys, conducted in 2024 and 2025, collected

molluscs at 12 sites in the ‘U’ and ‘W’ Water Management Areas of KwaZulu-Natal (Supplementary information Figure S5.4). IUCN Red List Category: Least Concern (LC). Year Assessed: 2017.

Genus *Tarebia* H. Adams and A. Adams, 1854

5. *Tarebia granifera* (Lamarck, 1816)

Type locality: Western part of Timor Island (Lamarck 1816). *Tarebia granifera* has become invasive in many places, including Venezuela, Florida, USA, several Caribbean Islands and South Africa (Appleton 2003). It has been reported in Mpumalanga Province and several localities in Northern KwaZulu-Natal (Appleton 2003). Our historical data showed 10 records scattered across the ‘U’ and ‘W’ Water Management Areas of KwaZulu-Natal, along the coast from Durban to Lake St. Lucia. Our recent surveys in 2024 and 2025 collected the mollusc at 11 sites in the three Water Management Areas of KwaZulu-Natal. The presence of the mollusc was recorded from the Mkomazi River to Mkuze, and inland up to the Umgeni River near Pietermaritzburg (Supplementary information Figure S5.5). IUCN Red List Category: Least Concern (LC). Year Assessed: 2010.

Genus *Thiara* Roding, 1798

6. *Thiara amarula* (Linnaeus, 1758)

Type locality: Asia. *Thiara amarula* inhabits rivers and streams just above the limit of tidal influence (Brown 1994). The mollusc is distributed in the Indo-Pacific coasts, including Madagascar and East Africa, from Somalia to KwaZulu-Natal, South Africa (Connolly 1939; Brown 1994). Our historical data showed eight records scattered in the ‘U’ and ‘W’ Water

Management Areas of KwaZulu-Natal, along the coast from Durban to Lake St. Lucia (Supplementary information Figure S5.6). Our recent surveys in 2024 and 2025 did not collect the mollusc (Chapter 4). IUCN Red List Category: Least Concern (LC). Year assessed: 2016.

Order Littorinimorpha A. N. Golikov and Starobogatov, 1975

Superfamily Truncatelloidea J. E. Gray, 1840

Family Tomichiidae Wenz, 1938

Genus *Tomichia* W. H. Benson, 1851

The genus *Tomichia* is primarily reported or known from the Congo (Verdcourt 1951), but three species have been described from KwaZulu-Natal (Brown 1967).

7. *Tomichia natalensis* (Connolly, 1939)

Type locality: Lower Umkomaas, KwaZulu-Natal, South Africa (Connolly 1939). *Tomichia natalensis* inhabits freshwater streams with pulmonates, on mud slopes shaded by vegetation (Brown 1980a, 1994; Davis 1981). In KwaZulu-Natal, records show Winkel Spruit (Connolly 1939); Inyezane and Ibati Rivers between Empangeni and Gingindlovu (Brown 1967, 1994). Our historical data showed only one record collected on the lower Tugela River; however, data from FBIS reveal four records collected near Pietermaritzburg and in Mtubatuba (Supplementary information Figure S5.7). Our recent surveys in 2024 and 2025 did not collect the mollusc (Chapter 4). IUCN Red List Category: Critically Endangered (CR). Year Assessed: 2007.

8. *Tomichia tristis* (Morelet, 1889)

Type locality: Gqeberha (Port Elizabeth), Eastern Cape Province, South Africa (Morelet 1889). *Tomichia tristis* inhabits amphibious areas, high on the shore of a saline lagoon (Davis 1981). The mollusc was also reported in Jeffreys Bay and possibly Port Alfred (Brown 1994). Our historical data showed three records collected in Umkomaas and near Port Shepstone. However, data from FBIS reveal one record collected in the Vumankala River in the Zululand (Supplementary information Figure S5.8). Our recent surveys in 2024 and 2025 did not collect the mollusc (Chapter 4). IUCN Red List Category: Critically Endangered (CR). Year Assessed: 2007.

9. *Tomichia ventricosa* (Reeve, 1842)

Type locality: Lakeside (Muizenberg Vlei), between Cape Town and Simonstown, South Africa (Reeve 1842). *Tomichia ventricosa* inhabits rivers, coastal wetlands, estuaries, as well as vleis and pans that dry out seasonally, becoming highly saline (Davis 1981; Brown 1994). Its distribution in South Africa spans the south-western coastal areas, where habitat destruction by anthropogenic causes a severe threat to the mollusc (Brown 1994). Our historical data showed two records of *T. ventricosa* collected at Albert Falls on the Umgeni River and Labuschagne's Kraal, Tugela River (Supplementary information Figure S5.9). Our recent surveys in 2024 and 2025 did not collect the mollusc (Chapter 4). IUCN Red List Category: Endangered (EN). Year Assessed: 2007.

Subclass Heterobranchia Burmeister, 1837

Superorder Hygrophila A. Férussac, 1822

Superfamily Lymnaeoidea Rafinesque, 1815

Family Bulinidae P. Fischer and Crosse, 1880

Subfamily Bulininae P. Fischer and Crosse, 1880

Genus *Bulinus* O. F. Müller, 1781

10. *Bulinus africanus* (Krauss, 1848)

Type locality: Port Natal, Durban, KwaZulu-Natal, South Africa (Krauss 1848). *Bulinus africanus* is common in streams and small dams, where the water is more permanent (Brown 1967; 1994). It is widely distributed from southern to Eastern Africa and can aestivate for long periods (Appleton and Miranda 2015). This species serves as an intermediate host for parasites that cause bilharzia in humans (Appleton and Miranda 2015) and schistosomiasis in both domesticated and wild bovines (Brown 1994; Appleton 1996; Rapalai 2024; Ziganira and Downs 2025). Our historical data showed 19 records collected across the three Water Management Areas of KwaZulu-Natal (Supplementary information Figure S5.10). However, our recent surveys in 2024 and 2025 did not collect *B. africanus* (Chapter 4). IUCN Red List Category: Least Concern (LC). Year Assessed: 2006.

11. *Bulinus forskalii* (Ehrenberg, 1831)

Type locality: Damietta, Egypt, Angola (Ehrenberg 1831) and Eastern Cape Province, South Africa (Krauss 1848; Melvill and Ponsonby 1897). *Bulinus forskali* is commonly found in temporary habitats such as rainpools, but is not confined to them (Appleton 1996). It is widely distributed in southern Africa, except in arid regions (Appleton 1996). Our historical data revealed 177 records of *E. forskalii* widely distributed across the three Water Management Areas of KwaZulu-Natal (Supplementary information Figure S11). Our recent surveys in 2024 and 2025 collected the molluscs at five sites in the ‘U’ Water Management Areas of KwaZulu-Natal. The presence of the mollusc was recorded on the Mkomazi River, Umgeni River and Lovu River

(Supplementary information Figure S5.11). IUCN Red List Category: Least Concern (LC). Year Assessed: 2006.

12. *Bulinus globosus* (Morelet, 1866)

Type locality: Dande River, Luanda Province, Angola (Morelet 1866). *Bulinus globosus* typically inhabits shallow water, where it may be found on bare substrates, but is more commonly associated with aquatic plants (Thomas and Tait 1984). The distribution of this species is highly temperature-dependent, with the snail being absent from areas that are too cool (Brown, 1966, 1994). *Bulinus globosus* is widely distributed across the Afrotropical region, from South Sudan to Senegal, to southern Africa (Mandahl-Barth 1958; Brown 1994). In South Africa, *B. globosus* is found in Mpumalanga Province (south eastern Transvaal) (Shutte and Frank 1964) around Lake Futululu and near Lake Nhlabane, Richards Bay district (Brown 1967, 1994). The snail is of medicinal importance because it is an intermediate host of *S. haematobium* in many areas of Africa (Brown 1994; Ziganira and Brown 2025). Our historical data showed eight records spread across Zululand and the KwaZulu-Natal Midlands (Supplementary information Figure S5.12). However, our recent surveys of 2024 and 2025 did not collect *B. globosus* (Chapter 4). IUCN Red List Category: Least Concern (LC). Year Assessed: 2017.

13. *Bulinus natalensis* (Kuster, 1841)

Type locality: streams in the Umgeni Valley, KwaZulu-Natal, South Africa (Krauss 1841). *Bulinus natalensis* inhabits small pools, slowly flowing rivers, and lakes and is tentatively identified from crater lakes in Cameroon (Mimpfoundi and Greer 1990). The distribution range of this mollusc extends from the coastal area of Durban to Lake Sibayi, north east of KwaZulu-Natal (Brown

1967, 1994). Our historical data showed 66 records of *B. natalensis* scattered along the east coast of KwaZulu-Natal (Supplementary information Figure S5.13). However, our recent surveys of 2024 and 2025 did not collect this snail (Chapter 4). IUCN Red List Category: Least Concern (LC). Year Assessed: 2017.

14. *Bulinus reticulatus* (Mandahl-Barth, 1954)

Type locality: Kanyakar Well, near Kisumu, Kenya (Mandahl-Barth 1954). *Bulinus reticulatus* prefers small, briefly-filled pools and is widely distributed in eastern and southern Africa. Our historical data showed one record collected in a dam near Mariasdaal, western KwaZulu-Natal (Supplementary information Figure S5.14). However, our recent surveys of 2024 and 2025 did not collect this snail (Chapter 4). IUCN Red List Category: Least Concern (LC). Year Assessed: 2016.

15. *Bulinus tropicus* (Krauss, 1848)

Type locality: Lepenula (Olifants) River, Mpumalanga Province, South Africa (Krauss 1848) (exact location unknown). *Bulinus tropicus* prefers small earth dams and residual pools in seasonally flowing streams. It is widely distributed in the highlands of eastern Africa and the Highveld of southern Africa, from Ethiopia to southern Africa (Brown 1994). In KwaZulu-Natal, *B. tropicus* is widely distributed but less frequent near coastal regions (Brown 1967). *Bulinus tropicus* is an intermediate host for *Schistosoma haematobium* (Bilharz 1852), which causes human urinary schistosomiasis (Albrecht et al. 2018). It also serves as the intermediate host for the conical fluke of cattle, *Caticophoron microbothrium* (Appleton 1996). Our historical data showed 294 records collected across the three Water Management Areas, KwaZulu-Natal (Supplementary information Figure S5.15). Our recent surveys in 2024 and 2025 collected the

molluscs at two sites in the ‘U’ Water Management Areas of KwaZulu-Natal on the Mkomazi River (Supplementary information Figure S5.15). IUCN Red List Category: Least Concern (LC). Year Assessed: 2017.

16. *Burnupia brunnea* (B. Walker, 1924)

Type locality: Zoutpansberg, Limpopo Province, South Africa (Walker 1924). *Burnupia brunnea* is also distributed in KwaZulu-Natal, and our historical data showed one record collected near Bulwer in the Midlands (Supplementary information Figure S5.16). However, our recent surveys of 2024 and 2025 did not collect this mollusc (Chapter 4). IUCN Red List Category: Data Deficient (DD). Year Assessed: 2007.

17. *Burnupia caffra* (Krauss, 1848)

Type locality: Pietermaritzburg, KwaZulu-Natal, South Africa (Krauss 1848). *Burnupia caffra* is usually found on stones or vegetation in streams (Brown 1994). It has been spotted in the Naukluftberge of Namibia, an isolated living population in 1982 (Brown 1994), and in Lake Tanganyika (Leloup 1953). Our historical data showed 43 records in KwaZulu-Natal, scattered across the three Water Management Areas (Supplementary information Figure S5.17). Our recent surveys of 2024 and 2025 located the molluscs on three sites in the ‘U’ Water Management Areas of KwaZulu-Natal on the Mkomazi River, Mlazi River and Lovu River (Supplementary information Figure S5.17). However, our recent surveys in 2024 and 2025 did not collect this mollusc. IUCN Red List Category: Least Concern (LC). Year Assessed: 2006.

18. *Burnupia capensis* (B. Walker, 1912)

Type locality: Lakeside, Cape Peninsula, Western Cape Province, South Africa (Walker 1912). It is also distributed as far as Lesotho, and across KwaZulu-Natal. Our historical data showed 43 records of *Burnupia capensis* collected across the three Water Management Areas of KwaZulu-Natal (Supplementary information Figure S5.18). However, our recent surveys in 2024 and 2025 did not collect this mollusc. IUCN Red List Category: Data Deficient (DD). Year Assessed: 2007.

19. *Burnupia capensis natalensis* (B. Walker, 1924)

Based on our historical data for KwaZulu-Natal, the freshwater mollusc *Burnupia capensis* natalensis was reported at the Nonoti River and Umhlali Beach (Supplementary Information, Figure S5.19). However, our recent surveys of 2024 and 2025 did not collect this mollusc. IUCN Red List Category: Data Deficient (DD). Year Assessed: 2007.

20. *Burnupia farquhari* (B. Walker, 1912)

Type locality: York, NE Cape, South Africa (Walker 1912). Our historical data showed two records of *Burnupia farquhari* found near Bulwer and Tugela Valley in the Midlands of KwaZulu-Natal (Supplementary information Figure S5.20). However, our recent surveys in 2024 and 2025 did not collect this mollusc. IUCN Red List Category: Data Deficient (DD). Year Assessed: 2007.

21. *Burnupia gordonensis* (Melvill and Ponsonby, 1903)

Type locality: Gordon Falls, KwaZulu-Natal, South Africa (Melvill and Ponsonby 1903). Our historical data showed 14 records of *Burnupia gordonensis* found in the Durban area, Pietermaritzburg, and the Tugela Valley in the Midlands of KwaZulu-Natal (Supplementary

information Figure S5.21). Our recent surveys in 2024 and 2025 collected the molluscs at three sites in the 'V' Water Management Areas of KwaZulu-Natal on the Slang River (Supplementary information Figure S5.21). IUCN Red List Category: Data Deficient (DD). Year Assessed: 2007.

22. *Burnupia mooiensis* (B. Walker, 1912)

Type locality: Mooi River at Potchefstroom, (West Transvaal), North West Province, South Africa (Walker 1912). In KwaZulu-Natal, our historical records showed only one specimen record of *Burnupia mooiensis*, sourced from the FBIS (FBIS 2022), collected in 1956 from the Nonoti River (Supplementary information Figure S5.22). However, our recent surveys of 2024 and 2025 did not collect this mollusc. IUCN Red List Category: Data Deficient (DD). Year Assessed: 2009.

23. *Burnupia nana* (B. Walker, 1912)

Type locality: Karkloof stream, KwaZulu-Natal, South Africa (Walker 1912). Our historical data showed eight records of *Burnupia nana* scattered across the KwaZulu-Natal Midlands and the Zululand north coast (Supplementary information Figure S5.23). However, our recent surveys of 2024 and 2025 did not collect this mollusc. IUCN Red List Category: Data Deficient (DD). Year Assessed: 2007.

24. *Burnupia ponsonbyi* (B. Walker, 1924)

Type locality: Umgeni River, KwaZulu-Natal, South Africa (Walker 1924). Our historical data revealed eight records of *Burnupia ponsonbyi* scattered throughout the KwaZulu-Natal Midlands, most notably on the Umgeni River. Similarly, in our surveys of 2024 and 2025, *B. ponsonbyi* was collected in the three Water Management Areas of KwaZulu-Natal in high abundance at certain

sites (Supplementary information Figure S5.24). IUCN Red List: Data Deficient (DD). Year Assessed: 2007.

25. *Burnupia stenochorias* (Melvill and Ponsonby, 1903)

Type locality: Gqeberha (Port Elizabeth), Eastern Cape Province, South Africa (Melvill and Ponsonby 1903). In KwaZulu-Natal, our historical data showed three records of *Burnupia stenochorias* collected in the Midlands (Supplementary information Figure S5.25). However, our recent surveys in 2024 and 2025 did not collect this mollusc. IUCN Red List Category: Data Deficient (DD). Year Assessed: 2007.

26. *Burnupia transvaalensis* (Craven, 1881)

Type locality: Mooi River (Vaal), (Transvaal), North West Province, South Africa (Craven 1881). In KwaZulu-Natal, our historical data showed nine records of *Burnupia transvaalensis* collected in the Midlands (Supplementary information Figure S5.26). However, our recent surveys in 2024 and 2025 did not collect this mollusc. IUCN Red List Category: Data Deficient (DD). Year Assessed: 2007.

Family Lymnaeidae Rafinesque, 1815

Subfamily Lymnaeinae Rafinesque, 1815

Genus *Galba* Schrank, 1803

27. *Galba truncatula* (O. F. Müller, 1774)

Type locality: Thangelstedt in Thuringia, near Weimar, Germany (Müller, 1774). *Galba truncatula* is widely distributed in Africa, mainly in the sub-Saharan region through migratory birds (Brown

1994). It has been confined to the higher parts of southern and central South Africa, including Lesotho. It also serves as the major intermediate host for the common liver fluke *Fasciola hepatica* (Brown 1994; Appleton 1996). In KwaZulu-Natal, our historical data showed eight records scattered in the Midlands and the Tugela Valley (Supplementary information Figure S5.27). However, our recent surveys in 2024 and 2025 did not collect this mollusc. IUCN Red List Category: Least Concern (LC). Year Assessed: 2013.

Genus *Pseudosuccinea* F. C. Baker, 1908

28. *Pseudosuccinea columella* (Say, 1817)

Type locality: Philadelphia, United States of America (Say 1817). *Pseudosuccinea columella* was introduced to many parts of the world, including Africa. It was found around the Cape Flats in the Western Cape Province in 1944 (Connolly 1939; Barnard 1948), and has become invasive in many rivers of southern Africa (Appleton 1996). *Pseudosuccinea columella* is an intermediate host for *Fasciola hepatica*, and its introduction to South Africa may have increased the prevalence of liver fluke in livestock (Brown 1994; Appleton 1996). We found 267 records in our historical data scattered across the three Water Management Areas of KwaZulu-Natal (Supplementary information Figure S5.28). However, our recent surveys in 2024 and 2025 did not collect this mollusc. IUCN Red List Category: Least Concern (LC). Year Assessed: 2012.

Subfamily Amphipepleinae Pini, 1877

Genus *Radix* Montfort, 1810

29. *Radix natalensis* (Krauss, 1848)

Type locality, KwaZulu-Natal, South Africa (Krauss 1848). *Radix natalensis* is most frequent in permanent streams and impoundments such as small dams (Brown 1994). In Africa, it is found over the eastern half of the sub-continent north (from Sudan to Senegal across the Sahara), and in southern Africa (Appleton 1996). *Radix natalensis* is the major intermediate host of the giant liver fluke *Fasciola gigantica* (Brown 1994). Our historical data showed 266 records scattered across KwaZulu-Natal in the three Water Management Areas (Supplementary information Figure S5.29). However, our recent surveys in 2024 and 2025 did not collect this mollusc. IUCN Red List Category: Least Concern (LC). Year Assessed: 2017.

30. *Radix rubiginosa* (Michelin, 1831)

Type locality: East Indies (Michelin 1831). *Radix rubiginosa* is an introduced and potentially invasive species that originated in sub-tropical regions of Asia but has been introduced to and thrives in artificially heated habitats in Europe (Appleton and Miranda 2015). *Radix rubiginosa* is of medical and veterinary importance in its native Southeast Asia, where it serves as the intermediate host for various trematodes (Appleton and Miranda 2015). *Radix rubiginosa* is tolerant of a wide range of temperatures, conductivity and pH, which may explain its occurrence in a variety of habitats such as rivers, lakes, ponds, rice fields and irrigation canals in its native region (Chitramvong et al. 1981). In KwaZulu-Natal, its distribution in our historical data showed one record collected on the Amatikulu River, 110 km northeast of Durban in 2013 (Supplementary information Figure S5.30). However, our recent surveys in 2024 and 2025 did not collect this mollusc. IUCN Red List Category: No data.

Family Physidae Fitzinger, 1833

Subfamily Physinae Fitzinger, 1833

Genus *Physella* Haldeman, 1842

31. *Physella acuta* (Draparnaud, 1805)

Type locality: River Garonne, France (Draparnaud, 1805). *Physella acuta* inhabits both stagnant and flowing waters in or near towns, and is a pollution-tolerant species (Brown 1994). It is believed that this species originated from the Americas and was introduced to Europe, and other parts of the world, including South Africa (Van Bruggen 1966). Its range includes South Western Europe, Egypt, eastern and southern Africa (Ehrmann 1953; Mandahl-Barth 1962; Brown 1965). In KwaZulu-Natal, it is distributed from the Durban district between the Mhlatuzane River and Stanger, and inland near New Hanover (Brown 1967). It is considered invasive in South Africa and an intermediate host for food-borne trematode diseases such as echinostomiasis and fascioliasis (Lawton et al. 2018; Rapalai, 2024). Our historical data showed 19 records of *P. acuta* scattered in the three Water Management Areas of KwaZulu-Natal (Supplementary information Figure S5.31). Similarly, our recent surveys in 2024 and 2025 collected this species across the three Water Management Areas of the province (Chapter 4). IUCN Red List Category: Least Concern (LC). Year Assessed: 2016.

Genus *Stenophysa* E. von Martens, 1898

32. *Stenophysa marmorata* (Guilding, 1828)

Type locality: St Vincent, Lesser Antilles, Caribbean Islands, Central America (Guilding, 1828), and invasive in South Africa (Appleton, 2003; Appleton and Miranda, 2015). *Stenophysa marmorata* prefers various standing and flowing waters, mostly modified by man and moderately

polluted (Thomas and Tait 1984; Ndifon and Ukoli 1989; Brown 1994). It is widely distributed in sub-Saharan Africa, in west and southern Africa, suggesting that Portuguese ships may have spread this species during the slave trade (Brown 1994; Appleton 1996). In South Africa, *S. marmorata* is distributed from artificial and semi-natural waterbodies around Tzaneen, Limpopo Province and Durban, KwaZulu-Natal. Our historical data showed nine records of *S. marmorata* scattered along the south and north coast of KwaZulu-Natal (Supplementary information Figure S5.32). However, our recent surveys in 2024 and 2025 did not collect this species (Chapter 4). IUCN Red List Category: Least Concern. Year Assessed: 2011.

Family Planorbidae Rafinesque, 1815

Subfamily Planorbidae Rafinesque, 1815

Genus *Afrogyrorbis* Starobogatov, 1967

33. *Afrogyrorbis natalensis* (Krauss, 1848)

Type localities: Easter Cape (Melvill and Ponsonby 1893), KwaZulu-Natal (Krauss 1848) (South Africa) and Kenya (Preston 1912). This freshwater mollusc is common in slowly flowing streams, rainpools and marshes of Kenya and the eastern coast of South Africa (Brown 1994). In KwaZulu-Natal, the mollusc is distributed in the Umgeni Valley, near Durban (Brown 1994). Historical records of this study showed a wide distribution across KwaZulu-Natal, from Mvoti Valley to the Midlands and South Coast (Supplementary information Figure S5.33). This distribution is wider than previously reported (Brown 1994; Appleton 1996), however, recent surveys did not collect it. IUCN Red List Category: Least Concern (LC). Year Assessed: 2017.

Genus *Biomphalaria* Preston, 1910

34. *Biomphalaria pfeifferi* (Krauss, 1848)

Type locality: Umgeni Valley, KwaZulu-Natal, South Africa (Krauss 1848). *B. pfeifferi* is of medical importance because it serves as the intermediate host for *Schistosoma mansoni*, the parasite causing intestinal bilharzia in humans (Brown, 1994). *Biomphalaria pfeifferi* is widely distributed in Africa: Ethiopia, Kenya, Madagascar, Mozambique, Namibia, South Africa and Zambia (molluscabase.org). In KwaZulu-Natal, it is present in the Umgeni Valley (Krauss 1848; Melvill and Ponsonby 1903; Brown 1994). Our historical data showed 94 records of *B. pfeifferi* scattered across KwaZulu-Natal, and many in northern KwaZulu-Natal (Supplementary information Figure S5.34). Our recent surveys in 2024 and 2025 collected this mollusc across the three Water Management Areas of KwaZulu-Natal. IUCN Red List Category: Least Concern (LC). Year Assessed: 2016.

Genus *Gyraulus* Charpentier, 1837

35. *Gyraulus andrussovi* (A. A. Ali-Zade and Kabakova, 1969)

Type locality: Azerbaijan (Ali-Zade and Kabakova, 1969). *Gyraulus andrussovi* prefers permanent waters with rich aquatic vegetation, floating lily leaves and amongst leaf litter on the bottom (Brown 1994). Its distribution is throughout tropical Africa (Brown and Mandahl-Barth 1973). In southern Africa, its range includes Namibia and eastern KwaZulu-Natal around Lake Sibayi and Pietermaritzburg (Appleton 1977). Our historical data showed three records of *G. andrussovi* collected in the pool near the Umgeni River mouth, Clairwood and Umhloti River (Supplementary information Figure S5.35). However, our recent surveys in 2024 and 2025 did not collect this mollusc. IUCN Red List Category: No data.

36. *Gyraulus chinensis* (Dunker, 1848)

Gyraulus chinensis is an introduced and potentially invasive species that originated in sub-tropical regions of Asia, but has been introduced to and thrives in artificially heated habitats in Europe (Appleton and Miranda 2015). In Africa, it was found in rice fields in Guinea-Bissau, West Africa, in 1989 (Appleton and Miranda 2015). In January of 1995, it was found in South Africa in a consignment of aquarium plants from Singapore (Appleton and Miranda 2015). In KwaZulu-Natal, *G. chinensis* was found in 2004 in an aquarium in the foyer of a building on Howard College Campus, University of KwaZulu-Natal, Durban Campus. Its distribution in our historical data showed one record collected on the Amatikulu River, 110 km northeast of Durban (Supplementary information Figure S5.36). However, our recent surveys in 2024 and 2025 did not collect this mollusc. IUCN Red List Category: Least Concern (LC). Year Assessed: 2010.

37. *Gyraulus connollyi* (D. S. Brown and Van Eeden, 1969)

Type localities of *Gyraulus connollyi* are in Gauteng, near Vereeniging (Brown and Van Eeden 1969) and the Northern Cape Province (Connolly 1939). In South Africa, this species is endemic to the southern and central Highveld plateau, the lower half of the Drakensberg escarpment and the Eastern Cape (Appleton 1996). Our historical data showed 44 records scattered across the whole KwaZulu-Natal in the north, south, east and the Midlands (Supplementary information Figure S5.37). However, our recent surveys in 2024 and 2025 did not collect this mollusc. Its habitat includes vegetation and stones in rivers and streams (Brown 1994). IUCN Red List Category: Least Concern (LC). Year Assessed: 2007.

38. *Gyraulus costulatus* (Krauss, 1848)

Type locality: Umgeni Valley, KwaZulu-Natal, South Africa (Krauss 1848). *Gyraulus costulatus* is distributed in sub-Saharan Africa, particularly in southern Africa, including Mozambique (Connolly, 1925), Namibia (Brown et al., 1992), and South Africa (Krauss, 1948). There are isolated living populations in southeastern Algeria, Libya, and Egypt, as well as across the Sahara from Ethiopia to Senegal (Brown 1994). *Gyraulus costulatus* is widely distributed in South Africa. Its habitat includes aquatic vegetation, marginal grass, and stones in slowly flowing streams and rivers, as well as large dams and lakes (Brown 1994). Our historical data showed 136 records of *G. costulatus* scattered across the entire KwaZulu-Natal, including the north, south, east, and Midlands (Supplementary information Figure S5.38). However, our recent surveys in 2024 and 2025 did not collect this mollusc. IUCN Red List Category: Least Concern (LC). Year Assessed: 2017.

Genus *Hovorbis* D. S. Brown and Mandahl-Barth, 1973

39. *Hovorbis coretus* (Blainville, 1826)

Type locality: Podor, Senegal (Blainville 1826). *Hovorbis coretus* is widely distributed in West and East Africa, southern Africa, specifically in Angola (Breure et al. 2018), Mozambique (Connolly 1925), Namibia (Brown et al. 1992), and South Africa (1977). In KwaZulu-Natal, *H. coretus* was found in the north around Lake Sibayi (Appleton 1977), and Pietermaritzburg (Brown 1994). This mollusc prefers permanent waters with rich aquatic vegetation, floating lily leaves and leaf litter on the bottom. Our historical data showed two records, one in the Midlands and one in the northwest of KwaZulu-Natal (Supplementary information Figure S5.39). However, our recent

surveys in 2024 and 2025 did not collect this mollusc. IUCN Red List Category: Least Concern (LC). Year Assessed: 2017.

Genus *Lentorbis* Mandahl-Barth, 1954

40. *Lentorbis carringtoni* (Azevedo, de Medeiros and M. C. Faro, 1961)

Type locality: Nacala, Mozambique (Azevedo, de Medeiros and M. C. Faro, 1961). This mollusc is also found in the southeast of the former Transvaal, now Mpumalanga, and possibly in the coastal region of KwaZulu-Natal, South Africa (Brown 1994). Only one record is recorded near Durban in our historical data (Supplementary information Figure S5.40). Our recent surveys in 2024 and 2025 did not collect this mollusc. IUCN Red List Category: Least Concern (LC). Year Assessed: 2009.

Subfamily Ancylinae Rafinesque, 1815

Genus *Pettancylus* Iredale, 1943

41. *Pettancylus burnupi* (B. Walker, 1912)

Type locality: Equeefa River, KwaZulu-Natal, South Africa (Walker 1912). In our historical data, six records of *Pettancylus burnupi* were found scattered along the south coast of KwaZulu-Natal, the Midlands and north-west of the province (Supplementary information Figure S5.41). However, our recent surveys in 2024 and 2025 did not collect this mollusc. IUCN Red List Category: Data Deficient (DD). Year Assessed: 2009.

42. *Pettancylus cawstoni* (B. Walker, 1924)

Type locality: Mooi River at Potchefstroom, KwaZulu-Natal, South Africa (Walker 1924). Our historical data showed one record of *Pettancylus cawstoni* collected in Camperdown, near Pietermaritzburg (Supplementary information Figure S5.42). However, our recent surveys in 2024 and 2025 did not collect this mollusc. IUCN Red List Category: Data Deficient (DD). Year Assessed: 2009.

43. *Pettancylus connollyi* (B. Walker, 1912)

Type locality: Black River at Maitland, Western Cape Province, South Africa (Walker 1912). Only records from South Africa, including the Eastern and Western Cape Provinces, are known. In KwaZulu-Natal, *P. connollyi* was reported in the Umbilo River at Sarnia (Brown 1967). Our historical data showed five records distributed around the Pietermaritzburg area (Supplementary information Figure S5.43). However, our recent surveys in 2024 and 2025 did not collect this mollusc. IUCN Red List Category: Data Deficient (DD). Year Assessed: 2009.

44. *Pettancylus fontinalis* (B. Walker, 1912)

Type locality: Ranjesfonterin, Pretoria district, South Africa (Walker 1912). Only records from South Africa, including the Free State and Western Cape Provinces, are known. In KwaZulu-Natal, *P. fontinalis* was reported around the Durban area (Brown 1967). Our historical data showed one record collected around the Durban area (Supplementary information Figure S5.44). However, our recent surveys in 2024 and 2025 did not collect this mollusc. IUCN Red List Category: Data Deficient (DD). Year Assessed: 2009.

45. *Pettancylus natalensis* (B. Walker, 1924)

Type locality: South Coast Junction, KwaZulu-Natal, South Africa (Walker 1924). Only records from South Africa, including the Free State and Western Cape Provinces, are known for *Pettancylus natalensis*. In KwaZulu-Natal, *P. natalensis* was reported around the Durban area (Brown 1967). Our historical data showed one record collected in South Coast Junction (Supplementary information Figure S5.45). However, our recent surveys in 2024 and 2025 did not collect this mollusc. IUCN Red List Category: Data Deficient (DD). Year Assessed: 2007.

46. *Planorbella duryi* (W. B. Marshall, 1926)

Type locality: Everglades of Florida, United States of America (Marshall 1926). *Planorbella duryi* is widely distributed in the Americas, Europe and Africa, from Egypt to Cape Town (Brown 1994). In southern Africa, *Planorbella* species were introduced by human activities, as most species were reportedly found in aquaria and ornamental waterbodies (Brown 1967; Appleton 1996, 2003). In KwaZulu-Natal, it has been reported in the coastal lowlands of the province, where water temperature is warmer (Appleton 2003). Our historical data showed three records collected in the Nagel Dam area and around Westville, Durban (Supplementary information Figure S5.46). However, our recent surveys in 2024 and 2025 did not collect this mollusc. IUCN Red List Category: Data Deficient (DD). Year Assessed: No data.

47. *Segmentorbis angustus* (Jickeli, 1874)

Type locality: Toquor River at Mekerka (west of Asmara), Eritrea (Jickel 1874). *Segmentorbis angustus* is widespread in tropical Africa and inhabits permanent marshes, on rocks in streams and the stony beaches (Brown 1994). In KwaZulu-Natal, the mollusc was reported near the coast

between the Makosi River, near Port Shepstone, and the Inyezane River, near Amatikulu (Brown 1967). Our historical data showed two records collected in the Umzinto River and in permanent water in Eshowe (Supplementary information Figure S5.47). However, our recent surveys in 2024 and 2025 did not collect this mollusc. IUCN Red List Category: Least Concern (LC). Year Assessed: 2017.

48. *Segmentorbis kanisaensis* (Preston, 1914)

Type locality: Kanisa, Nile, South Sudan (Preston 1914). *Segmentorbis kanisaensis* is widespread in tropical Africa and inhabits permanent marshes and temporary rain pools (Brown 1994). In KwaZulu-Natal, *S. kanisaensis* was reported in Merebank near Durban and Ngoboseleni Lake, near Sodwana Bay (Connolly 1939; Brown 1967). Our historical data showed four records collected in Yengweni Pan, Ubombo, Mkhuze Nature Reserve and Merebank, Durban (Supplementary information Figure S5.48). However, our recent surveys in 2024 and 2025 did not collect this mollusc. IUCN Red List Category: Least Concern (LC). Year Assessed: 2017.

49. *Segmentorbis planodiscus* (Melvill and Ponsonby, 1897)

Type locality: uMgeni Valley, KwaZulu-Natal, South Africa (Melvill and Ponsonby 1897). Possible range of *Segmentorbis planodiscus* in South Africa includes the Eastern Cape Province and Mpumalanga (Connolly 1939; Brown 1967). In KwaZulu-Natal, *S. planodiscus* has been recorded in coastal localities between the Umbogintwini and Mtubatuba districts (Brown 1967, 1994). Our historical data showed two records collected at the Erasmus Dam in the lower Tugela River and the mouth of the uMgeni River, near Durban (Supplementary information Figure S5.49).

However, our recent surveys in 2024 and 2025 did not collect this mollusc. IUCN Red List Category: Least Concern (LC). Year Assessed: 2009.

Subclass Neritimorpha Koken, 1896

Oorder Cycloneritida Frýda, 1998

Superfamily Neritoidea Rafinesque, 1815

Family Neritidae Rafinesque, 1815

Subfamily Neritininae Poey, 1852

Genus *Neritina* Lamarck, 1816

50. *Neritina pulligera* (Linnaeus, 1767)

Type locality: not given. *Neritina pulligera* is distributed in East Africa, Mozambique and South Africa, including the African islands of the East (Brown 1994). In KwaZulu-Natal, the mollusc is distributed around the Durban area and Zululand (Appleton 1996). Our historical data showed six records of *N. pulligera* found on the South Coast and North Coast of KwaZulu-Natal (Supplementary information Figure S5.50). Similarly, our surveys in 2024 and 2025 collected this mollusc from a pool on the Mkomazi River, as well as from the Umgeni River in the rural community of Nkanyezini, and from the Matigulu and Mlazi rivers (Chapter 4). IUCN Red List Category: Conservation status: Least Concern (LC). Year Assessed: 2016.

Genus *Septaria* J. B. Férussac, 1807

Species *Septaria porcellana* (Linnaeus, 1758)

51. *Septaria porcellana borbonica* (Bory de Saint-Vincent, 1804)

Type locality: not given. *Septaria porcellana borbonica* inhabits streams on the coastal regions of KwaZulu-Natal, South Africa (Brown 1994). It is also distributed in the Indian Ocean Islands (Brown 1994). In KwaZulu-Natal, it has been recorded on the north coast between Mtunzini and Tongaat (Appleton 1996). Our historical data showed two records of the mollusc collected in Mtunzini and the Mzamba River. However, our surveys in 2024 and 2025 collected *S. porcellana borbonica* on the Mkomazi River in a pool, near the river mouth (Supplementary information Figure S5.51). IUCN Red List Category: No data.

52. *Septaria tessellaria* (Lamarck, 1816)

Type locality: Australia, Philippines, Sri Lanka (Lamarck 1816). *Septaria tessellaria* is widely distributed in Australia, the Philippines, Sri Lanka, Madagascar and South Africa. In KwaZulu-Natal, the mollusc is found in coastal localities between Amanzimtoti and the Mkomazi River (Connolly 1939; Brown 1967). Our historical data showed one record of the mollusc collected in the Nyoni Estuary, Amatikulu area, KwaZulu-Natal. However, our surveys in 2024 and 2025 collected *S. tessellaria* on the Mkomozi River (Supplementary information Figure S5.52). IUCN Red List Category: Least Concern (LC). Year Assessed: 2010.

Genus *Vittina* H. B. Baker, 1923

53. *Vittina gagates* (Lamarck, 1822)

Type locality: not given. *Vittina gagates* inhabits streams near tidal influence, on stones in currents (Starmühlner, 1969, 1983). It is distributed in the African Indian Ocean Islands, on the mainland between Mozambique and Mzamba in the Eastern Cape Province, South Africa (Brown, 1967,

1994; Appleton 1996). In KwaZulu-Natal, *V. gagates* was found in Tongaat, the Mkomazi River, and the Umgeni lagoon (Connolly 1939; Brown 1967). Our historical data showed three records sampled on the Umgeni River, Mkomazi River and Mzamba River. However, our recent surveys in 2024 and 2025 collected the mollusc in a pool of the Mkomazi River (Supplementary information Figure S5.53). IUCN Red List Category: Least Concern (LC). Year Assessed: 2016.

54. *Vittina natalensis* (Reeve, 1855)

Type locality: Umgeni River (near Durban), KwaZulu-Natal, South Africa (Reeve 1855). *Vittina natalensis* distribution range includes Mozambique and the Pangani River, Tanganyika (Pilsbry and Bequaert 1927; Brown 1967). In KwaZulu-Natal, the mollusc was previously found on the Mtamvuna River, Umzimkulu River and Umlalazi River (Connolly 1928; Brown 1967; Appleton 1996). Our historical data showed one record of *V. natalensis* collected on the Pongolo River in the North Coast of KwaZulu-Natal. Our recent surveys in 2024 and 2025 collected the mollusc in a pool on the Mkomazi River (Supplementary information Figure S5.54). IUCN Red List Category: No data.

Order Architaenioglossa Haller, 1892

Superfamily Viviparoidea Gray, 1847

Family Viviparidae J. E. Gray, 1847

Subfamily Bellamyinae Rohrbach, 1937

Genus *Bellamya* Jousseaume, 1886

55. *Bellamya capillata* (Frauenfeld, 1865)

Type locality: Lake Malawi, Malawi (Frauenfeld 1865). *Bellamya capillata* prefers lakes, rivers, and smaller water bodies if they are permanent. Its distribution ranges from Tanzania southwards into north-eastern KwaZulu-Natal, South Africa, and into the Lower DRC, Angola, the Okavango River, and Mozambique (Brown et al. 1992). Distribution in South Africa includes the southeastern former Transvaal, now Mpumalanga Province (Schutte and Frank 1964) and Lake Sibayi (Connolly 1939) in KwaZulu-Natal. Our historical data showed 16 records of *B. capillata* collected in the Pongolo River, Lake Sibayi, Ndumo Nature Reserve and Maputaland. Our recent surveys in 2024 and 2025 collected two specimens on the Pongolo River (Supplementary information Figure S5.55). IUCN Red List Category: Least Concern (LC). Year Assessed: 2017.

Class Bivalvia

Subclass Autobranchia Grobben, 1894

Order Mytilida A. Férussac, 1822

Superfamily Mytiloidea Rafinesque, 1815

Family Mytilidae Rafinesque, 1815

Subfamily Brachidontinae F. Nordsieck, 1969

Genus *Brachidontes* Swainson, 1840

56. *Brachidontes virgiliae* (Barnard, 1964)

Type locality: Keurbooms River, Western Cape Province, South Africa (Barnard 1964). *Brachidontes virgiliae* is a brackwater mussel that is conspicuous and largely attaches itself to rocks in large numbers (Appleton and Miranda 2015). The mollusc is widely distributed along the southern and eastern coast from South Africa to Mozambique (https://molluscabase.org). Our

historical data showed five records of *B. virgiliae* collected in the Ifafa, Amahlongwana, Mzinto and Illovo Rivers, and Lake St. Lucia. Our recent surveys in 2024 and 2025 collected *B. virgiliae* from the lower Mlazi, Mkomazi, and Tugela rivers (Supplementary information Figure S5.56). IUCN Red List Category: No data.

Order Unionida Gray, 1854

Superfamily Etherioidea Deshayes, 1832

Family Iridinidae Swainson, 1840

Subfamily Aspathariinae Modell, 1942

Genus *Chambardia* Bourguignat, 1891

57. *Chambardia wahlbergi* (Krauss, 1848)

Type locality: Apies River, a tributary of the Limpopo River, South Africa (Krauss 1848). *Chambardia wahlbergi* is the largest mussel species in southern Africa. It was recorded in West and East Africa, Kunene River, Botswana, southern Zimbabwe, Mozambique and South Africa (Brown 1967; Appleton 1996; Rapalai 2024). In KwaZulu-Natal, *C. wahlbergi* was recorded in the Enseleni River (Connolly 1939), Msunduzi River and south of Mtubatuba (Brown 1967). Our historical data showed 11 records of *C. wahlbergi* collected in the Ndumo Nature Reserve, Ubombo, Mkuze, the Eseleni River, the Pongola River, and sites in Pietermaritzburg (Supplementary information, Figure S5.57). Our recent surveys in 2024 and 2025 did not collect data on this species. IUCN Red List Category: Least Concern (LC). Year Assessed: 2018.

Superfamily Unionoidea Rafinesque, 1820

Family Unionidae Rafinesque, 1820

Subfamily Parreysiinae J. Henderson, 1935

Genus *Coelatura* Conrad, 1853

58. *Coelatura mossambicensis* (E. von Martens, 1860)

Type locality: Mozambique (Martens 1860). *Coelatura mossambicensis* has been recorded in Botswana, Malawi, Tanzania, Zimbabwe, Mozambique, and South Africa (molluscabase.org). Our historical data showed one record of *C. mossambicensis* collected in the Ngwavuma River (Supplementary information Figure S5.58). Our recent surveys in 2024 and 2025 did not collect data on this species. IUCN Red List Category: Least Concern (LC). Year Assessed: 2006.

Subfamily Unioninae Rafinesque, 1820

Genus *Unio* Philipsson, 1788

59. *Unio caffer* (Krauss, 1848)

Type locality: KwaZulu-Natal, South Africa (Krauss 1848). *Unio caffer* is endemic to southern Africa and widely distributed in this African region (Brown 1967; Rapalai 2024). *Unio caffer* usually inhabits rivers (seasonal and perennial), dams, and lakes (Appleton 1996). Our historical data showed eight records of *U. caffer* collected across the three Water Management Areas of KwaZulu-Natal, in the Slang, Umsunduzi, and the Little Tugela Rivers, and in Zululand (Supplementary information Figure S5.59). Our recent surveys in 2024 and 2025 collected the mollusc in the Mkomazi River (Chapter 4). IUCN Red List Category: Least Concern (LC). Year Assessed: 2007.

Subclass Autobranchia Grobben, 1894

Superorder Imparidentia Bieler, P. M. Mikkelsen and Giribet, 2014

Order Venerida Gray, 1854

Superfamily Cyrenoidea J. E. Gray, 1840

Family Cyrenidae J. E. Gray, 1840

Genus *Corbicula* Megerle von Mühlfeld, 1811

60. *Corbicula africana* (Krauss, 1848)

Type locality: Gauritz River, Western Cape Province, South Africa (Krauss 1848). *Corbicula africana's* distribution range extends from the Eastern and Western Cape Provinces in South Africa to the East African Great Lakes (Connolly 1939; Brown 1967). In KwaZulu-Natal, the mollusc is widely distributed in the eastern region along the coast from the Ifafa River and inland at Nagle Dam, near Pietermaritzburg (Brown 1967). Our historical data showed 19 records scattered in the 'U' and 'V' Water Management Areas of KwaZulu-Natal. Our recent surveys in 2024 and 2025 identified C. africana in the Mkomazi River, Mdloti River, Umgeni River, and Msunduzi River (Supplementary information Figure S5.60). IUCN Red List Category: Least Concern (LC). Year Assessed: 2018.

61. *Corbicula astartina* (E. von Martens, 1860)

Type locality: Geounit, Mozambique (von Martens 1860). The distribution range of *Corbicula astartina* extends from Zimbabwe, Mozambique and South Africa (Appleton 1996). Its range in South Africa is suspected to be widespread beyond the Cape Region, KwaZulu-Natal and Mpumalanga Provinces (Appleton 1996). Our historical data showed one record collected in Zululand, specifically in the Mkhuze Nature Reserve, from small pools on the dry bed of a river. Our recent surveys in 2024 and 2025 identified the mollusc on the Mlazi River and the Msunduzi

River in the rural community of Nkanyezini (Supplementary information Figure S5.61). IUCN Red List Category: Least Concern (LC). Year Assessed: 2006.

62. *Corbicula fluminalis* (O. F. Müller, 1774)

Type locality: Guangzhou (Canton), Guangdong Province, China (Müller, 1774). *Corbicula fluminalis* is widely distributed in Africa, Asia and Europe. It inhabits rivers, lakes, and dams across southern Africa, except in the arid western parts (Appleton 1996). Our historical data showed 11 records scattered across the three water management areas of KwaZulu-Natal. Our surveys in 2024 and 2025 identified this mollusc in the 'U' and 'V' Water Management Areas, which extend from the South Coast, Midlands, and the Tugela Valley (Supplementary information Figure S5.62). IUCN Red List Category: Least Concern (LC). Year Assessed: 2016.

Order Sphaeriida Lemer, Bieler and Giribet, 2019

Superfamily Sphaerioidea Deshayes, 1855 (1820)

Family Sphaeriidae Deshayes, 1855 (1820)

Subfamily Sphaeriinae Deshayes, 1855 (1820)

Genus *Euglesa* Jenyns, 1832

63. *Euglesa costulosa* (Connolly, 1931)

Type locality: Rhenoster River at Rustfontein, Free State, South Africa (Connolly 1931). This species is known from South Africa only, with a range extending from Western Cape Province, Free State, and the northern regions (Brown 1967). In KwaZulu-Natal, *E. costulosa* is widely distributed, particularly in areas with altitudes below 500 m (Kuiper 1966). Our historical data showed 10 records scattered from the KwaZulu-Natal Midlands to the Mvoti River. Our recent

surveys in 2024 and 2025 identified this mollusc on the Msunduzi River in the rural community of Nkanyenzini (Supplementary information Figure S5.63). IUCN Red List Category: No data.

64. *Euglesa langleyana* (Melvill and Ponsoby, 1891)

Type locality: Gqeberha (Port Elizabeth), Eastern Cape Province (Melvill and Ponsoby 1891). Native range of *Euglesa langleyana* is South Africa, and the extent of the range includes Eastern Cape Province and the Northern provinces historically known as Transvaal (Kuiper 1966). In KwaZulu-Natal, *E. langleyana* is widely distributed in the Durban area (Kuiper 1966). However, our historical data showed seven records of *E. langleyana* widely distributed from the KwaZulu-Natal Midlands to the Mvoti River and the lower Tugela River (Supplementary information Figure S5.64). Our recent surveys in 2024 and 2025 did not locate this mollusc (Chapter 4). IUCN Red List Category: No data.

65. *Euglesa ovampica* (Ancey, 1890)

Type locality: Omambonde River (Ovampoland), Namibia (Ancey 1890). *Euglesa ovampica* is widely distributed in the Eastern and Western Cape Provinces, (Eastern Transvaal) Mpumalanga Province, South Africa, (Swaziland) eSwatini (Brown and Kuiper unpublished observations), Uganda, Congo and Ethiopia (Brown 1967; Kuiper 1964). In KwaZulu-Natal, *E. ovampica* was found in Stanger (Brown 1967; Brown and Kuiper unpublished observations). Data from the FBIS show that one specimen record was collected in 1967 in the Mavivane River, Stanger, KwaZulu-Natal (FBIS, 2022; Supplementary information Figure S5.65). Our recent surveys in 2024 and 2025 did not collect this mollusc. IUCN Red List Category: Least Concern (LC). Year Assessed: 2016.

66. *Euglesa viridaria* (Kuiper, 1956)

Type locality: Near Nairobi, Kenya (Kuiper 1956). *Euglesa viridaria* is widely distributed in eastern and southern Africa, from Ethiopia to Western Cape Province of South Africa (Kuiper 1964; Brown 1967; Rapalai 2024). In KwaZulu-Natal, the snail is distributed from the coast to the foothills of the Drakensberg escarpment (Brown 1967). Our historical data showed six records of *E. viridaria* scattered in the Midlands and Zululand areas (Supplementary information Figure S5.66). However, our recent surveys in 2024 and 2025 did not locate any of this species (Chapter 4). IUCN Red List Category: No data.

Genus *Sphaerium* Scopoli, 1777

67. *Sphaerium capense* (Krauss, 1848)

Type locality: In Knysna River, Western Cape Province, South Africa (Krauss 1848). *Sphaerium capense* inhabits calm sandy substrates in lakes, rivers and streams (Van Damme et al. 2016). The distribution in sub-Saharan Africa includes Congo (Haas 1936) and the southern African region (Connolly 1939; Rapalai 2024). In KwaZulu-Natal, the mollusc is widely distributed in the northern area along the coast, from Tongaat to Lake St. Lucia and the Empangeni area (Haas 1936; Brown 1967). Our historical data showed six records of *S. capense* distributed in northern KwaZulu-Natal, including Maputaland, Lake Sibayi, Eshowe, the Umfolozi River, Lake Zilonde, and Lake Bangazi (Supplementary information Figure S5.67). Our surveys in 2024 and 2025 found *S. capense* across the three Water Management Areas of KwaZulu-Natal, suggesting a range expansion (Chapter 4). IUCN Red List Category: Least Concern (LC). Year Assessed: 2016.

68. *Sphaerium incomitatum* (Kuiper, 1966)

Type locality: Type locality: McIlwaine Lake outside Harare, Zimbabwe (Kuiper 1966). *Sphaerium incomitatum* is widely distributed in southern Africa, including the Democratic Republic of the Congo (Brown 1994). The mollusc is usually found in high densities and can tolerate freshwater bodies with low oxygen (Van Damme 2011). In KwaZulu-Natal, the mollusc was reported in the north-eastern region of the province (Appleton 1996). Our historical data showed *S. incomitatum* in the three Water Management Areas: Maputaland, Lake Zilonde, Mooi River and the Mzimkulu River (Supplementary information Figure S5.68). However, our surveys in 2024 and 2025 did not find this species (Chapter 4). IUCN Red List Category: Least Concern (LC). Year Assessed: 2009.

Subfamily Euperinae Heard, 1965

Genus *Eupera* Bourguignat, 1854

69. *Eupera ferruginea* (Krauss, 1848)

Type locality: Knysna River, Western Cape Province, South Africa (Krauss 1848). *Eupera ferruginea* is widely distributed in southern Africa (Brown 1967; Appleton 1996). In KwaZulu-Natal, its distribution includes localities near the coast as far south as Illovo Lagoon (Connolly 1939; Brown 1969). Our historical data showed two records collected on the Illovo River in KwaZulu-Natal. Similarly, our 2024 and 2025 surveys located this mollusc on the Mkomazi River (Supplementary information Figure S5.69). IUCN Red List Category: Least Concern (LC). Year Assessed: 2018.

5.6 Discussion

The publication of F. Krauss's "Die südafrikanischen Mollusken" in 1848, was the first major step to studying the molluscan fauna in South Africa (Kilburn 1999; Ziganira and Downs 2025). Some amateur malacologists, such as W.H. Turton, began collecting shells in the Eastern Cape and KwaZulu-Natal to send them overseas towards the end of the 19th century (Kilburn 1999). However, that rapidly changed in the 20th century and beyond as local interest increased (Kilburn 1999; Ziganira and Downs 2025). Historical freshwater mollusc data for KwaZulu-Natal indicate that the family Planorbidae comprised 17 species, whereas only one species was recorded at sites in our most recent surveys. Similarly, the family Burnupidae has 11 species historically recorded; however, only one species of this family was reported in our surveys in 2024 and 2025. Interestingly, five species of the family Neritidae were reported historically, and all were found during our latest surveys (Figure 5.2).

The absence of many freshwater mollusc species in our recent surveys at our REMP study sites (Chapter 4), totalling 45 species, suggests that the species composition of freshwater ecosystems in KwaZulu-Natal may be declining. Our surveys in 2024 and 2025 recorded 24 freshwater mollusc species out of 69 historically known species in the province (Chapter 4), with 13 species mapped at our REMP study sites (Chapter 4). In addition, no new species records for the KwaZulu-Natal have been reported since 2007, and likely, many of these historical voucher specimens are preserved in the South African museums (Chapter 3).

Our study has collected all available data to compile a checklist of the 69 freshwater mollusc species of KwaZulu-Natal (55 gastropods and 14 bivalves) belonging to 16 families (11 gastropods and five bivalves). The list includes historical records, online sources and our latest research samplings, which recovered 24 species. Family Planorbidae amongst the gastropods was

the most diverse (17 species), while family Sphaeriidae was the most diverse within the bivalves (seven species). The 'U' water management area harbours the most diverse mollusc community, with a total of 54 species (43 gastropods and 11 bivalves). There are 18 local endemic species, 16 of which are gastropods and two bivalves (Brown 1967; 1994; Appleton 1996; Herbert 1998). Most of these endemic freshwater mollusc species were recorded in the 'U' water management area of KwaZulu-Natal in our recent surveys. This area was found to have 25 sampling sites, nearly half of our total number of sites visited during our study. The high number of sampling sites in this area contributed to a higher mollusc diversity than in the 'V' and 'W' water management areas. Interestingly, three sampling sites situated near rural human settlements in the 'U' water management area exhibited high mollusc diversity because of potentially increased biotope availability, reduced competition and lower predation (Chapter 4). Unlike the 'W' water management area, freshwater molluscs were recorded across seven out of eight sites in the 'V' water management area, while 10/18 (56%) of sites in the 'W' water management area did not have molluscs. It is believed that a high proportion of sites without molluscs during our surveys contributed to low diversity in this region because of drought conditions. This observation was supported by Agboola et al. (2020a), who found that many rivers in the northern KwaZulu-Natal (in 'W' water management area), had limited biotope availability because of either river bank modification or prevailing drought in the region (Chapter 4).

The gastropods *Tomichia natalensis* (Connolly, 1939) and *Tomichia tristis* (Morelet, 1889) are listed as Critically Endangered (CR) and *Tomichia ventricosa* (Reeve, 1842) Endangered (EN) on the IUCN Red List; while the vast majority of freshwater molluscs were either Least Concern (LC) or Data Deficient (DD). A total of 15 non-native species have been identified in KwaZulu-Natal (Appleton and Miranda 2015; Chapter 3). Of those, four species are known invasive species

(*Physella acuta, Stenophysa marmorata, Tarebia granifera, Pseudosuccinea columella*) that were introduced into KwaZulu-Natal by people from different parts of the world, including Asia, Australia, East Africa, and North, Central and South America (Appleton and Miranda 2015; Lawton et al. 2018). The IUCN status of the four invasive species, i.e., *P. acuta*, *P. columella*, *T. granifera* and *S. marmorata*, is 'Least Concern' (LC) from the latest assessments of 2016, 2012, 2010 and 2011, respectively.

Previous work on freshwater Mollusca in South Africa and the KwaZulu-Natal is well documented, and includes recent distribution range and taxonomic work (Conolly 1939; Mandahl-Barth 1958, 1960; Kuiper 1964, 1966; Van Eeden and Brown 1966; Brown 1967, 1994; Appleton 1996; Herbert 1998; Nwoko et al. 2022). However, ca. 69 freshwater mollusc species have previously been reported in KwaZulu-Natal (Brown 1967, 1994; Appleton 1996). In comparison with the previous freshwater mollusc checklist by Appleton (1996), a total of ten species were added to this study: *Euglesa costulosa* (Connolly, 1931), *Euglesa langleyana* (Melvill and Ponsoby, 1891), *Euglesa viridaria* (Kuiper, 1956), *Tomichia natalensis* (Connolly, 1939), *Tomichia tristis* (Morelet, 1889), *Tomichia ventricosa* (Reeve, 1842) and *Gyraulus chinensis* (Dunker, 1848), *Stenophysa marmorata* (Guilding, 1828), and *Tarebia granifera* (Lamarck, 1816), including 11 *Burnupia* species.

Twenty-four freshwater molluscs recovered in our recent surveys of KwaZulu-Natal suggest a decline in species diversity, in line with global and regional trends in anthropogenic activities such as urbanisation, agriculture, industrialisation, damming, and sand mining (Alexander et al., 2021; Böhm et al., 2020; Lopes-Lima et al., 2021). However, only 13 species were recorded at the 52 historically mapped REMP sites, compared with 24 species collected in this study. This highlights the importance of identifying and including more sites in REMP

(Chapter 4). This way, REMP could explore new sites rich in biodiversity, as the majority of historical key biodiversity coastal regions in KwaZulu-Natal are presently not part of REMP because of anthropogenic activities. The prevalence of invasive species in highly organic-polluted freshwater ecosystems might have displaced endemic species. We also believed that predation and competition had favoured invasive species over the survival of endemic species. Climate change, in the form of natural disasters such as droughts and floods in KwaZulu-Natal (Appleton and Miranda, 2015; Agboola et al., 2020a), along with other factors, may also contribute to lower freshwater mollusc diversity in the province.

5.7 References

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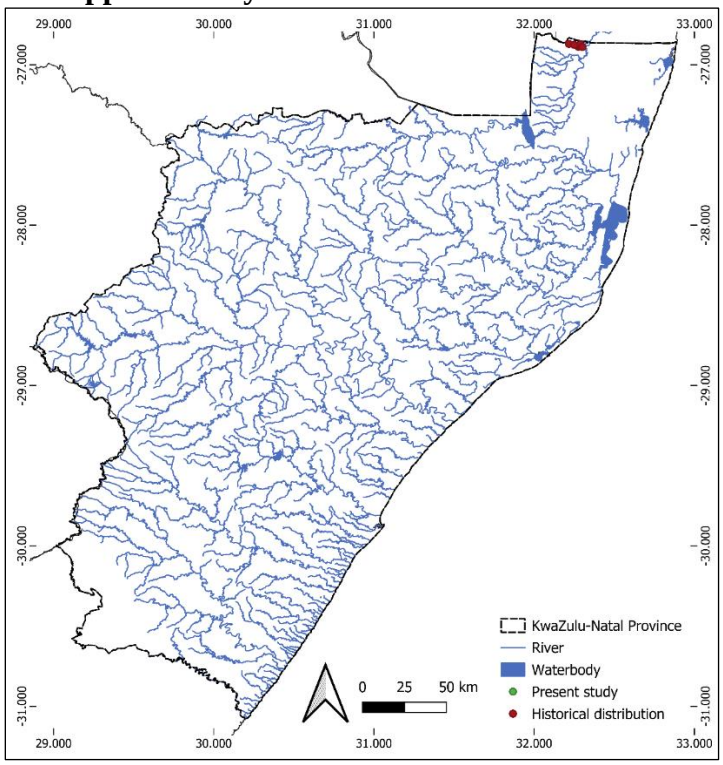
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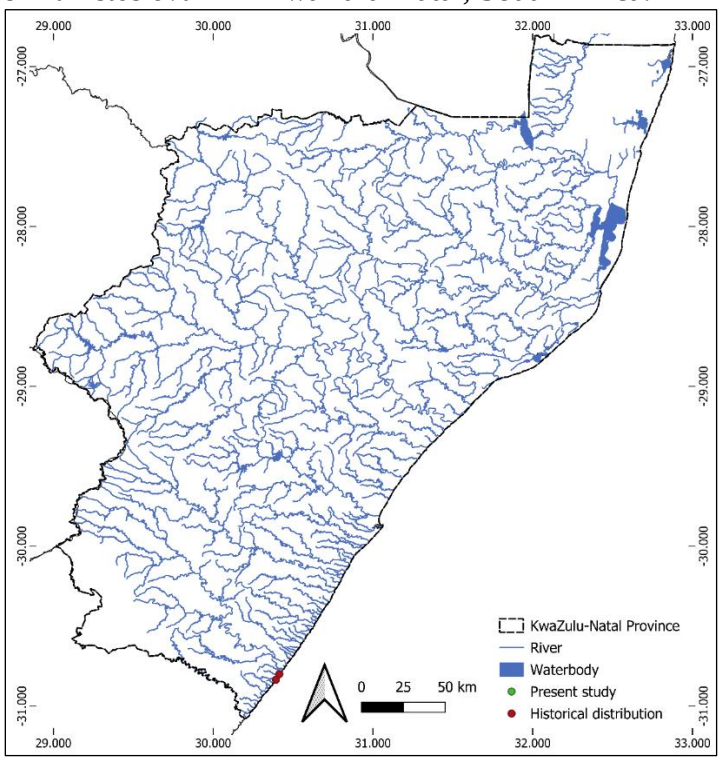
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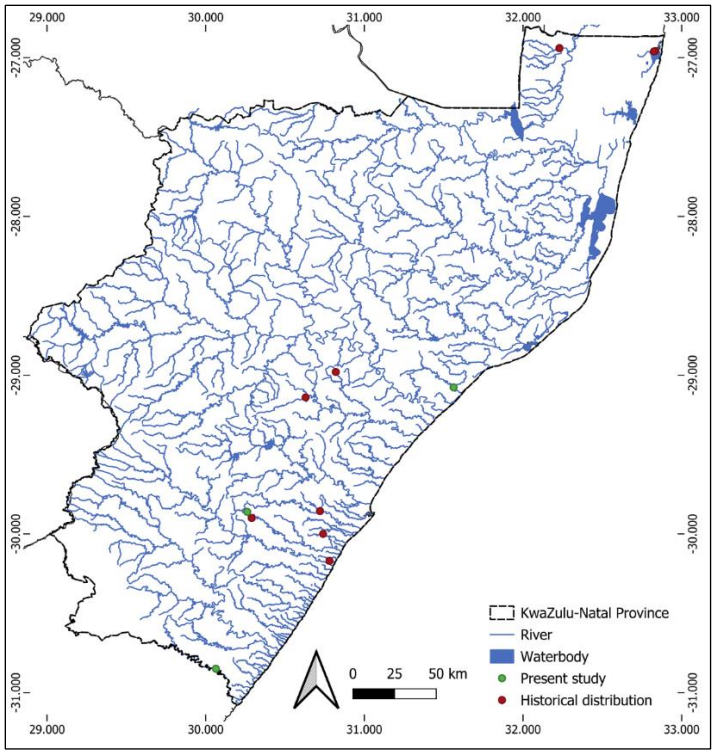
5.8 Supplementary information



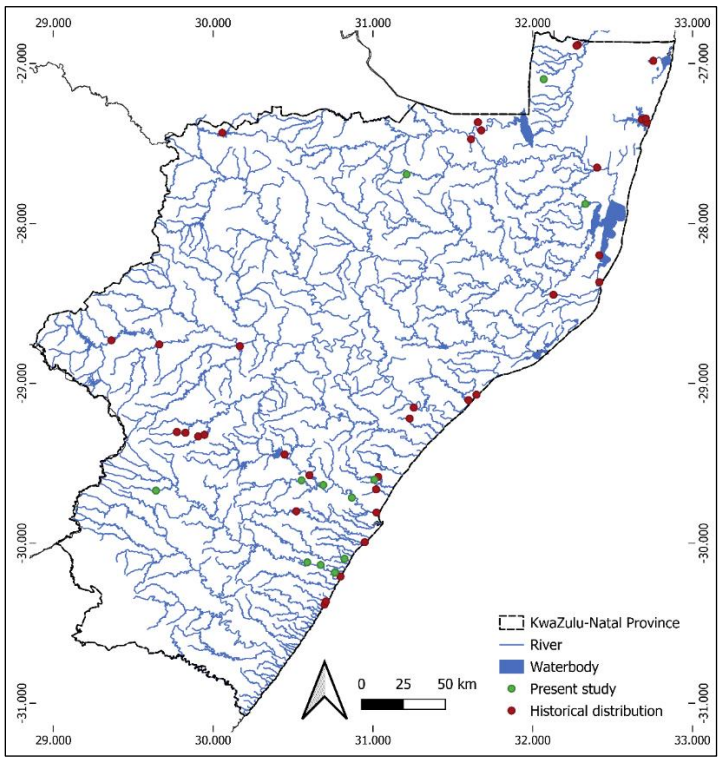
Supplementary Information Figure S5.1: Spatial distribution showing historical sampling sites of *Lanistes ovum* in KwaZulu-Natal, South Africa.



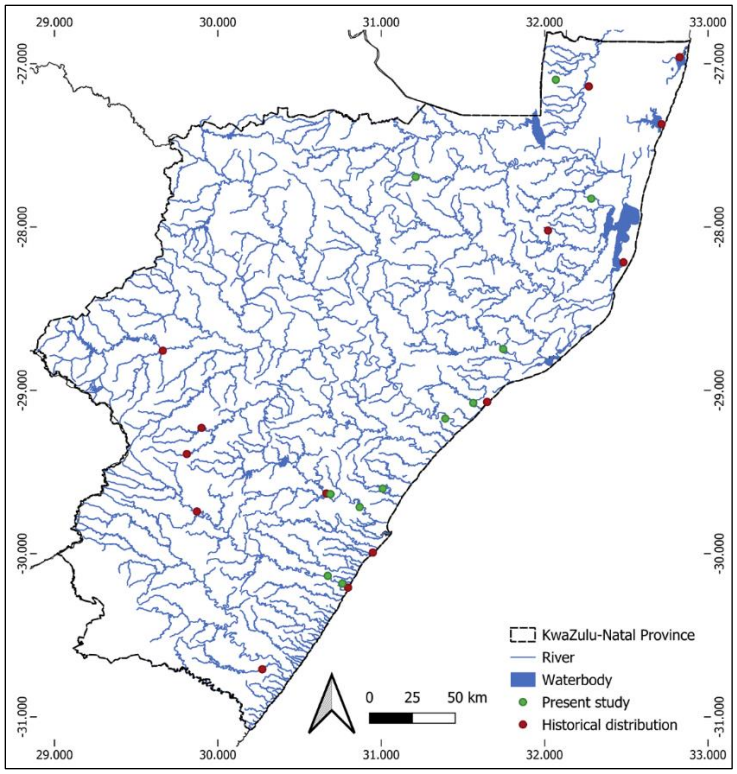
Supplementary Information Figure S5.2: Spatial distribution showing historical sampling sites of *Pomacea bridgesii* in KwaZulu-Natal, South Africa.



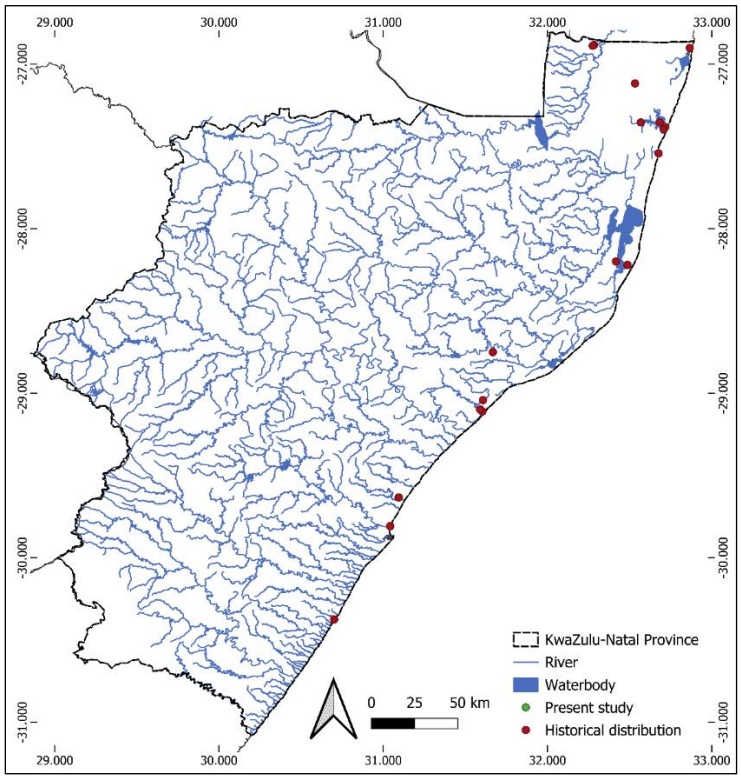
Supplementary Information Figure S5.3: Spatial distribution showing historical and recent sampling sites of *Cleopatra ferruginea* in KwaZulu-Natal, South Africa.



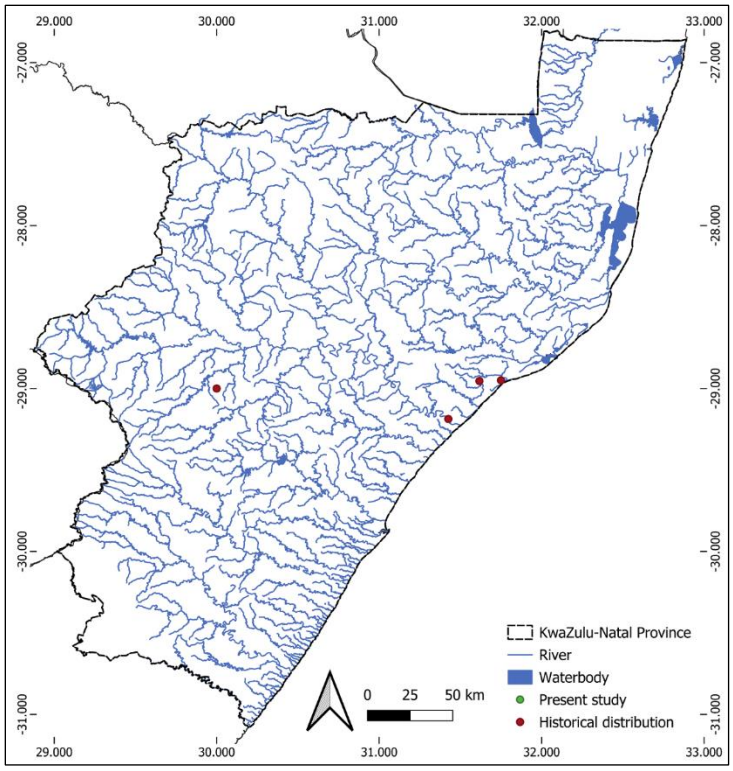
Supplementary Information Figure S5.4: Spatial distribution showing historical and recent sampling sites of *Melanoides tuberculata* in KwaZulu-Natal



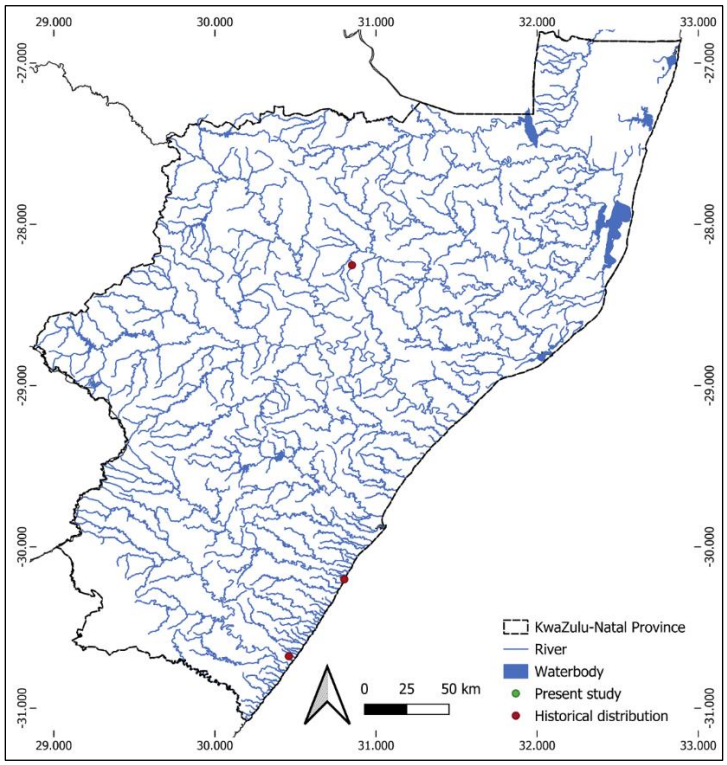
Supplementary Information Figure S5.5: Spatial distribution showing historical and recent sampling sites of *Tarebia granifera* in KwaZulu-Natal, South Africa.



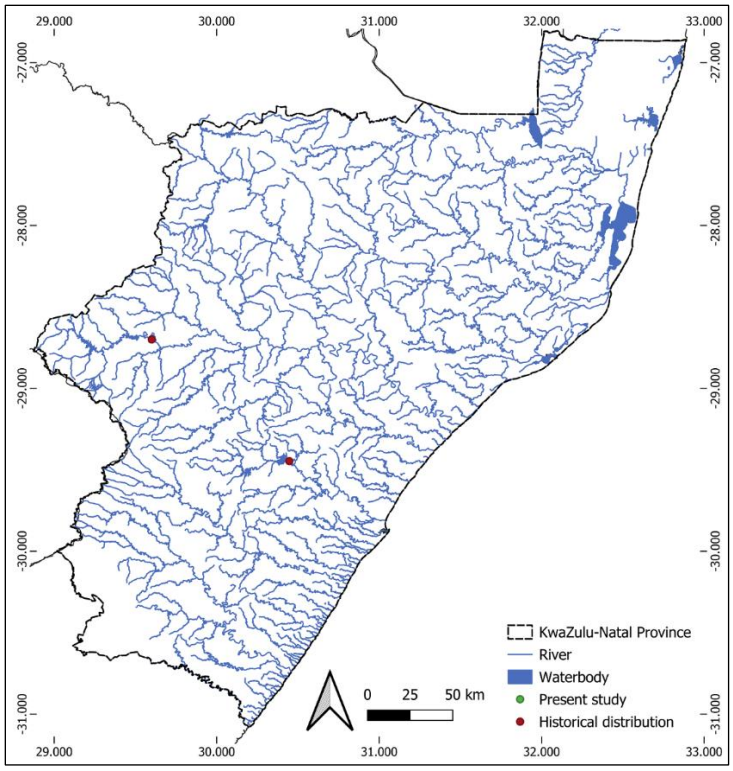
Supplementary Information Figure S5.6: Spatial distribution showing historical sampling sites of *Thiara amarula* in KwaZulu-Natal, South Africa.



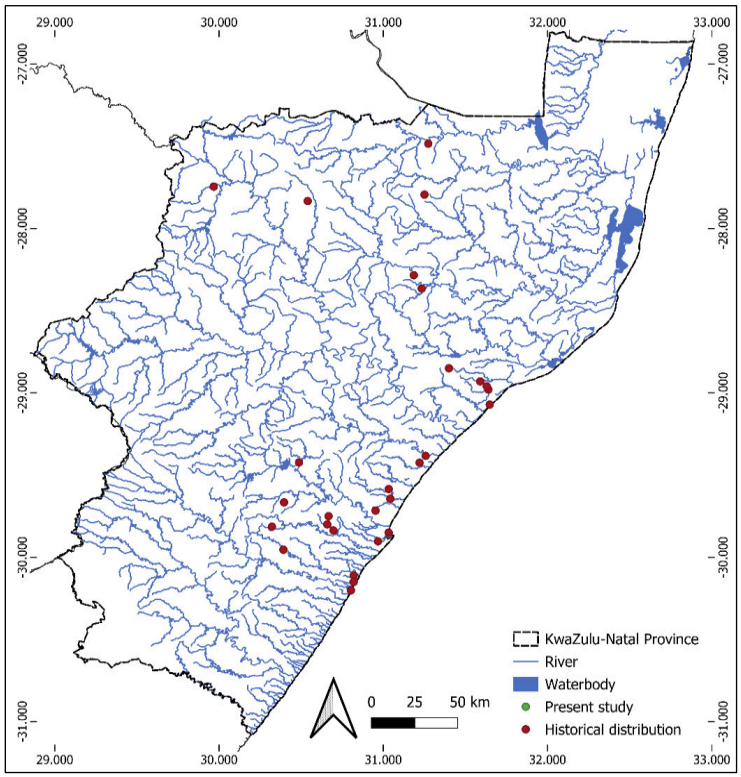
Supplementary Information Figure S5.7: Spatial distribution showing historical sampling sites of *Tomichia natalensis* in KwaZulu-Natal, South Africa.



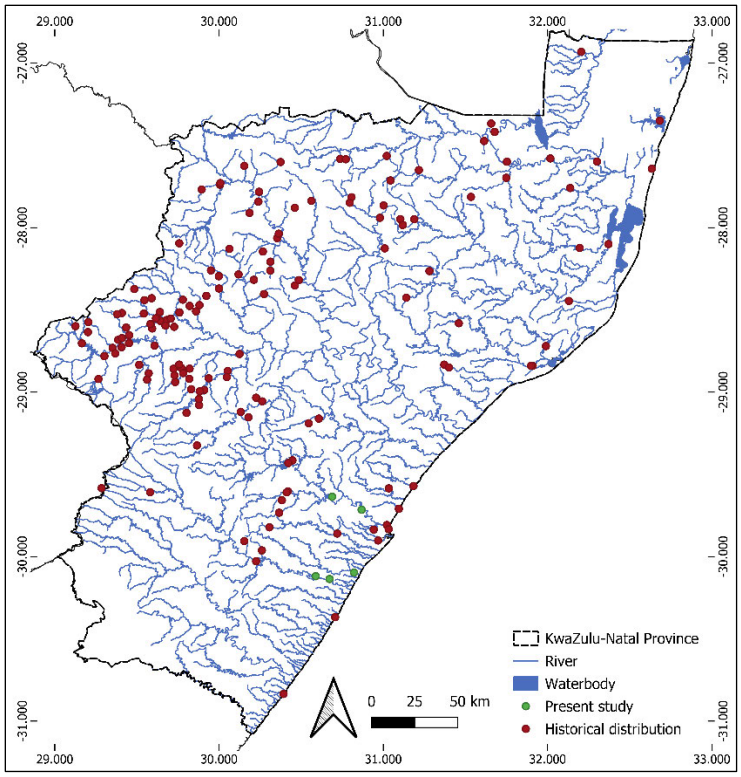
Supplementary Information Figure S5.8: Spatial distribution showing historical sampling sites of *Tomichia tristis* in KwaZulu-Natal, South Africa.



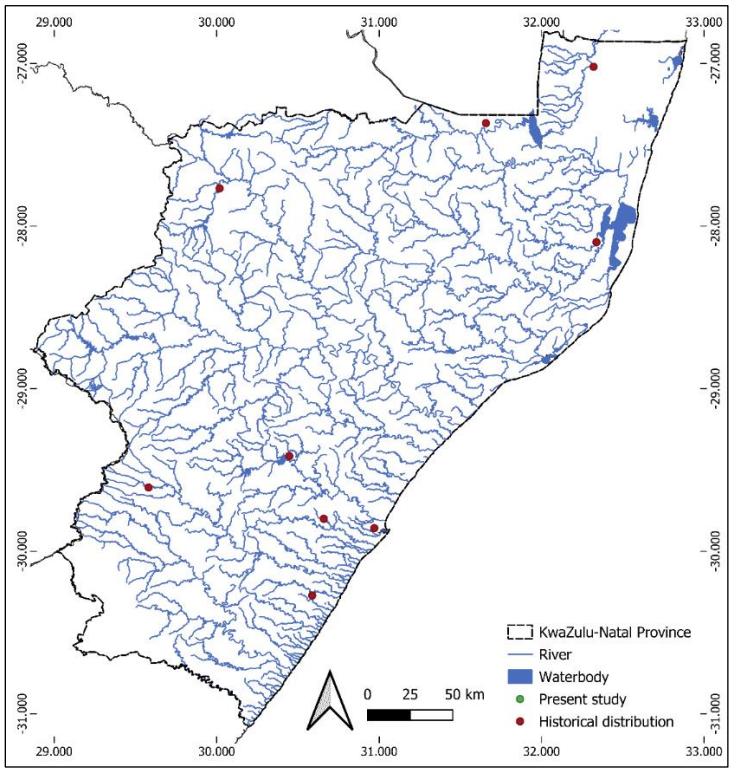
Supplementary Information Figure S5.9: Spatial distribution showing historical sampling sites of *Tomichia ventricosa* in KwaZulu-Natal, South Africa.



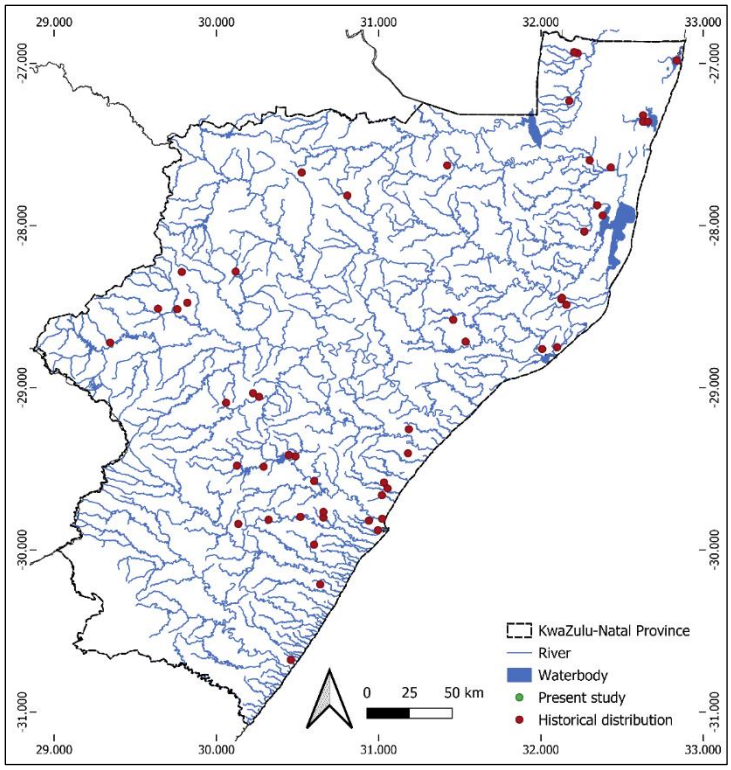
Supplementary Information Figure S5.10: Spatial distribution showing historical sampling sites of *Bulinus africanus* in KwaZulu-Natal, South Africa.



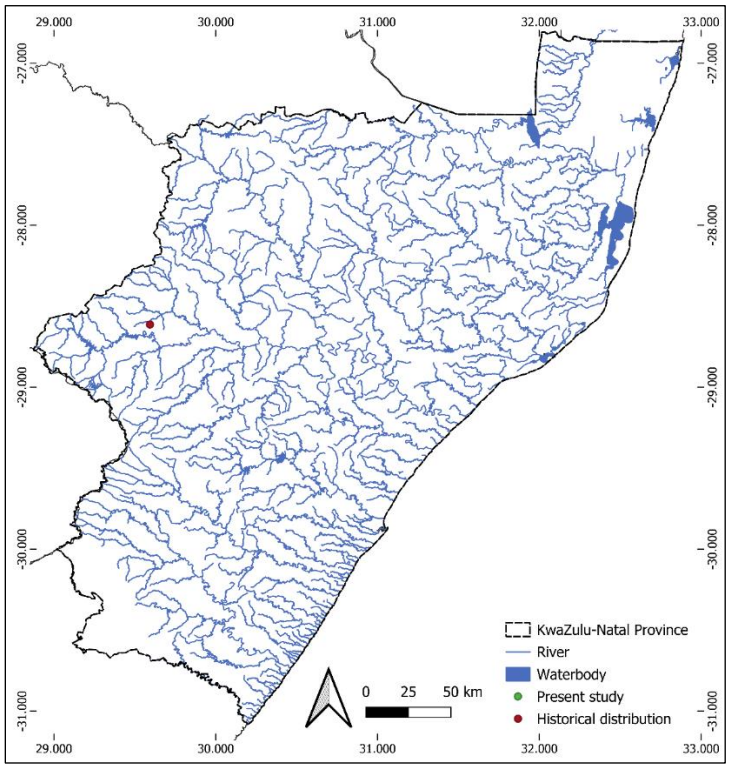
Supplementary Information Figure S5.11: Spatial distribution showing historical sampling sites of *Bulinus forskalii* in KwaZulu-Natal, South Africa.



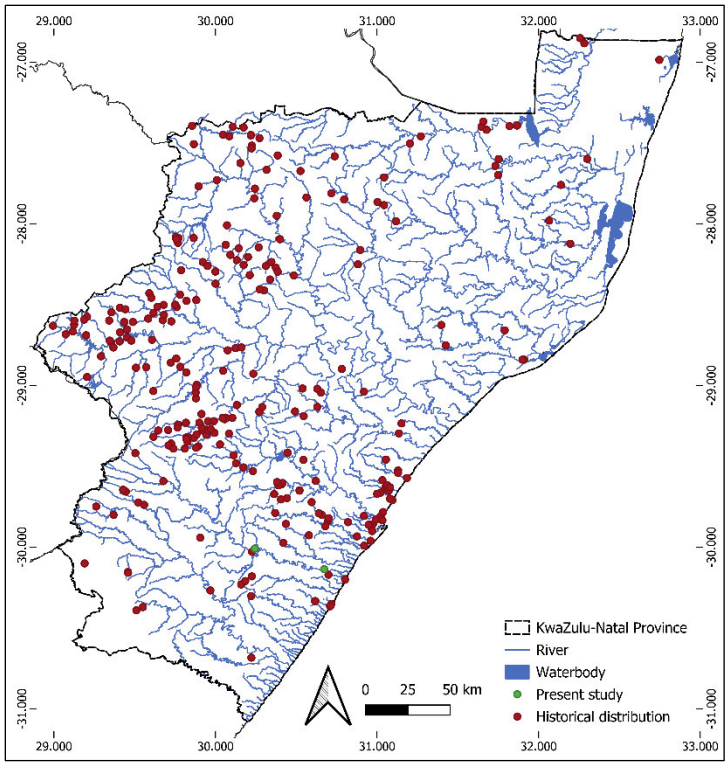
Supplementary Information Figure S5.12: Spatial distribution showing historical sampling sites of *Bulinus globosus* in KwaZulu-Natal, South Africa.



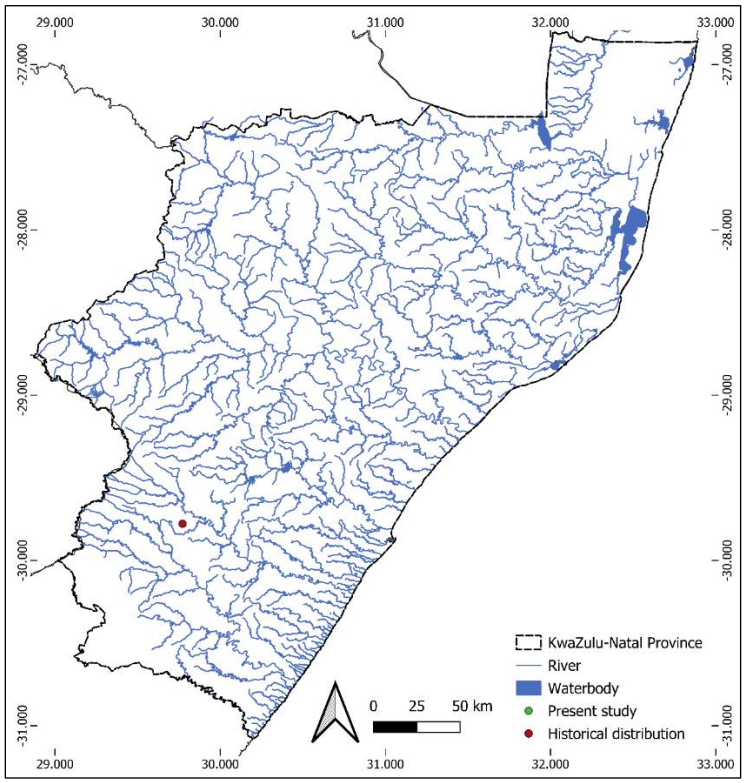
Supplementary Information Figure S5.13: Spatial distribution showing historical sampling sites of *Bulinus natalensis* in KwaZulu-Natal, South Africa.



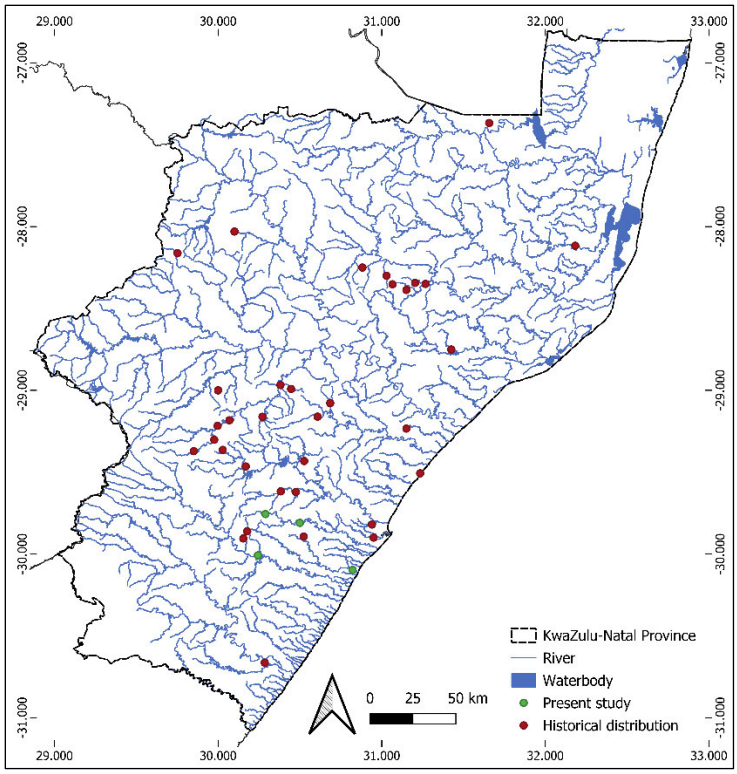
Supplementary Information Figure S5.14: Spatial distribution showing historical sampling sites of *Bulinus reticulatus* in KwaZulu-Natal, South Africa.



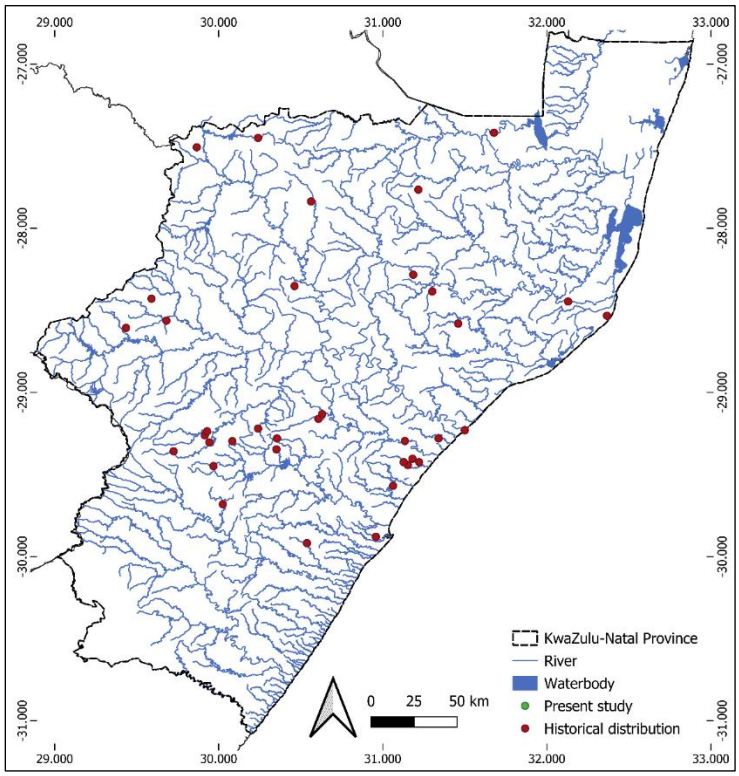
Supplementary Information Figure S5.15: Spatial distribution showing historical sampling sites of *Bulinus tropicus* in KwaZulu-Natal, South Africa.



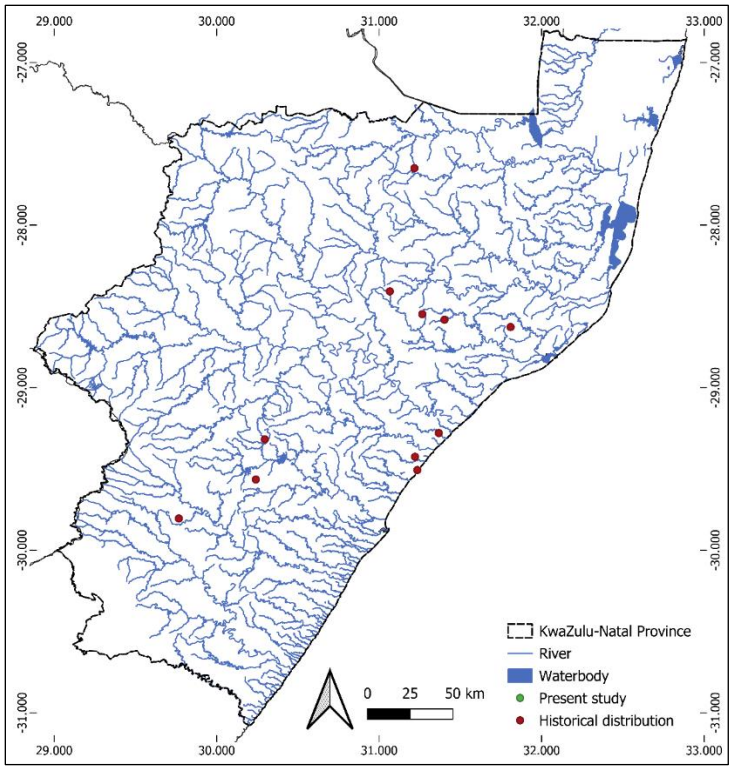
Supplementary Information Figure S5.16: Spatial distribution showing historical sampling sites of *Burnupia brunnea* in KwaZulu-Natal, South Africa.



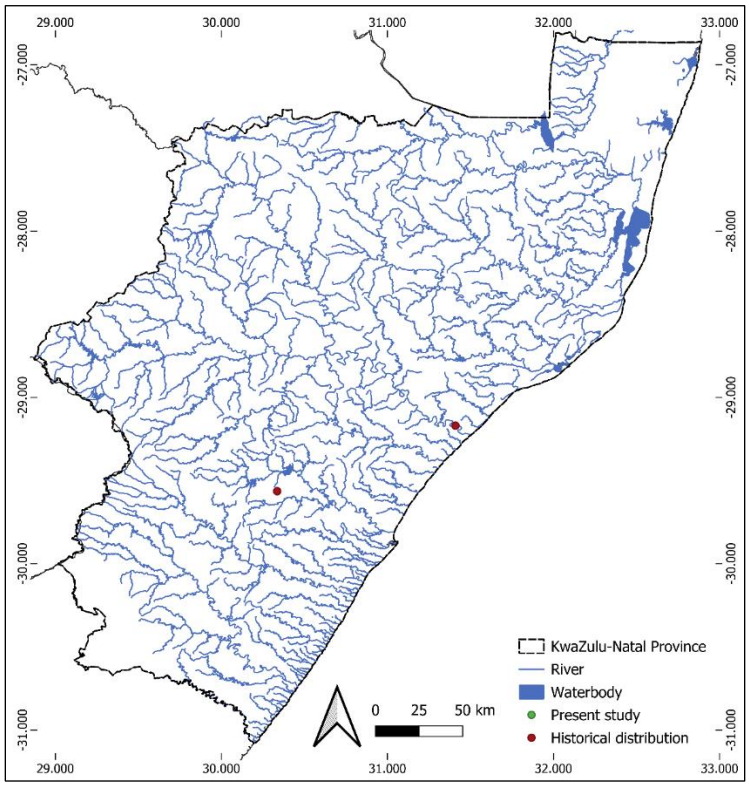
Supplementary Information Figure S5.17: Spatial distribution showing historical sampling sites of *Burnupia caffra* in KwaZulu-Natal, South Africa.



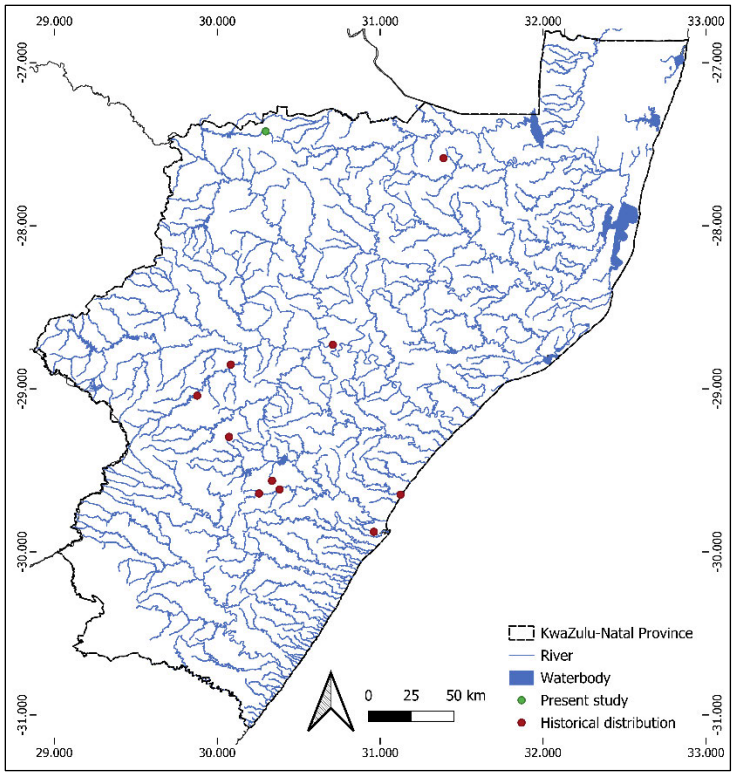
Supplementary Information Figure S5.18: Spatial distribution showing historical sampling sites of *Burnupia capensis* in KwaZulu-Natal, South Africa.



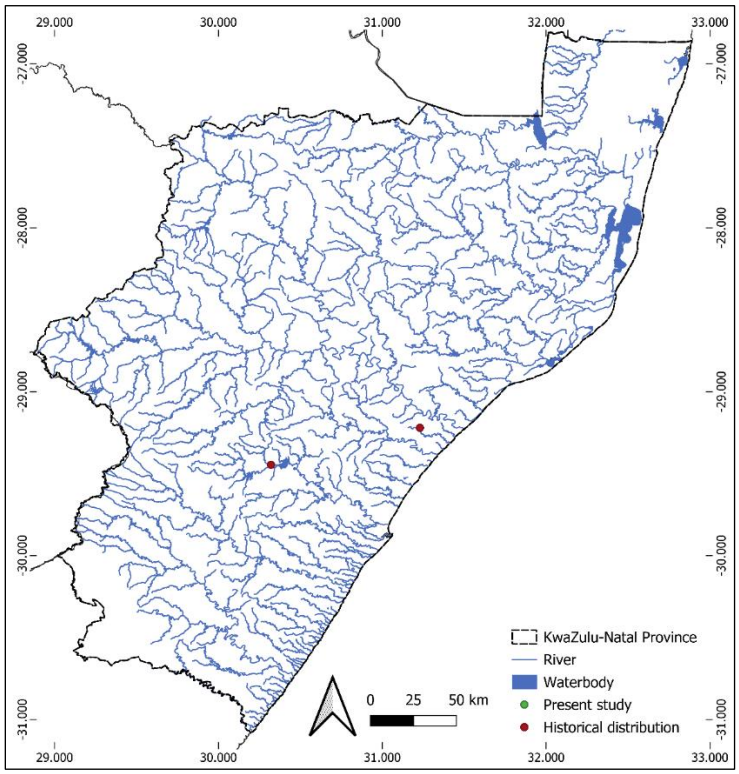
Supplementary Information Figure S5.19: Spatial distribution showing historical sampling sites of *Burnupia capensis natalensis* in KwaZulu-Natal, South Africa.



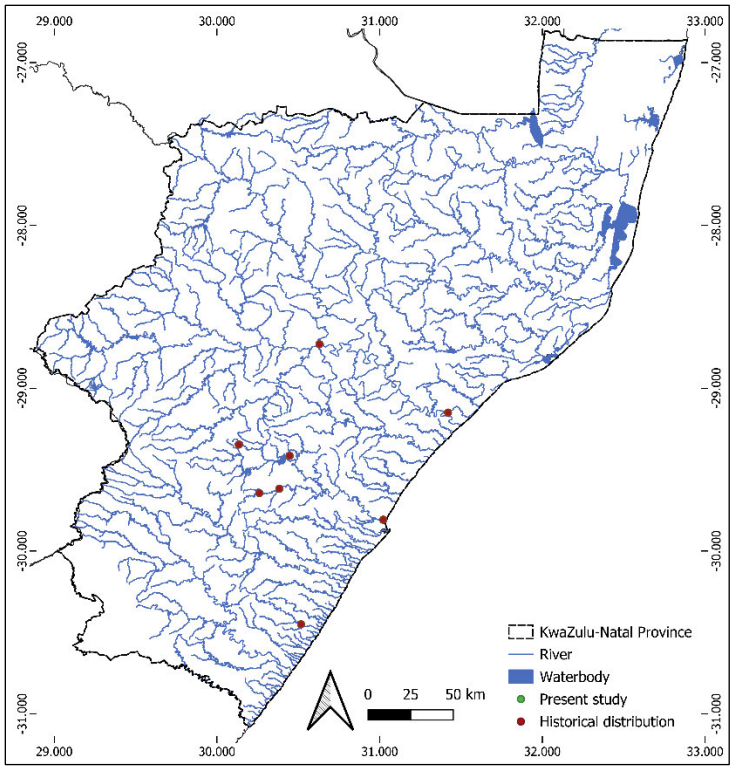
Supplementary Information Figure S5.20: Spatial distribution showing historical sampling sites of *Burnupia farquhari* in KwaZulu-Natal, South Africa.



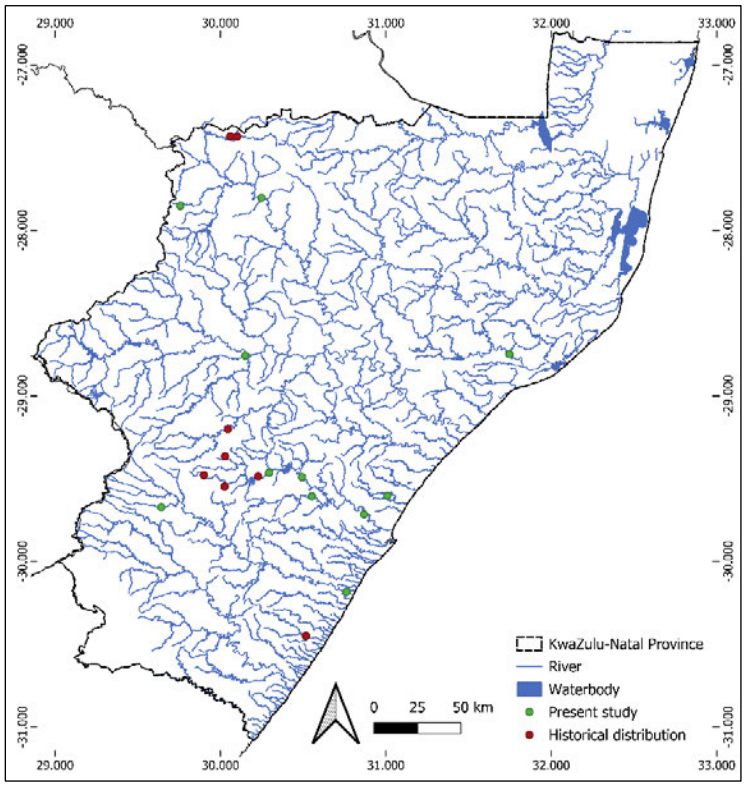
Supplementary Information Figure S5.21: Spatial distribution showing historical sampling sites of *Burnupia gordonensis* in KwaZulu-Natal, South Africa.



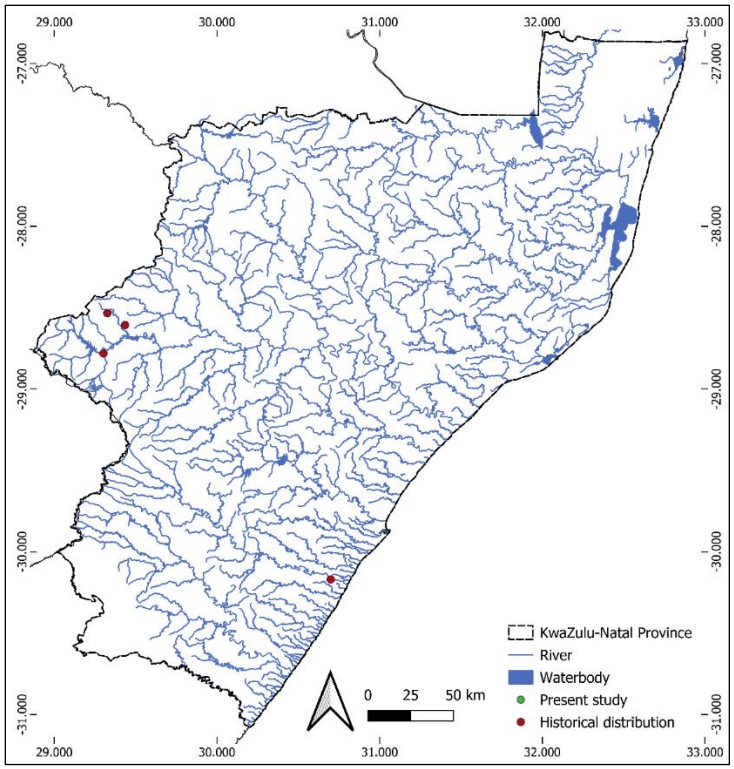
Supplementary Information Figure S5.22: Spatial distribution showing historical sampling sites of *Burnupia mooiensis* in KwaZulu-Natal, South Africa.



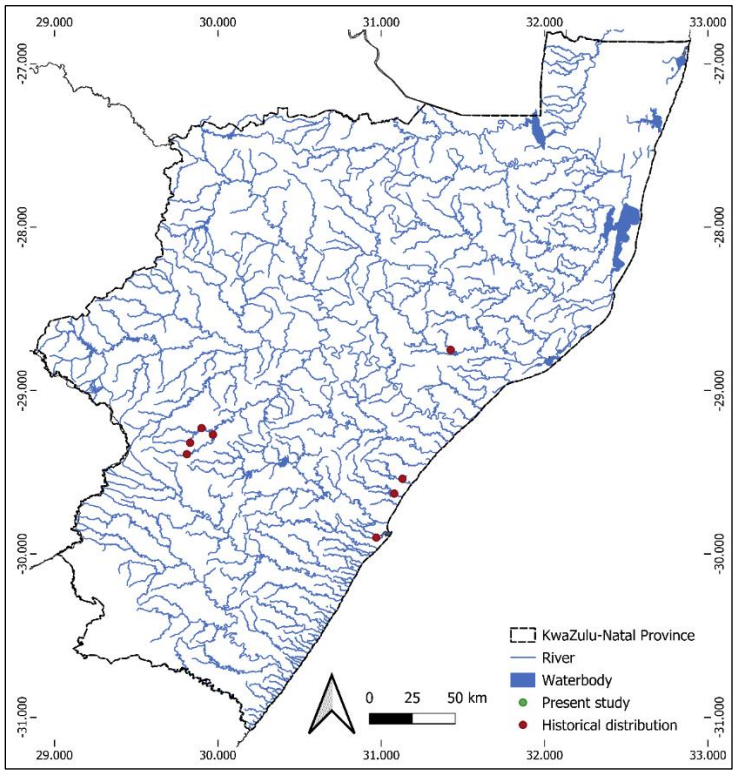
Supplementary Information Figure S5.23: Spatial distribution showing historical sampling sites of *Burnupia nana* in KwaZulu-Natal, South Africa.



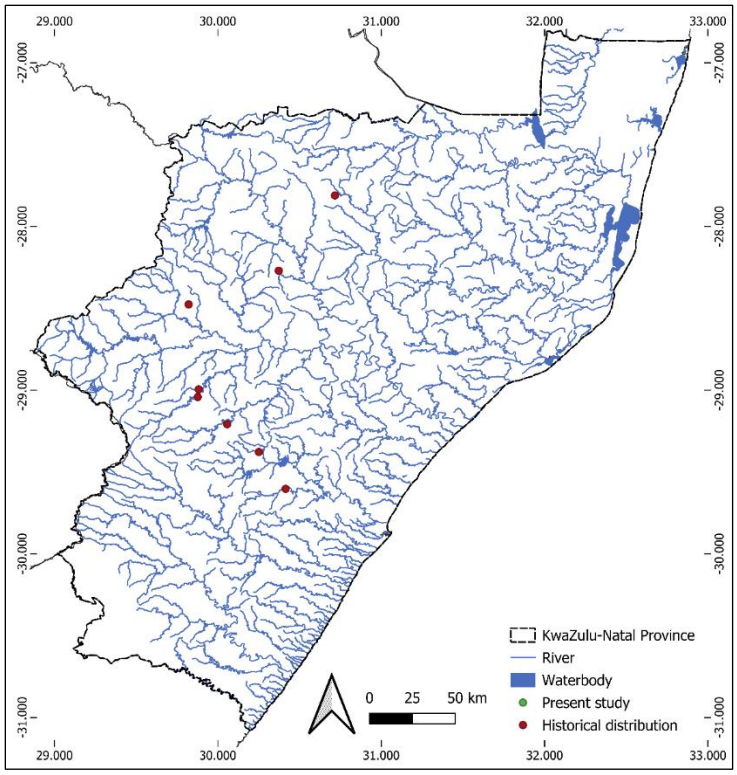
Supplementary Information Figure S5.24: Spatial distribution showing historical and recent sampling sites of *Burnupia ponsonbyi* in KwaZulu-Natal, South Africa.



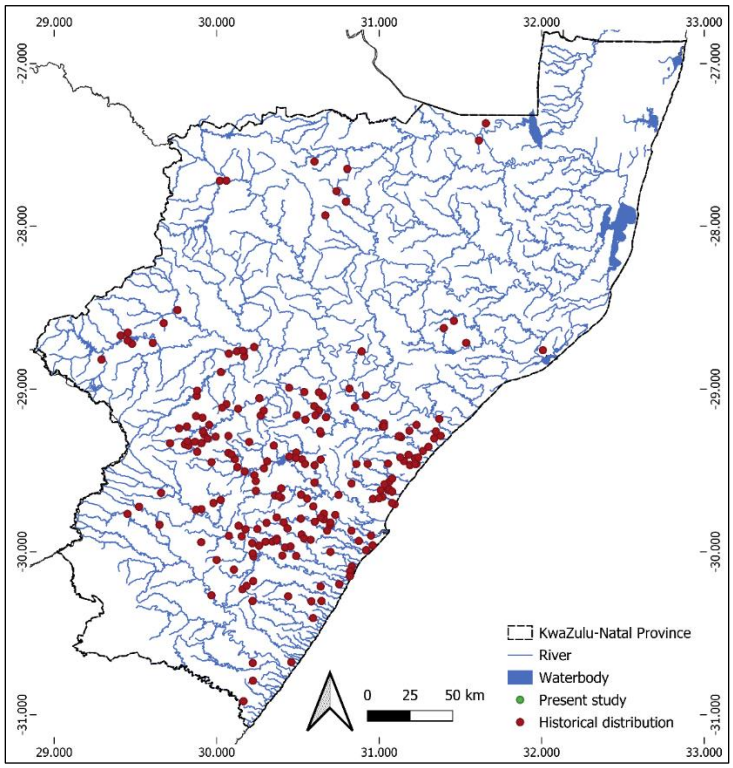
Supplementary Information Figure S5.25: Spatial distribution showing historical sampling sites of *Burnupia stenochorias* in KwaZulu-Natal, South Africa.



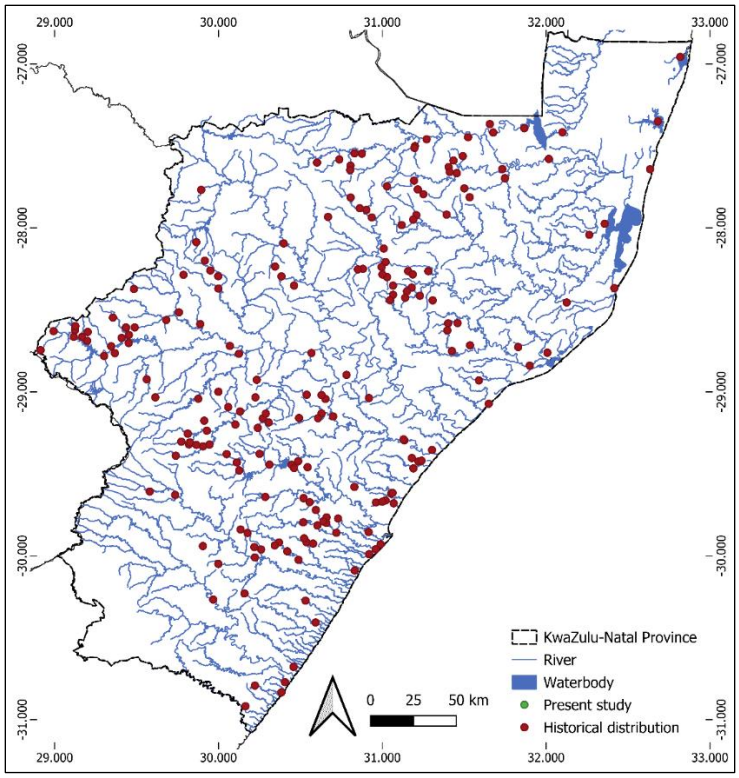
Supplementary Information Figure S5.26: Spatial distribution showing historical sampling sites of *Burnupia transvaalensis* in KwaZulu-Natal, South Africa.



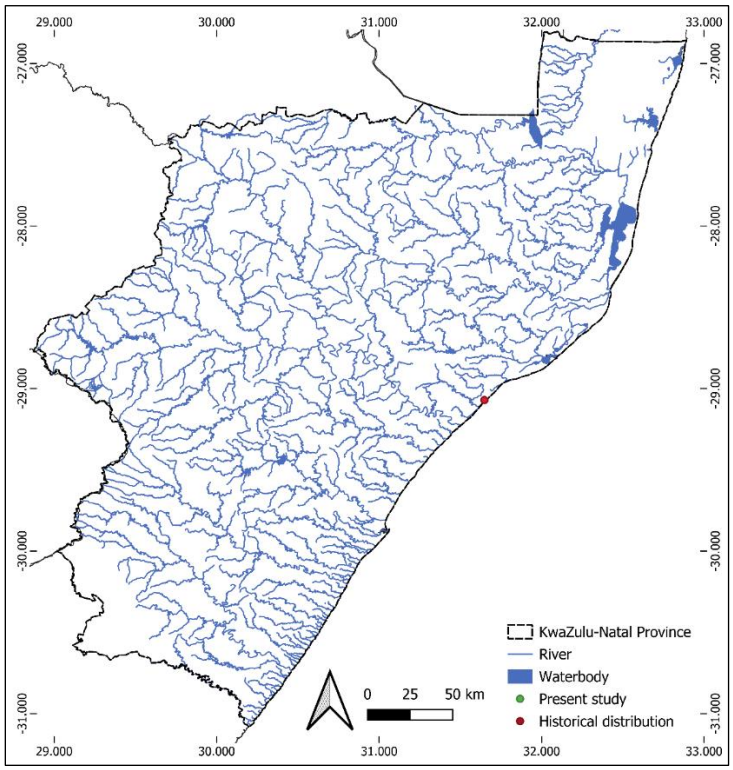
Supplementary Information Figure S5.27: Spatial distribution showing historical sampling sites of *Galba truncatula* in KwaZulu-Natal, South Africa.



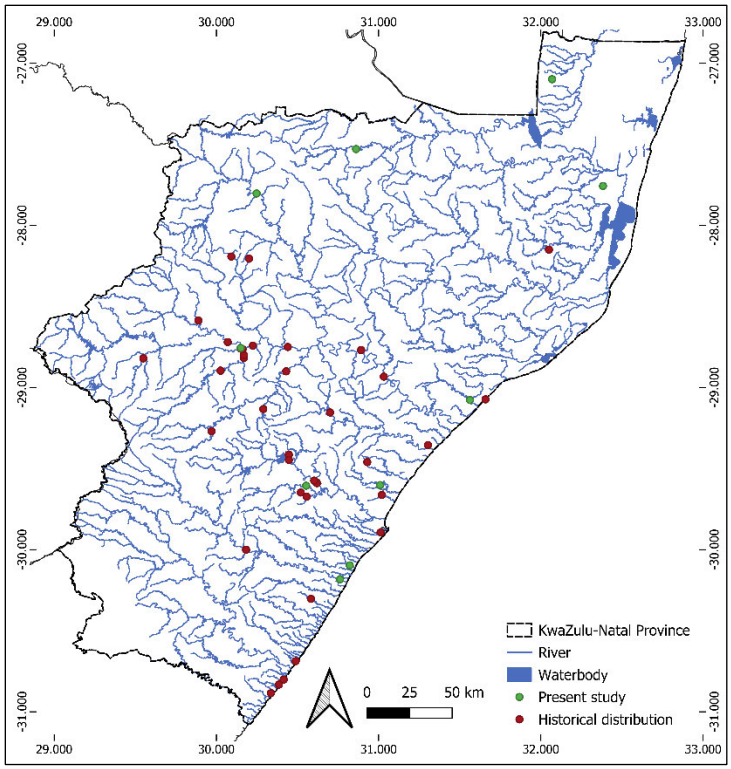
Supplementary Information Figure S5.28: Spatial distribution showing historical sampling sites of *Pseudosuccinea columella* in KwaZulu-Natal, South Africa.



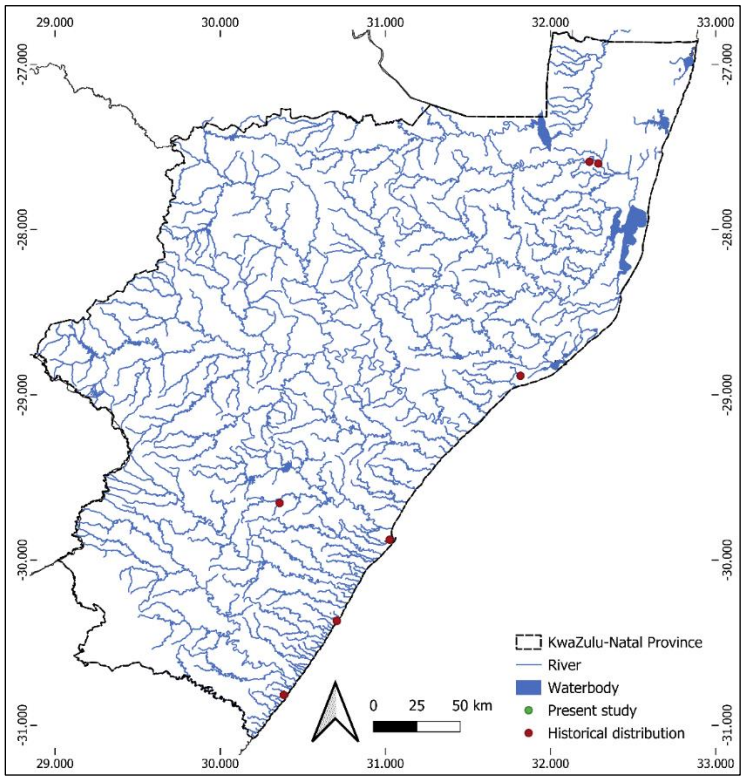
Supplementary Information Figure S5.29: Spatial distribution showing historical sampling sites of *Radix natalensis* in KwaZulu-Natal, South Africa.



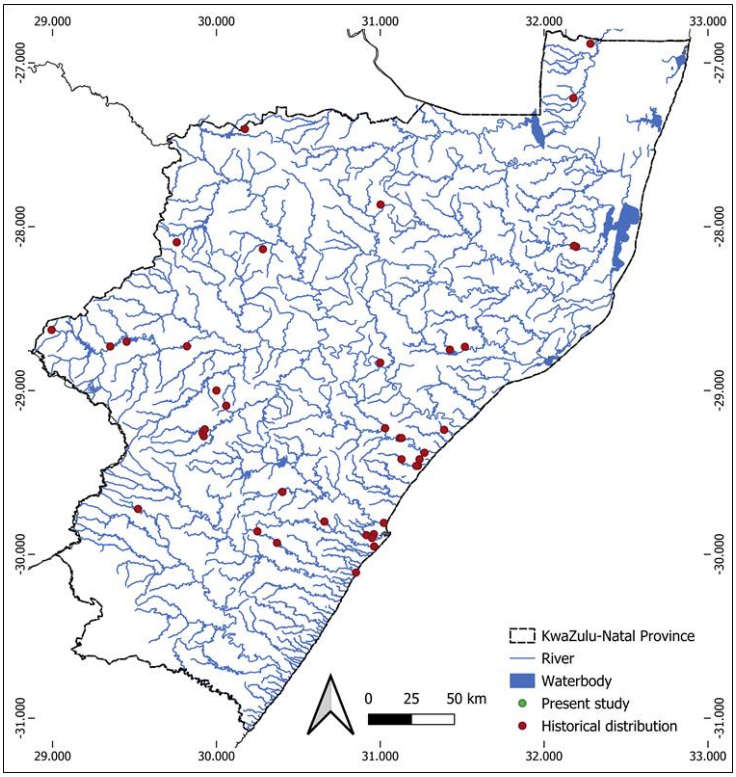
Supplementary Information Figure S5.30: Spatial distribution showing historical sampling sites of *Radix rubiginosa* in KwaZulu-Natal, South Africa.



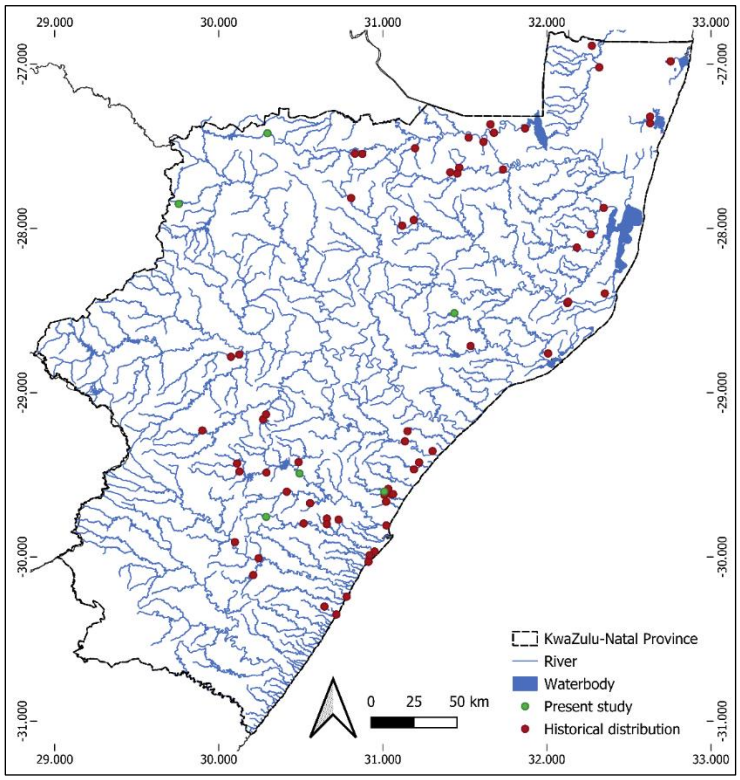
Supplementary Information Figure S5.31: Spatial distribution showing historical sampling sites of *Physella acuta* in KwaZulu-Natal, South Africa.



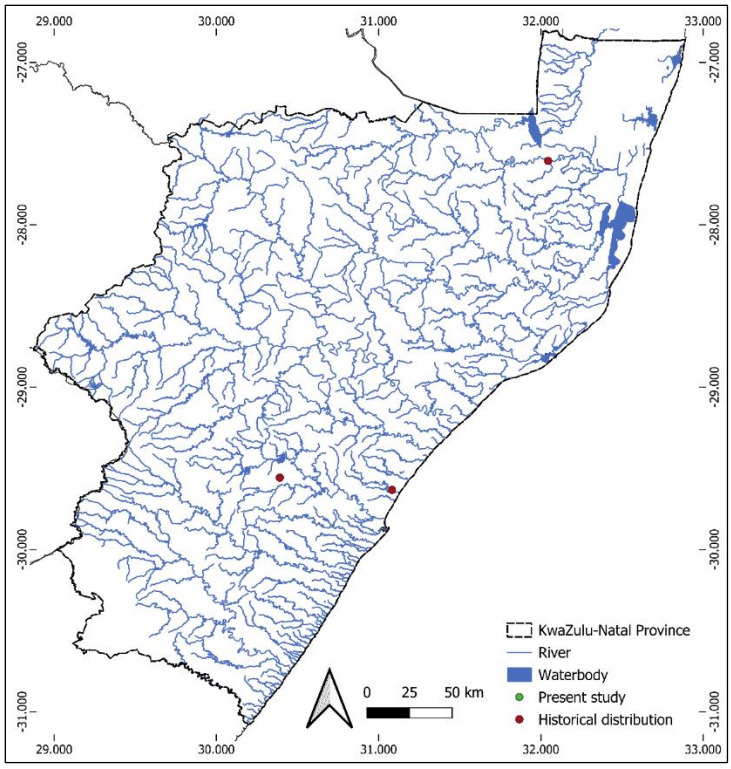
Supplementary Information Figure S5.32: Spatial distribution showing historical sampling sites of *Stenophysa marmorata* in KwaZulu-Natal, South Africa.



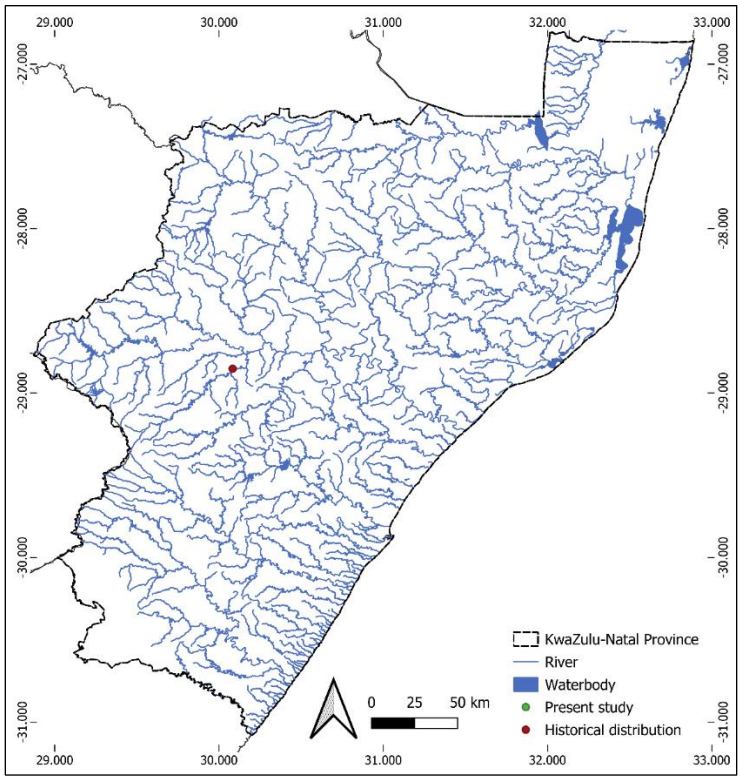
Supplementary Information Figure S5.33: Spatial distribution showing historical sampling sites of *Afrogyrorbis natalensis* in KwaZulu-Natal, South Africa.



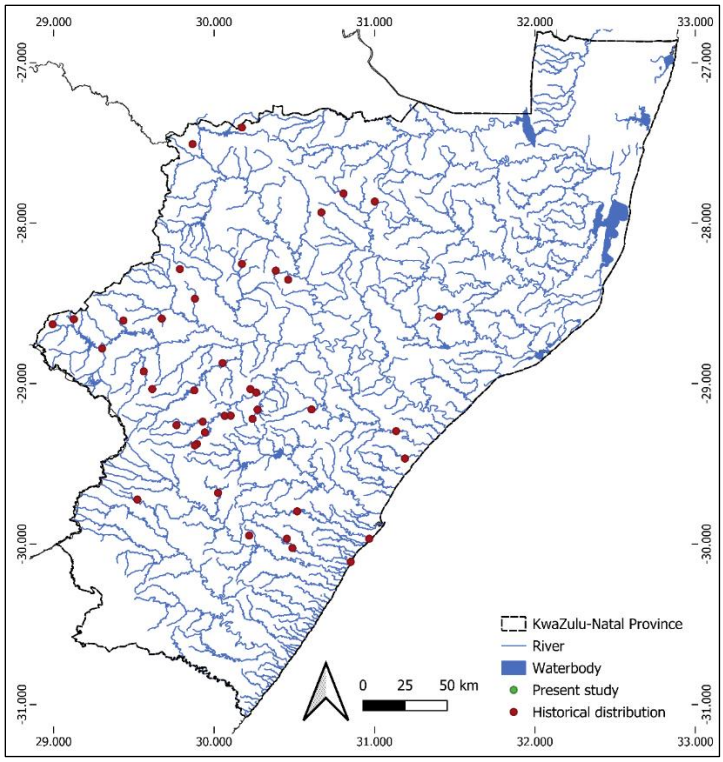
Supplementary Information Figure S5.34: Spatial distribution showing historical and recent sampling sites of *Biomphalaria pfeifferi* in KwaZulu-Natal, South Africa.



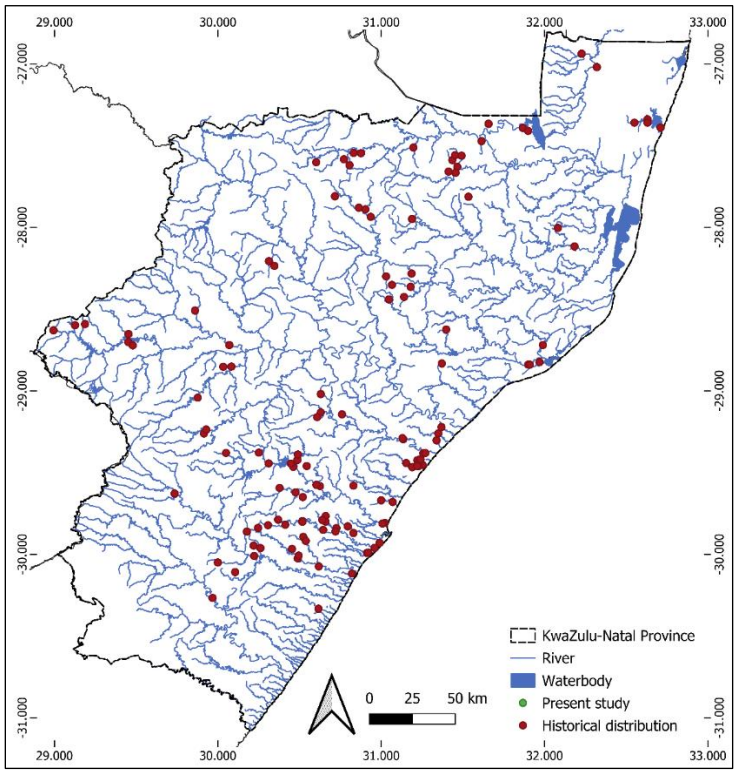
Supplementary Information Figure S5.35: Spatial distribution showing historical sampling sites of *Gyraulus andrussovi* in KwaZulu-Natal, South Africa.



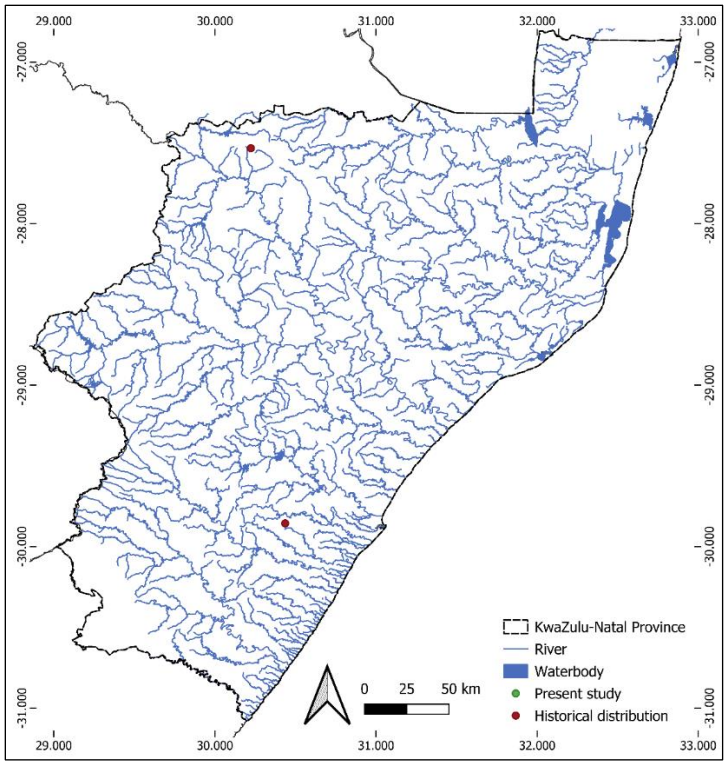
Supplementary Information Figure S5.36: Spatial distribution showing historical sampling sites of *Gyraulus chinensis* in KwaZulu-Natal, South Africa.



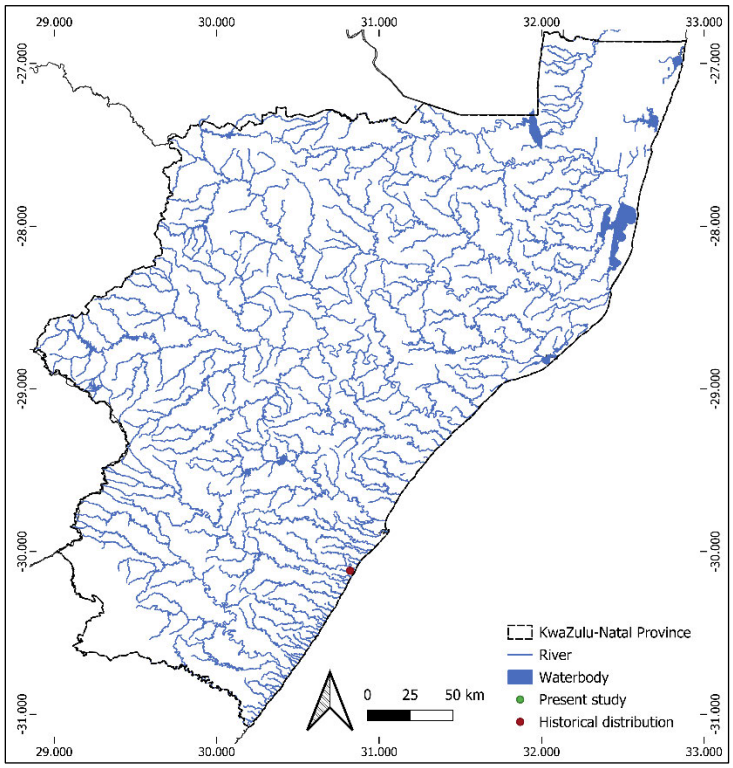
Supplementary Information Figure S5.37: Spatial distribution showing historical sampling sites of *Gyraulus connollyi* in KwaZulu-Natal, South Africa.



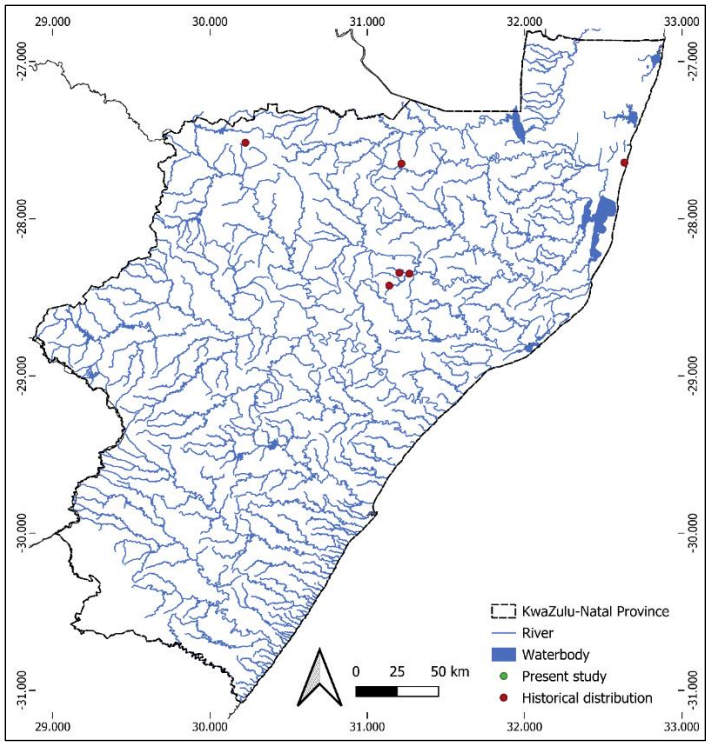
Supplementary Information Figure S5.38: Spatial distribution showing historical sampling sites of *Gyraulus costulatus* in KwaZulu-Natal, South Africa.



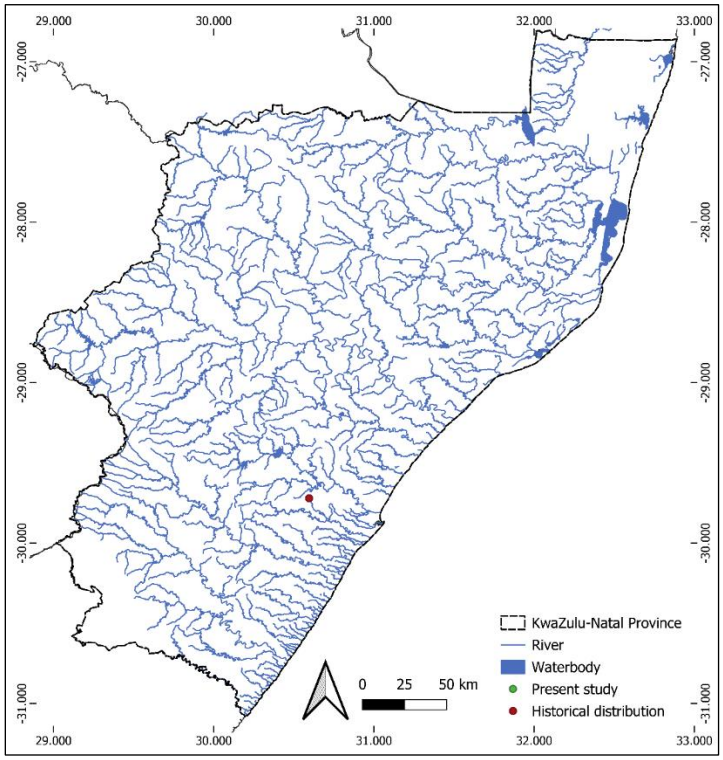
Supplementary Information Figure S5.39: Spatial distribution showing historical sampling sites of *Hovorbis coretus* in KwaZulu-Natal, South Africa.



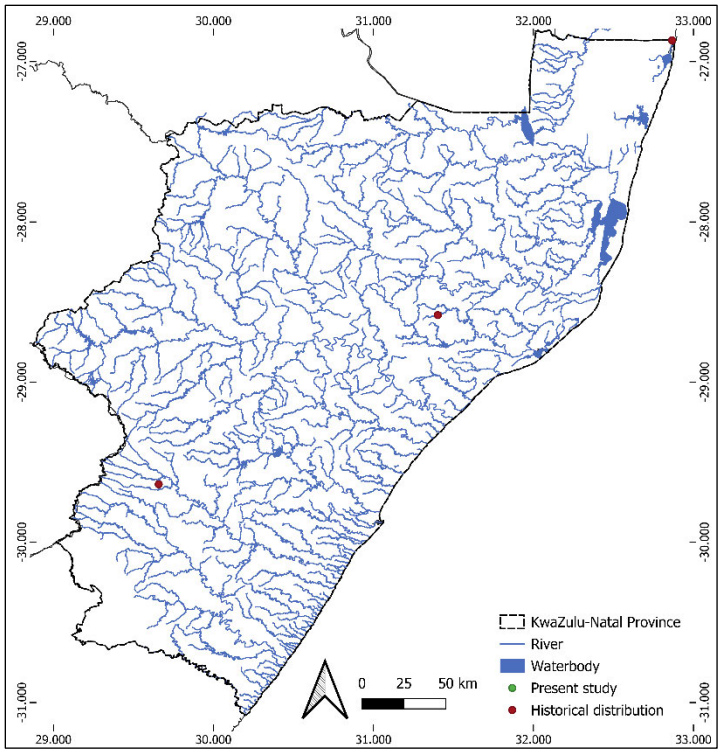
Supplementary Information Figure S5.40: Spatial distribution showing historical sampling sites of *Lentorbis carringtoni* in KwaZulu-Natal, South Africa.



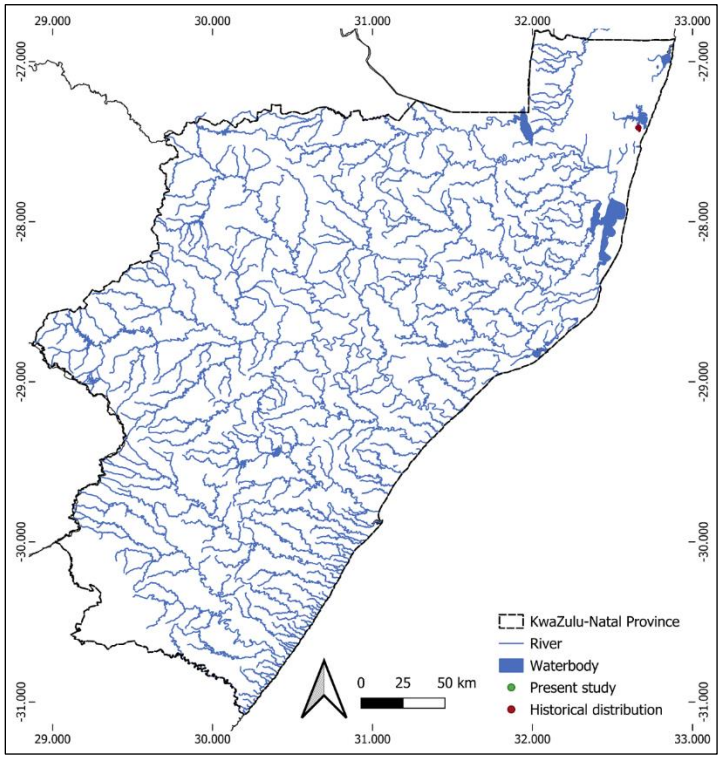
Supplementary Information Figure S5.41: Spatial distribution showing historical sampling sites of *Pettancylus burnupi* in KwaZulu-Natal, South Africa.



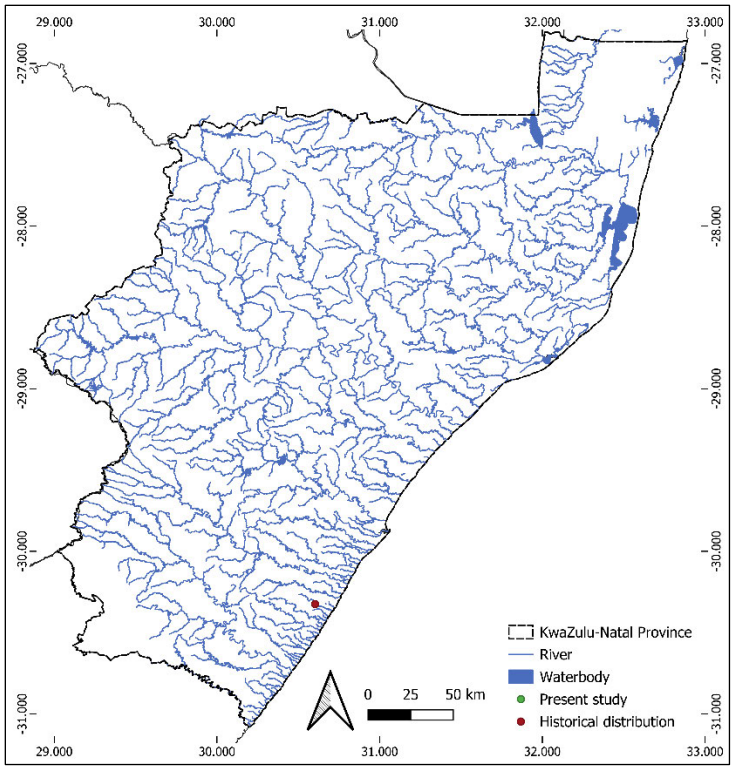
Supplementary Information Figure S5.42: Spatial distribution showing historical sampling sites of *Pettancylus cawstoni* in KwaZulu-Natal, South Africa.



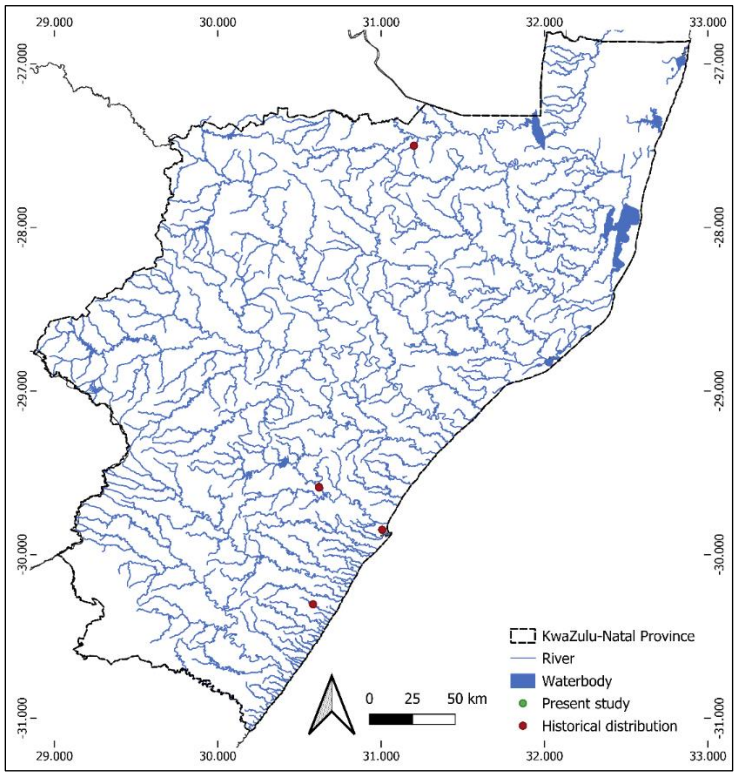
Supplementary Information Figure S5.43: Spatial distribution showing historical sampling sites of *Pettancylus connollyi* in KwaZulu-Natal, South Africa.



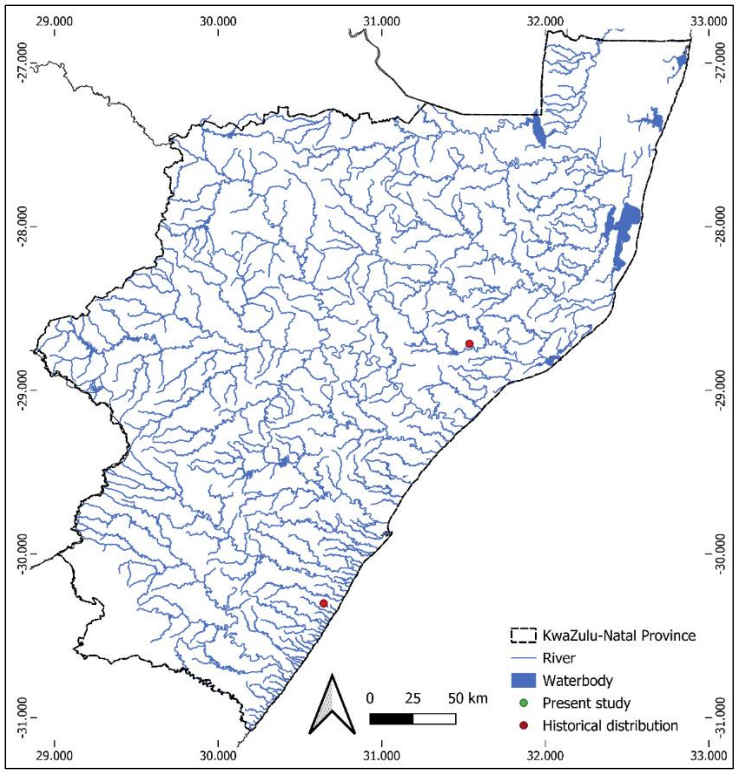
Supplementary Information Figure S5.44: Spatial distribution showing historical sampling sites of *Pettancylus fontinalis* in KwaZulu-Natal, South Africa.



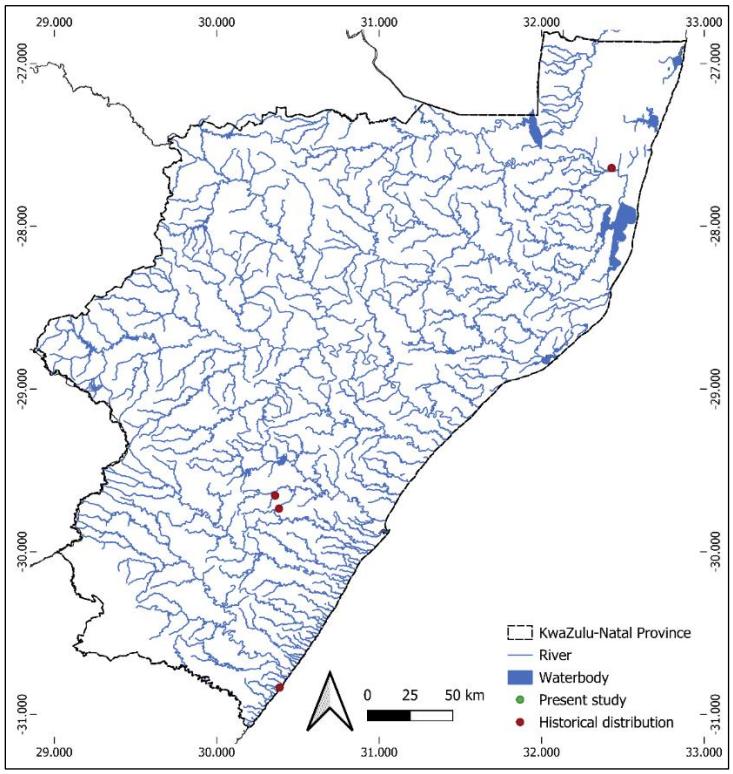
Supplementary Information Figure S5.45: Spatial distribution showing historical sampling sites of *Pettancylus natalensis* in KwaZulu-Natal, South Africa.



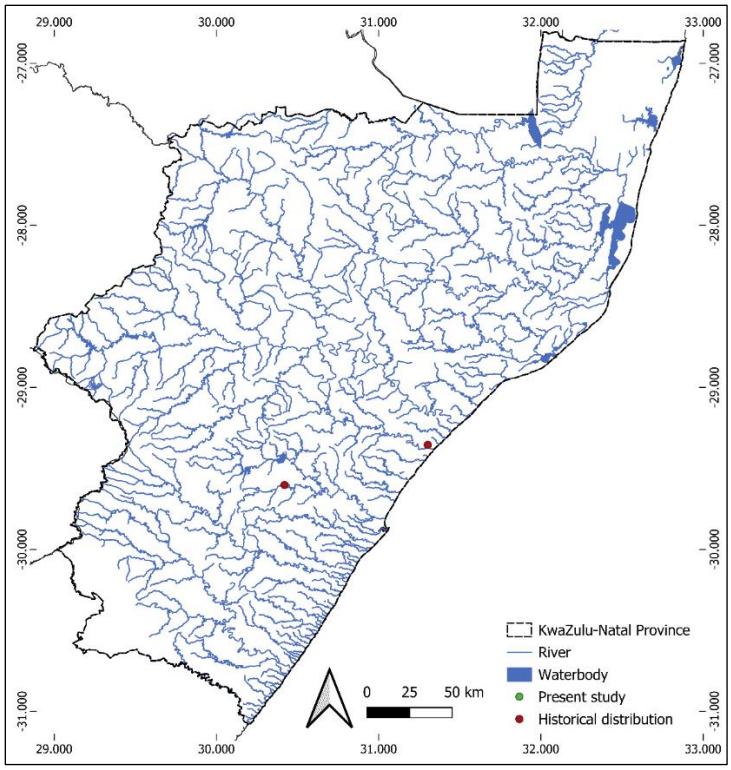
Supplementary Information Figure S5.46: Spatial distribution showing historical sampling sites of *Planorbella duryi* in KwaZulu-Natal, South Africa.



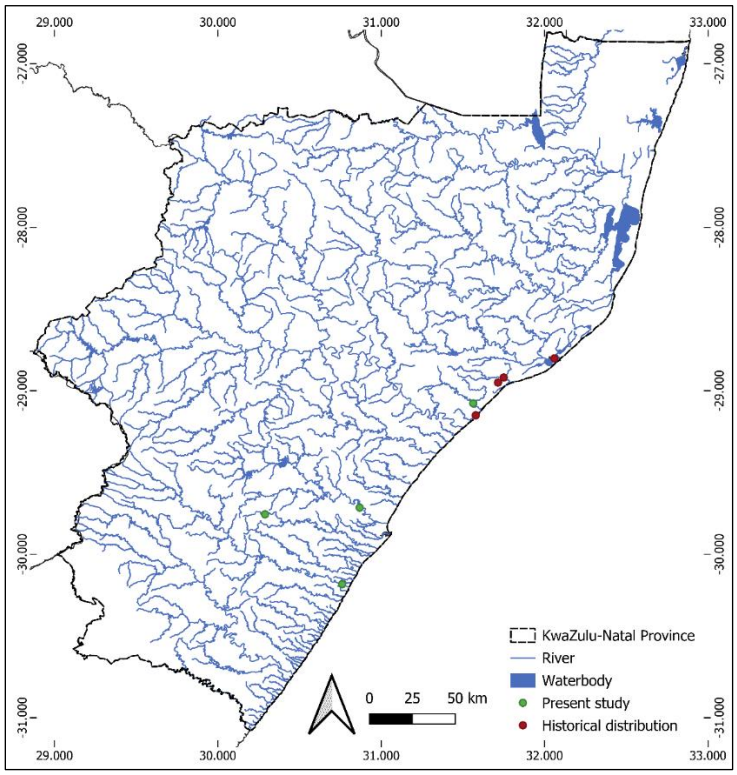
Supplementary Information Figure S5.47: Spatial distribution showing historical sampling sites of *Segmentorbis angustus* in KwaZulu-Natal, South Africa.



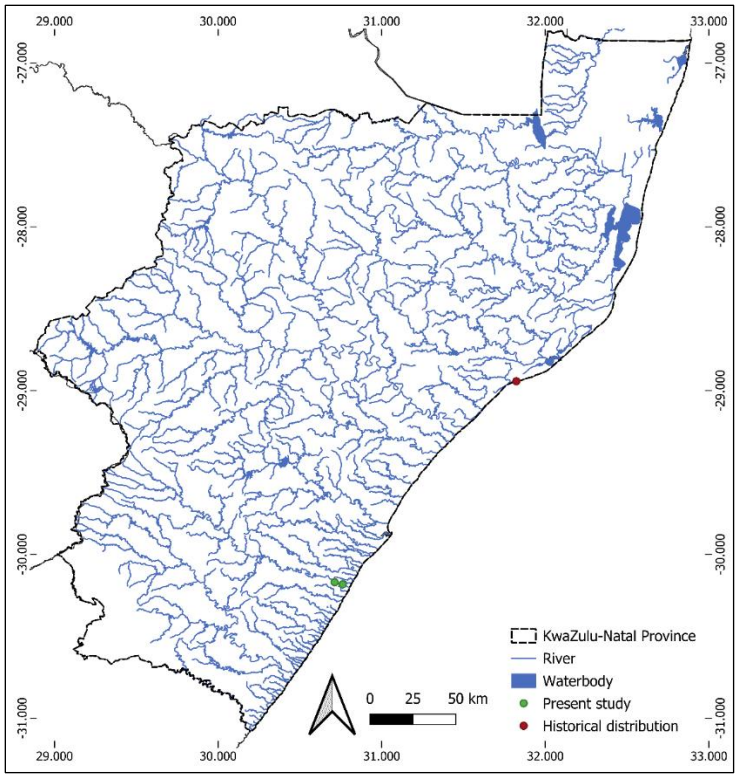
Supplementary Information Figure S5.48: Spatial distribution showing historical sampling sites of *Segmentorbis kanisaensis* in KwaZulu-Natal, South Africa.



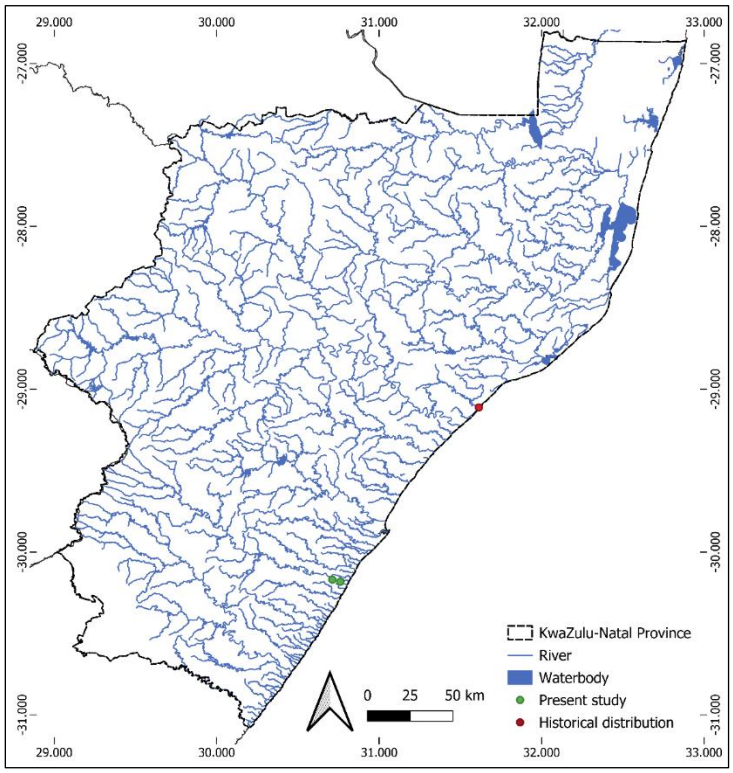
Supplementary Information Figure S5.49: Spatial distribution showing historical sampling sites of *Segmentorbis planodiscus* in KwaZulu-Natal, South Africa.



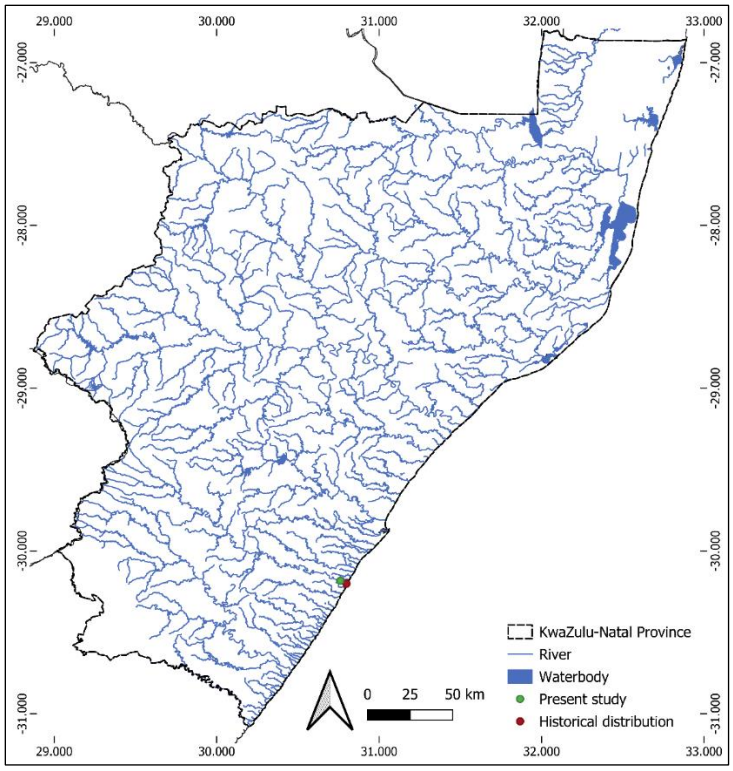
Supplementary Information Figure S5.50: Spatial distribution showing historical and recent sampling sites of *Neritina pulligera* in KwaZulu-Natal, South Africa.



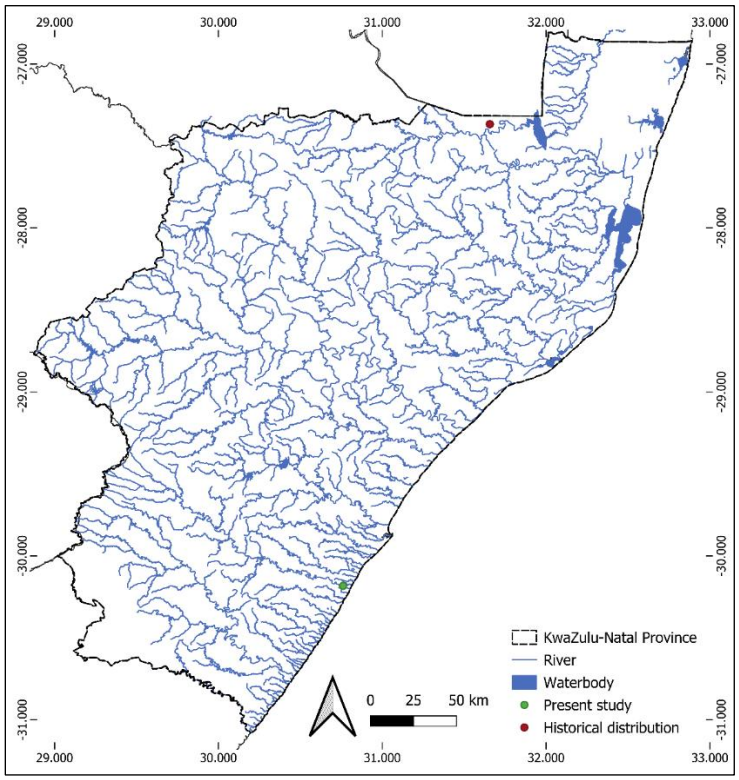
Supplementary Information Figure S5.51: Spatial distribution showing historical and recent sampling sites of *Septaria porcellana borbonica* in KwaZulu-Natal, South Africa.



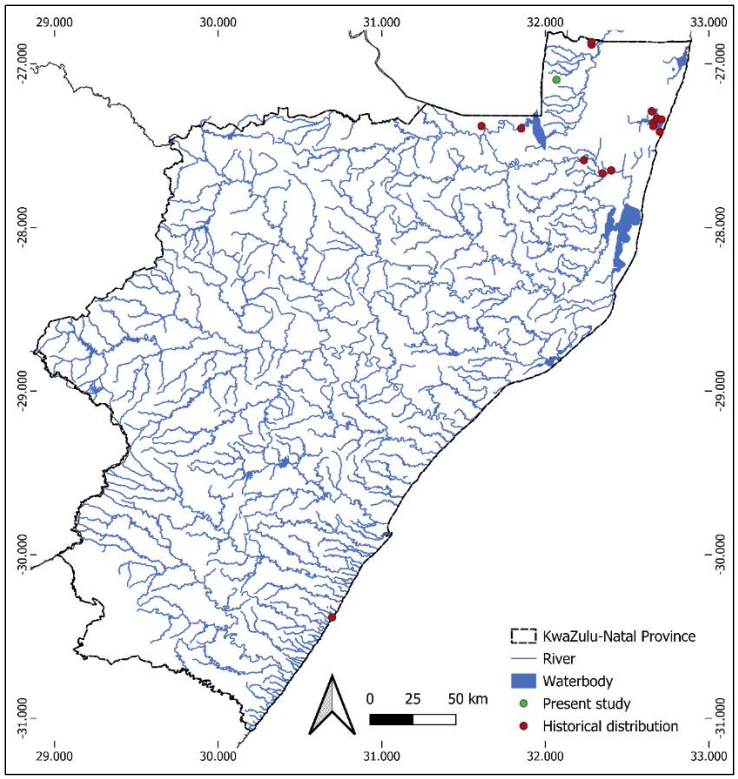
Supplementary Information Figure S5.52: Spatial distribution showing historical and recent sampling sites of *Septaria tessellaria* in KwaZulu-Natal, South Africa.



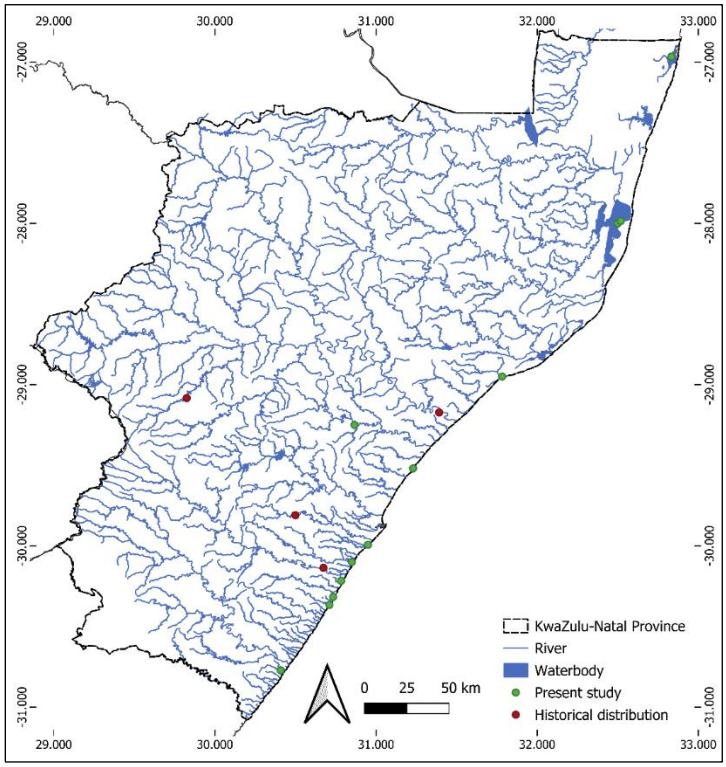
Supplementary Information Figure S5.53: Spatial distribution showing historical and recent sampling sites of *Vittina gagates* in KwaZulu-Natal, South Africa.



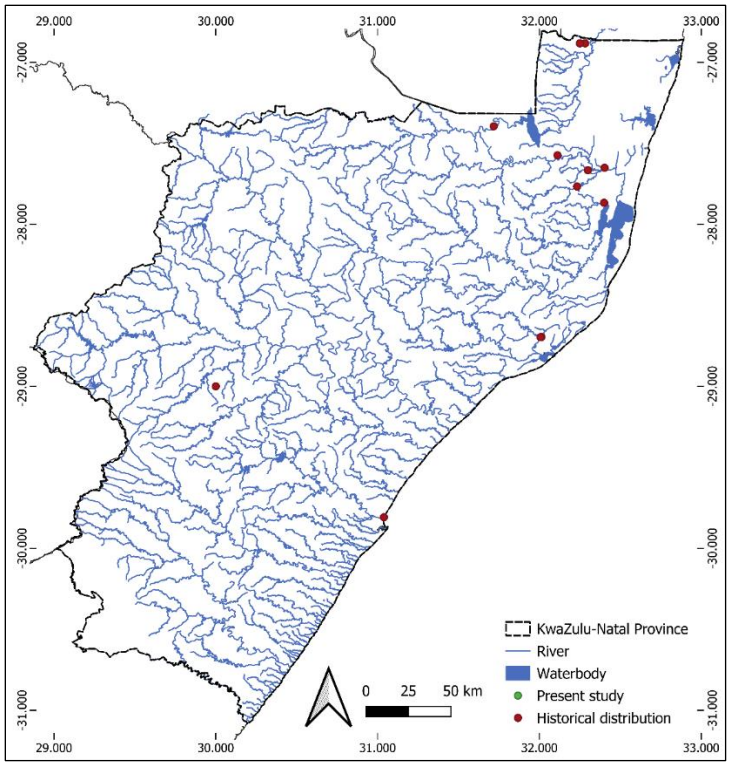
Supplementary Information Figure S5.54: Spatial distribution showing historical and recent sampling sites of *Vittina natalensis* in KwaZulu-Natal, South Africa.



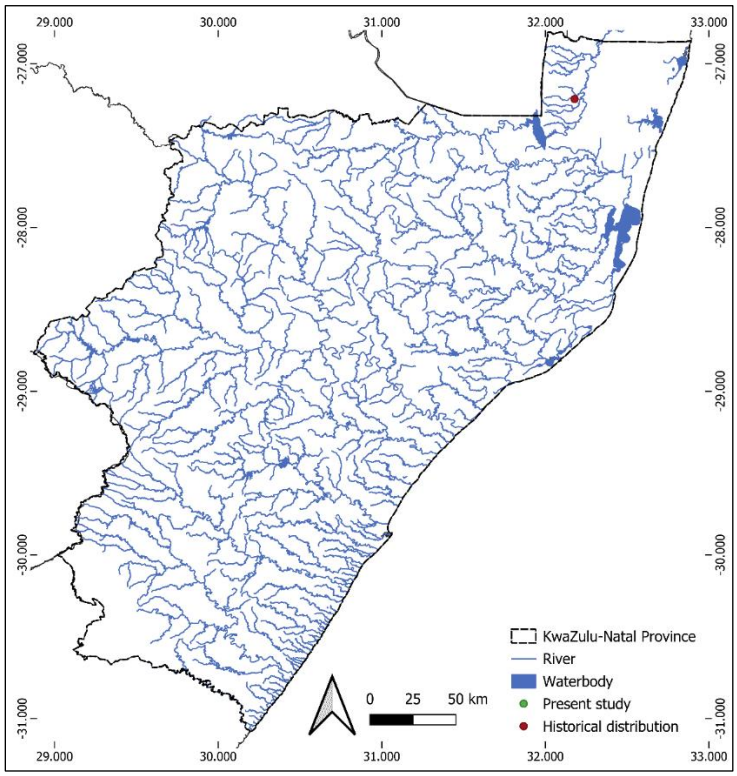
Supplementary Information Figure S5.55: Spatial distribution showing historical and recent sampling sites of *Bellamya capillata* in KwaZulu-Natal, South Africa.



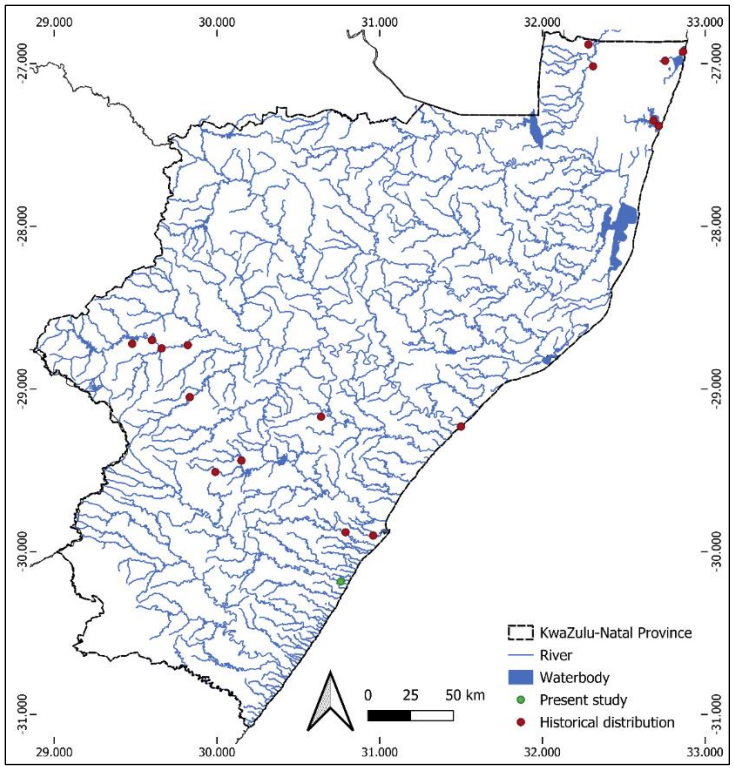
Supplementary Information Figure S5.56: Spatial distribution showing historical and recent sampling sites of *Brachidontes virgiliae* in KwaZulu-Natal, South Africa.



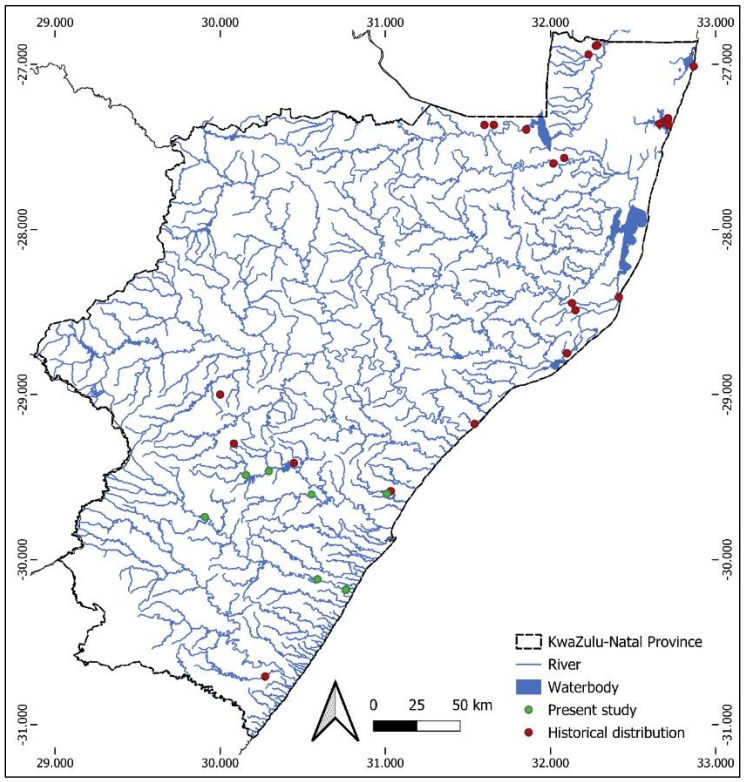
Supplementary Information Figure S5.57: Spatial distribution showing historical sampling sites of *Chambardia wahlbergi* in KwaZulu-Natal, South Africa.



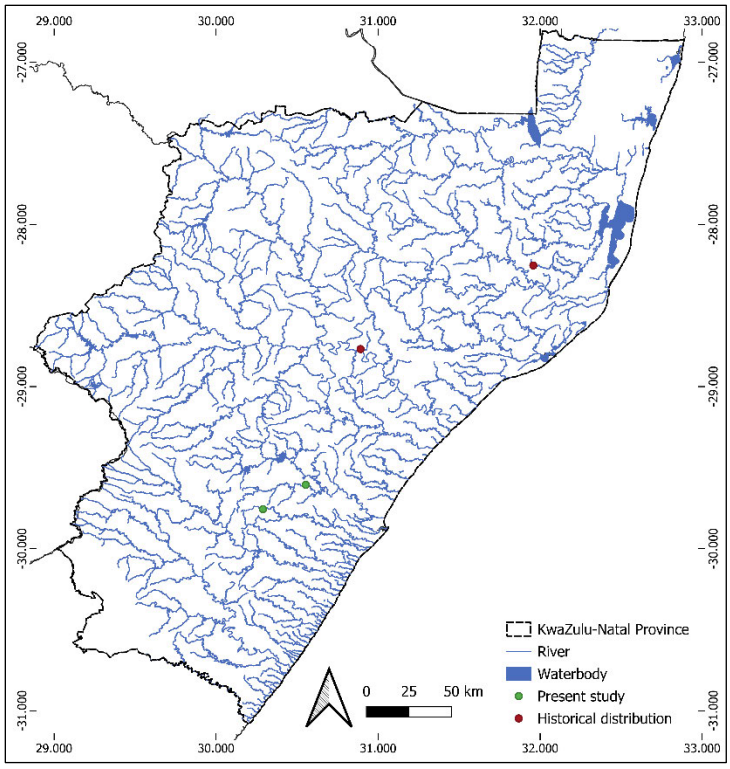
Supplementary Information Figure S5.58: Spatial distribution showing historical sampling sites of *Coelatura mossambicensis* in KwaZulu-Natal, South Africa.



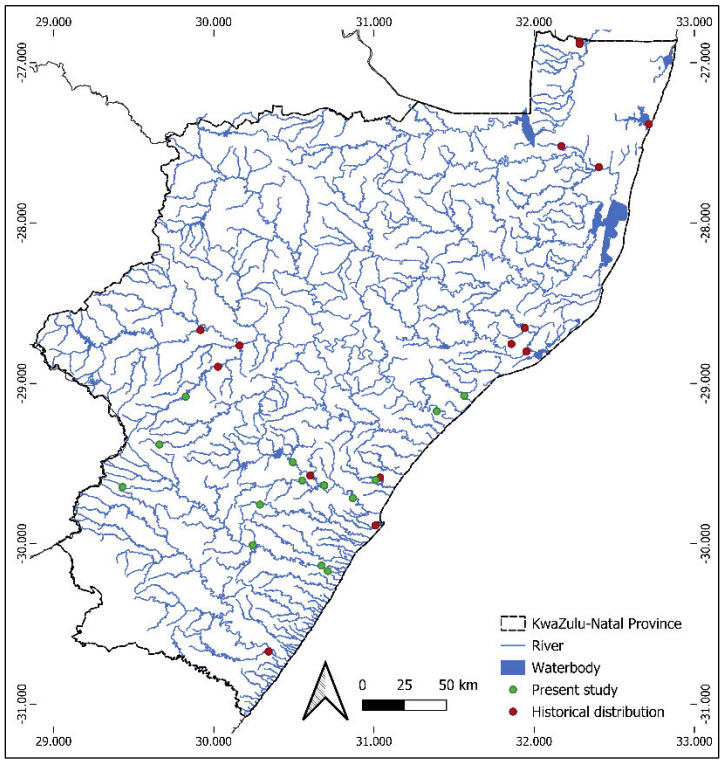
Supplementary Information Figure S5.59: Spatial distribution showing historical and recent sampling sites of *Unio caffer* in KwaZulu-Natal, South Africa.



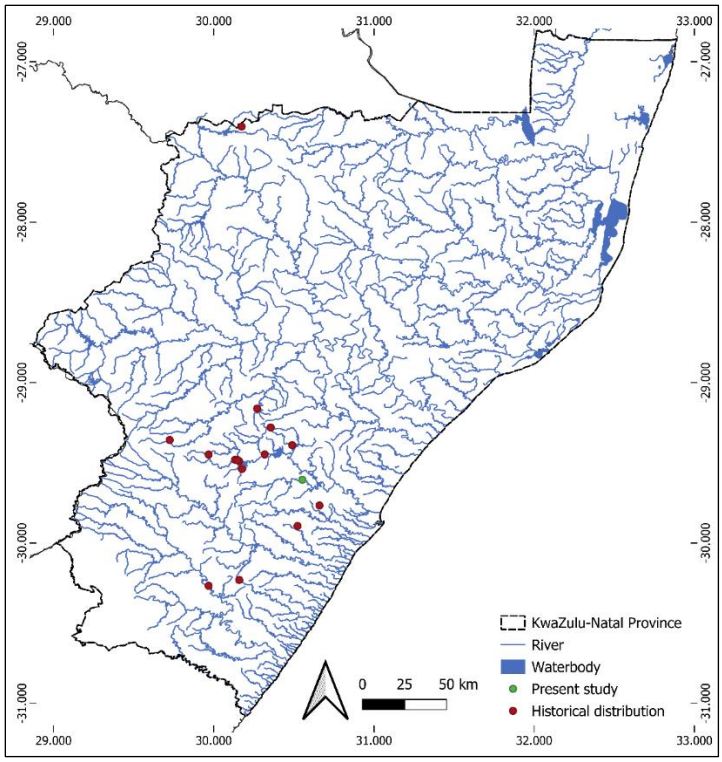
Supplementary Information Figure S5.60: Spatial distribution showing historical and recent sampling sites of *Corbicula africana* in KwaZulu-Natal, South Africa.



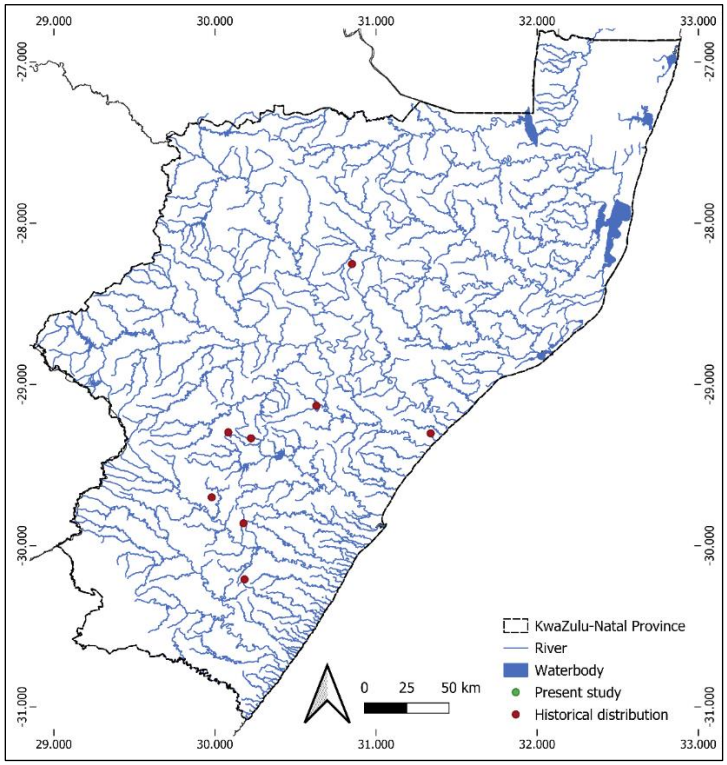
Supplementary Information Figure S5.61: Spatial distribution showing historical and recent sampling sites of *Corbicula astartina* in KwaZulu-Natal, South Africa.



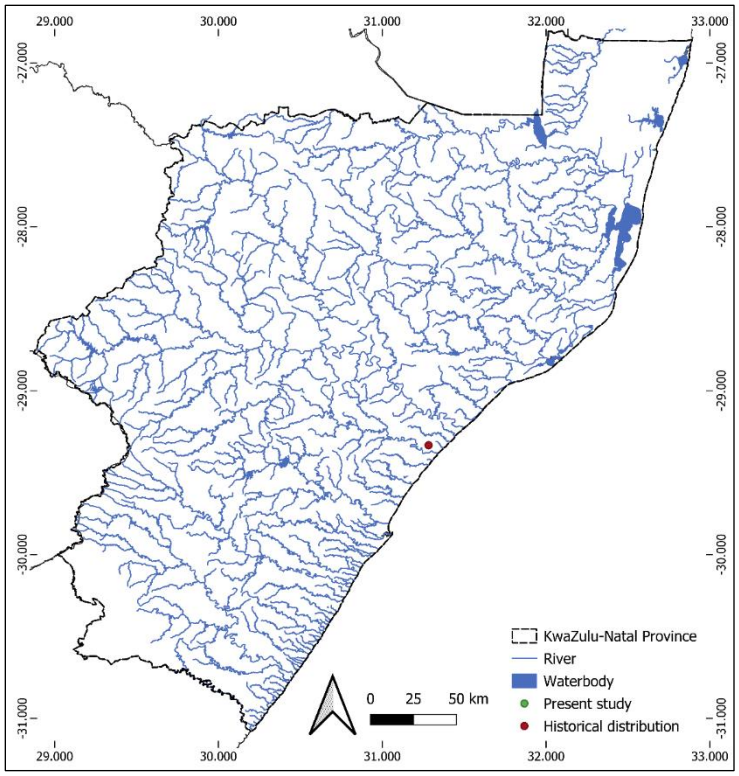
Supplementary Information Figure S5.62: Spatial distribution showing historical and recent sampling sites of *Corbicula fluminalis* in KwaZulu-Natal, South Africa.



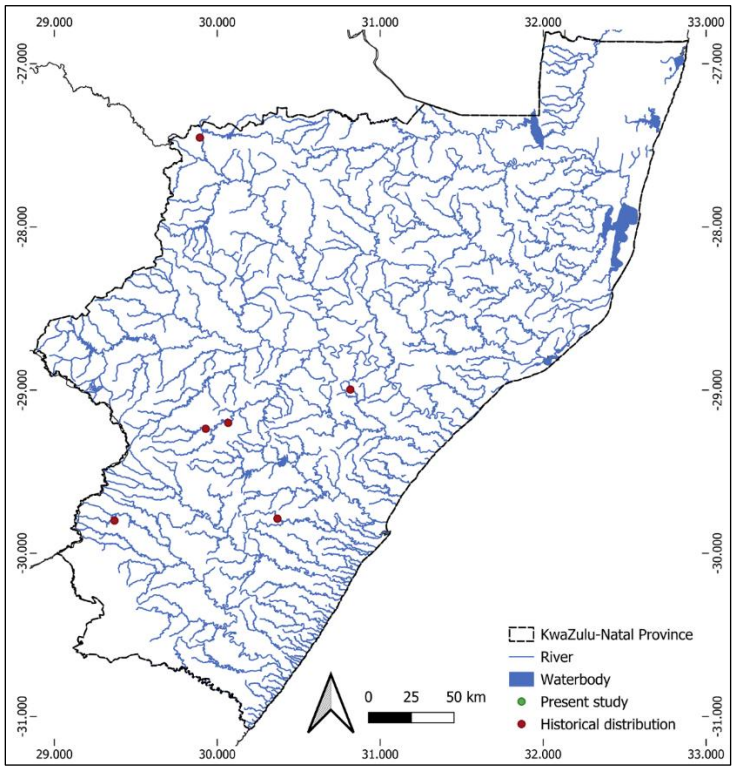
Supplementary Information Figure S5.63: Spatial distribution showing historical and recent sampling sites of *Euglesa costulosa* in KwaZulu-Natal, South Africa.



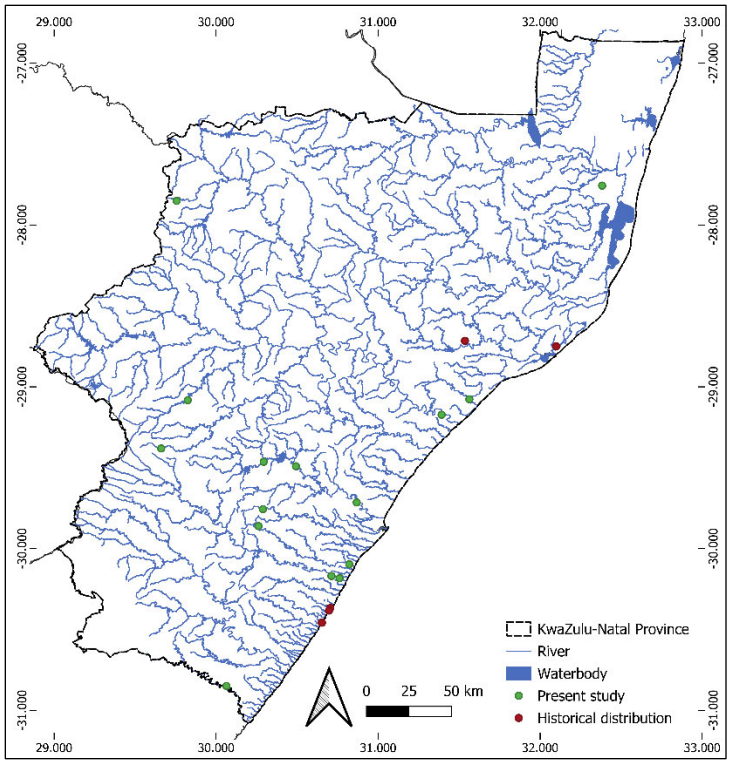
Supplementary Information Figure S5.64: Spatial distribution showing historical sampling sites of *Euglesa langleyana* in KwaZulu-Natal, South Africa.



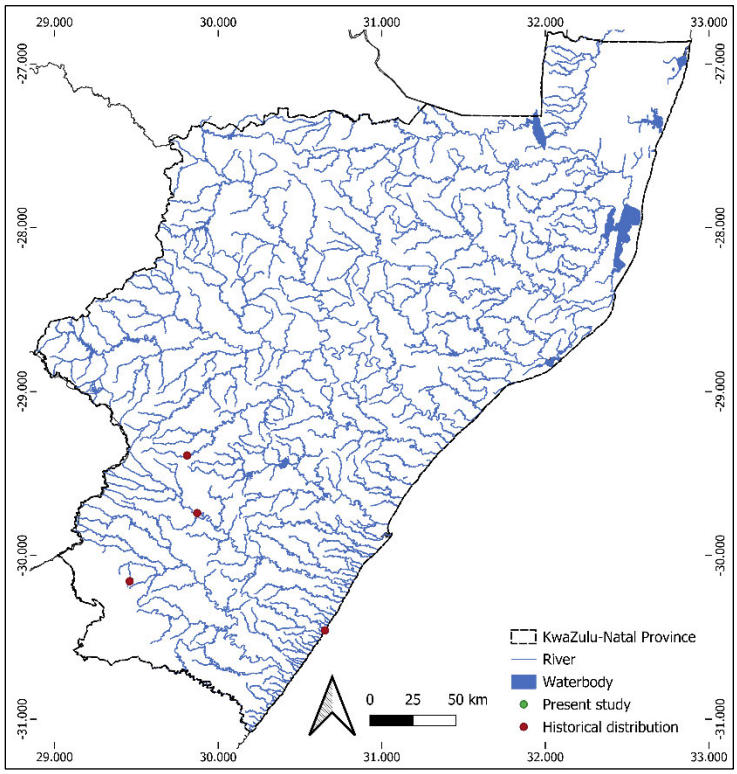
Supplementary Information Figure S5.65: Spatial distribution showing historical sampling sites of *Euglesa ovampica* in KwaZulu-Natal, South Africa.



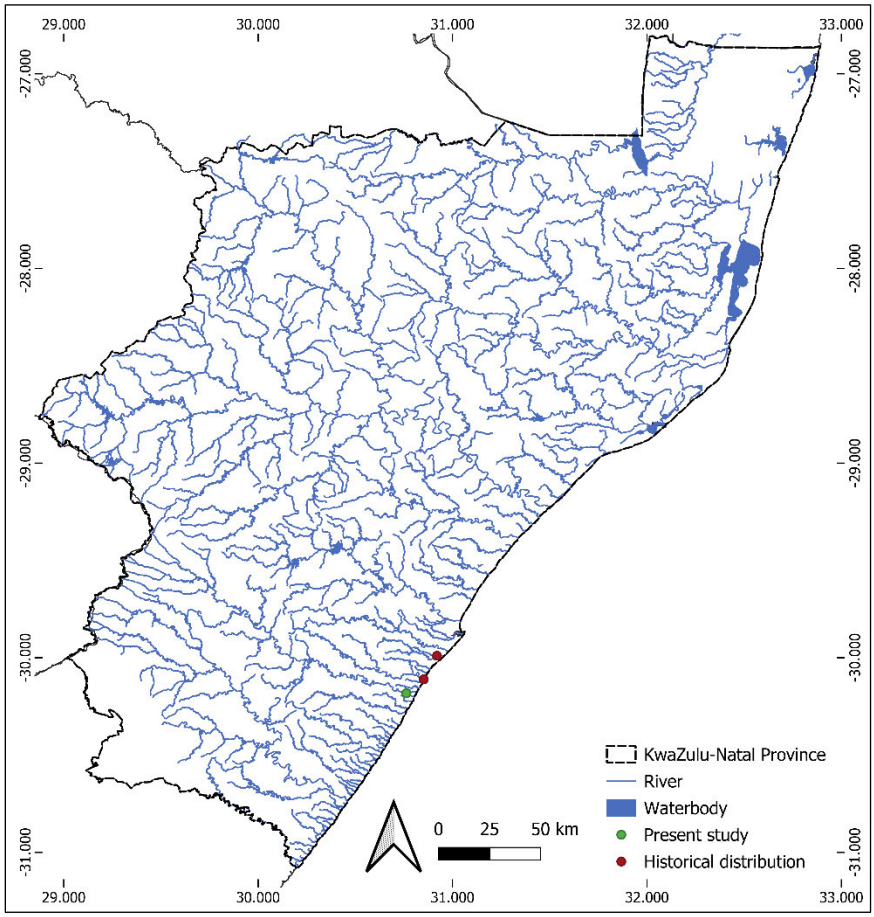
Supplementary Information Figure S5.66: Spatial distribution showing historical sampling sites of *Euglesa viridaria* in KwaZulu-Natal, South Africa.



Supplementary Information Figure S5.67: Spatial distribution showing historical and recent sampling sites of *Sphaerium capense* in KwaZulu-Natal, South Africa.



Supplementary Information Figure S5.68: Spatial distribution showing historical sampling sites of *Sphaerium incomitatum* in KwaZulu-Natal, South Africa.



Supplementary Information Figure S5.69: Spatial distribution showing historical and recent sampling sites of *Eupera ferruginea* in KwaZulu-Natal, South Africa.

CHAPTER 6

General discussion, summary findings, conclusions and recommendations

6.1 Background

This chapter summarises and discusses the main findings of the research in relation to the aim and objectives of the present study. The benefits of using natural history collections and recent field data in analysing past and present changes in the diversity and distribution of freshwater molluscs in KwaZulu-Natal, particularly at River Eco-Status Monitoring Programme (REMP) sites, are discussed. Based on the study's outcomes, raising awareness of the existence of museum collections, collaboration among museum researchers and academics, increasing funding and capacity building, and including more mollusc families in REMP are advocated. In addition, the relatively low freshwater mollusc diversity across KwaZulu-Natal's freshwater ecosystems suggests that the majority of present habitats and water quality parameters are not suitable for supporting high mollusc diversity. However, compared with historical records at the 52 REMP sites, only 13 species were mapped, while this study recovered 24 species, with high or low diversity recorded at some sites. With increased urbanisation along the east coast of KwaZulu-Natal, where most historical sampling took place, national programs such as REMP and the Freshwater Biodiversity Information System (FBIS) have the opportunity to identify and include new key biodiversity sites for biomonitoring of biodiversity and the emergence of future diseases. Thus, an increase in financial and skills investment would facilitate the monitoring of biodiversity, emergence of future diseases and climate change in KwaZulu-Natal, and South Africa as a whole. This study will hopefully assist decision-makers in the district municipalities of KwaZulu-Natal in establishing a sustainable balance in the management of freshwater ecosystems.

Scientific study of African freshwater molluscs began nearly 260 years ago, with the arrival of European traders and explorers (Brown, 1994). Significant advances have been made in all the main fields of research, including conservation, taxonomy, genetics, climate change, ecology, public health, and more. Despite these, there are still gaps that need to be addressed, including (1) a lack of mollusc life history studies with regard to freshwater basin-connectivity on the continent; (2) a lack of categorisation of fields of study in publication records over the past four centuries. It could be suggested that research on freshwater molluscs is under-represented in some African regions and has been largely sidelined compared with terrestrial and marine molluscs. To date, little has been done to document the significant progress in the study of African freshwater molluscs over the past 260 years.

Globally, freshwater biodiversity is declining in major river basins (Turak et al., 2017; Böhm et al., 2020; Lopes-Lima et al., 2021). As a whole, South Africa is not exempt from this trend, the rivers of KwaZulu-Natal are being impacted by various anthropogenic activities that threaten their sustainability (Du Plessis, 2019; Agboola et al., 2020; Evans et al., 2022; Burnett et al., 2025), the leading causes of natural land cover loss and the ultimate decline in environmental functionality and connectivity in KwaZulu-Natal (Alexander et al., 2021). While the importance of natural history collections for research is generally appreciated (Shultz et al., 2021), the use of freshwater mollusc collections to analyse changes in occurrence and distribution in South Africa, particularly in KwaZulu-Natal, is lacking. Validating information from museum specimen records with online databases, such as the Global Biodiversity Information Facility (GBIF) and the Freshwater Biodiversity Information System (FBIS), can potentially aid in understanding long-term faunal changes in freshwater ecosystems in South Africa.

Previous work on freshwater Mollusca in South Africa and the KwaZulu-Natal is well documented, including recent distribution range and taxonomic work (Conolly, 1939; Mandahl-Barth, 1958, 1960; Kuiper, 1964, 1966; Van Eeden and Brown, 1966; Brown, 1967; Appleton, 1996; Herbert, 1998; Nwoko et al., 2022). There are ca. 69 species of freshwater Mollusca distributed across the province of KwaZulu-Natal, supported by 124 years of historical collection data (Brown, 1967, 1994; Appleton, 1996; Chapter 3). It has been reported that freshwater molluscs' distribution is influenced by the availability of suitable aquatic biotopes and depends on water quality (De Kock and Wolmarans, 1998; Dallas, 2007; Zeybek et al., 2012). These biotopes are constantly under threat from anthropogenic activities (Vaughn and Taylor, 1999; De Klerk et al., 2012; DWA, 2012; Kemp et al., 2016). In addition, since the establishment of the River Eco-Status Monitoring Programme (REMP) in the last decade, aquatic macroinvertebrates, including several mollusc families, have been utilised for biomonitoring freshwater ecosystems in South Africa using the South African Scoring System 5 (SASS 5) (Dickens and Graham, 2002) methodology. However, the SASS 5 score sheet lists only 11 families of freshwater molluscs (eight gastropods and three bivalves), whereas historical records have reported 16 families (11 gastropods and five bivalves). As a result, five freshwater mollusc families have been left out of the SASS 5 score sheet, and using microscopic identification of collected molluscs through the SASS 5 method has not been evaluated. The results of this study will increase our understanding of mollusc changes in faunal composition reported in the latest two years (2024 – 2025) of comprehensive surveys in the province, compared with historical records (Brown, 1967, 1994; Appleton, 1996; Nwoko et al., 2022), mapped at similar REMP sites. Additionally, this study aims to provide recommendations for identifying and including new sites for REMP and for increasing the number of mollusc families on the SASS 5 score sheet to broaden our understanding of mollusc diversity

and distribution changes. We believe this approach will make biomonitoring in KwaZulu-Natal and across South Africa more inclusive.

With its diverse geology and climate, KwaZulu-Natal harbours a high diversity of freshwater mollusc species, including endemic taxa (Brown, 1967, 1994; Herbert, 1998). The previous checklist of freshwater molluscs of KwaZulu-Natal included ca. 60 species (Brown, 1967, 1980, 1994; Mandahl-Barth, 1988; Appleton, 1996), but the list did not seem exhaustive, as some species mentioned in this study (e.g., invasive species) were omitted, as their presence was noticed in the late 1990s. It has been more than 20 years since checklists of freshwater molluscs in KwaZulu-Natal were compiled (Brown, 1967, 1994; Appleton, 1996). There is an urgent need to protect freshwater ecosystems in South Africa, and particularly in KwaZulu-Natal. Research that compiles a comprehensive checklist of freshwater malacofauna can assist conservation decision-makers in protecting these critical natural resources and tracing the emergence of future diseases and invasive species.

6.2 Research findings

The most notable pioneer in the study of plant and animal biodiversity in Africa in the 18th century was Michel Adanson (Carteret, 2012). Nearly 260 years ago (1757), the first study volume dedicated to molluscs was published, and his real contribution covered fifteen years of his work, from *Histoire naturelle du Sénégal* (published in 1757) to the *Cours d'histoire naturelle* (concerning zoology) which he taught between 1772 and 1774 (Fischer-Piette, 1942; Carteret, 2012). This component of the overall study found that the number of published studies on freshwater snails conducted in Africa between 1757 and 2024 increased gradually. The highest increase was recorded over the last 23 years (2001-2024), with 44.3% of publications on

freshwater snails conducted in Africa during this period (Chapter 2). Although new fields of study focus have emerged in the last 50 years, it was interesting to note that the majority of snail study objectives were related to conservation and taxonomy of species (Chapter 2), while the Nile and the Congo Basins dominated the percentage contribution of African freshwater mollusc studies. This study has established that understanding the history of the subject matter and documenting the significant efforts invested are paramount, as they inform future researchers about how we arrived at our present state, while acknowledging the pioneers and all their contributions. With the global decline of taxonomists, Africa, and South Africa in particular, are not exempt from this trend. Therefore, it is important for African malacology to evolve and adapt to a new technological era, and to strive to reinvent itself through the opportunities presented by multidisciplinary research.

The second objective of the overall study was to analyse the information on specimen records provided by natural history collections in order to determine changes in the relative diversity and distribution of freshwater molluscs of KwaZulu-Natal, and validate the results by comparing our database with two data repositories, the FBIS and GBIF relative trends (FBIS, 2022). To assess long-term changes in freshwater mollusc communities in KwaZulu-Natal, we compiled a database of records from the Albany Museum in Makanda (AMM), East London Museum in East London (ELM), KwaZulu-Natal Museum in Pietermaritzburg (KZNM) and the National Freshwater Snail Collection (NFSC) of South Africa in Potchefstroom (Chapter 3). This study identified 69 freshwater mollusc species from KwaZulu-Natal that are presently preserved in museum collections in South Africa. The greatest increase in specimen deposition occurred during the 1960s and 1970s, peaking at 77% before declining thereafter. A large proportion of specimens collected during this period were deposited at the National Freshwater Snail Collection

of South Africa (NFSC) in Potchefstroom. A national survey of the freshwater Mollusca of South Africa was conducted between 1960 and 1980 by the Bilharzia Research Group of the Council for Scientific and Industrial Research (Brown, 1967; Hadfield, 2020). These results highlighted that the availability of financial and skill resources can support and move forward scientific research, especially when clear objectives are defined. Three species were predominantly the most abundant, *Bulinus tropicus* (Krauss, 1848), followed by *Radix natalensis* (Krauss, 1848) and *Pseudosuccinea columella* (Say, 1817). It was also found that there was a significant disconnect between museum specimens in natural history collections in South Africa and online data repositories such as GBIF and FBIS, as most of the data used were not published on these two open, collaborative data infrastructures. However, it is believed that the data compiled in the present study will, without a doubt, assist national and global efforts to mobilise and make biodiversity data available worldwide. Thus, advancing research on freshwater Mollusca in South Africa and across Africa. In addition, the present study found that the majority of species recorded as 'declining' were endemic molluscs, which highlights the importance of including more freshwater mollusc families in national monitoring programmes, such as REMP, using SASS 5. Regrettably, most species in our database had 'Data Deficient' or 'No Data' statuses, and their International Union for Conservation of Nature (IUCN) Red List statuses were 'Unknown'. Finally, the present study highlighted these data gaps and called for urgent systematic assessment of the IUCN Red List status of these mollusc taxa, for which information is incomplete. The list of freshwater molluscs, including both endemic and invasive species, has been updated with new localities. This study acknowledged limitations in our methodologies but advocated substantial efforts to increase financial support and taxonomic capacity for institutions housing natural history collections, including national infrastructures such as FBIS, so that large-scale, continuous monitoring

programs can be strategically implemented in South Africa. Additionally, collections-based research and data sharing are encouraged to build capacity in the field.

Freshwater mollusc surveys in South Africa and the KwaZulu-Natal in particular are well documented, and supported by 124 years of historical collections data (Connolly, 1939; Mandahl-Barth, 1958, 1960; Kuiper, 1964, 1966; Van Eeden and Brown, 1966; Brown, 1967, 1994; Appleton, 1996; Herbert, 1998, Chapters 3 and 4). However, most recent and ongoing surveys in the province have recorded fewer freshwater mollusc species than previously documented, suggesting a decline of mollusc diversity in KwaZulu-Natal. Additionally, since the establishment of the River Eco-Status Monitoring Programme (REMP) in the last decade, aquatic macroinvertebrates, including 11 mollusc families, have been utilised for biomonitoring freshwater ecosystems in South Africa (DWS, 2016). Yet, historical records of KwaZulu-Natal have reported 16 mollusc families, and no higher-resolution data have been used to assess mollusc diversity at REMP sites in KwaZulu-Natal. Thus, the third objective of the overall study was to assess the composition and distribution of freshwater malacofauna in major freshwater ecosystems of KwaZulu-Natal, in relation to water quality, and whether these patterns had changed over time (Chapter 4). Historical mollusc taxa were mapped to the nearest 10 km radius, based on their locality descriptions and coordinates, to match the REMP sites in KwaZulu-Natal. Additionally, 52 sites were sampled four times between February 2024 and September 2025 and were part of the REMP surveys. The sampling sites belonged to the three water management areas ‘U’, V’, and ‘W’ of KwaZulu-Natal, and some of them overlapped with historical localities (see Chapter 4, Section 4.3.1 for details on the three water management areas). Only a total of 24 freshwater mollusc species were recorded across the three water management areas of KwaZulu-Natal, compared with 69 known species (Chapter 4). However, 13 taxa were recorded on the historically

mapped REMP sites, compared with 24 taxa recorded in the present study. Although more species were recorded in this study than in recent studies and in the FBIS's ongoing surveys over the past five years (2020 – 2025), the present study recorded 45 fewer species than historical data. The 'U' recorded the highest number of species, followed by 'W' and 'V' water management areas. This study reports a potential decline in freshwater mollusc species diversity across KwaZulu-Natal, based on recent and ongoing surveys. Interestingly, *Corbicula fluminalis* (O. F. Müller, 1774) and *Tarebia granifera* are introduced species that were the most abundant recorded (Chapter 4). A total of 1371 individuals were recorded in this study, of which 42% were *Tarebia granifera.* Biotope availability, habitat characteristics, and the presence of predators and competitors were the primary variables determining the abundance and distribution of molluscs (Min et al., 2022). This study revealed that the availability of vegetation biotope and the total dissolved solids (TDS), significantly influenced mollusc species diversity, distribution, and composition (Chapter 4). However, compared with historical records for KwaZulu-Natal, the vast majority of endemic freshwater molluscs reported historically were not recorded across the province during our surveys, whereas invasive species diversity and composition increased. Sampling freshwater molluscs in the low flow season recorded lower mollusc diversity compared with high flow, suggesting that freshwater mollusc species composition and diversity were higher in summer and autumn, compared with winter and spring. Compared with historical records mapped at the 52 REMP sites (13 species), this study recovered 24 mollusc taxa, with high or low diversity recorded at some sites. Many historical sites were located along the coastal regions of KwaZulu-Natal, and are no longer part of REMP because of anthropogenic activities. Landscape changes at many sites were observed during the surveys because of human activities such as agriculture, urbanisation, and sand mining (Chapter 4). The present study acknowledges limitations in our methodologies

but suggests that the low mollusc diversity in KwaZulu-Natal may also be attributed to inadequate sampling and a lack of a long-term monitoring program at selected sites over the past decade (Chapter 4). A high proportion of sites lacked molluscs, suggesting that freshwater mollusc species richness and composition may be influenced by both natural and anthropogenic disturbances (Chapter 4). Anthropogenic sewage discharge favoured the proliferation of select tolerant freshwater mollusc species, while less tolerant taxa were negatively affected, leading to degradation of critical ecosystem processes and river health (Chapter 4). Anthropogenic factors such as chemical pollution and sedimentation, competition and predation amongst aquatic species, and tolerance and sensitivity to urban pollution, significantly impacted the diversity, abundance, and composition of molluscs (Agboola et al., 2020; Böhm et al., 2020; Lopes-Lima et al., 2021) as was found in the present study (Chapter 4).

It has been more than 20 years since the last checklists on freshwater molluscs of KwaZulu-Natal were compiled (Brown, 1967, 1994; Appleton, 1996). Since then, there have been rapid changes in the freshwater ecosystems of KwaZulu-Natal, and a revised checklist of freshwater malacofauna was lacking. Recent studies on freshwater ecosystems in KwaZulu-Natal suggested that the sustainability of these ecosystems and all living organisms inhabiting them is under severe anthropogenic pressure (Agboola et al., 2020; Evans et al., 2022; Burnett et al., 2025; Chapter 4). Thus, protecting freshwater ecosystems is paramount, and relying on up-to-date information is crucial for informed conservation decision-making.

The fourth objective of the overall study was to update information on the ecology and taxonomy of freshwater molluscs across major freshwater ecosystems of KwaZulu-Natal (Chapter 5). This study presented an updated checklist of 69 freshwater mollusc species of KwaZulu-Natal (55 gastropods and 14 bivalves) belonging to 16 families (11 gastropods and five bivalves). The

list included historical records, online sources and our latest research surveys, which recorded 24 species (Chapter 5). Family Planorbidae amongst the gastropods was the most diverse (17 species), while Sphaeriidae was the most diverse within the bivalves (seven species). The 'U' water management area harbours the most diverse mollusc community, with a total of 54 species (43 gastropods and 11 bivalves) (Chapter 5). The gastropods *Tomichia natalensis* (Connolly, 1939) and *Tomichia tristis* (Morelet, 1889) are listed Critically Endangered, and *Tomichia ventricosa* (Reeve, 1842) Endangered, on the IUCN Red List; while the vast majority of freshwater molluscs are listed as either Least Concern or Data Deficient (Chapter 5). In addition, this study found that, in comparison with the previous freshwater mollusc checklist by Appleton (1996), a total of ten species are added: *Euglesa costulosa* (Connolly, 1931), *Euglesa langleyana* (Melvill & Ponsoby, 1891), *Euglesa ovampica* (Ancey, 1890), *Euglesa viridaria* (Kuiper, 1956), *Tomichia natalensis* (Connolly, 1939), *Tomichia tristis* (Morelet, 1889), *Tomichia ventricosa* (Reeve, 1842) and *Gyraulus chinensis* (Dunker, 1848), *Stenophysa marmorata* (Guilding, 1828), and *Tarebia granifera* (Lamarck, 1816), including eleven *Burnupia* species (Chapter 5).

6.3 Conclusions

This study has contributed to the field of freshwater Mollusca in South Africa by demonstrating that the role of natural history collections in scientific research should remain appreciated when all comprehensive collections are used in the study. It highlighted the limitations of using natural history collections but focused on the importance of these collections with regard to the types of data that could be extracted and how to utilise them, the individuals who built the collections and for what purpose, why these collections should continue to exist, as well as what future research should focus on (Chapters 2 and 3). This study compiled a comprehensive database of freshwater

molluscs of KwaZulu-Natal, dated between 1897 and 2025 (128 years). Additionally, this study may assist national and global efforts to mobilise and share biodiversity data, identify and include new key biodiversity sites for biomonitoring, and track the emergence of future diseases. This study also updated the status of endemic and invasive freshwater mollusc species in KwaZulu-Natal. From field surveys in 2024 and 2025, this study recorded 24 out of 69 known mollusc taxa, but the collection was higher than the historical 13 mollusc taxa recorded at the 52 REMP mapped sites (Chapter 4). The two years of surveys (2024 – 2025) were comprehensive and reported more freshwater molluscs than recent studies (eight species) and ongoing surveys (19 species) in the province, highlighting the robustness of our sampling method, while acknowledging limitations to our approach. Finally, it was essential to compile a checklist of all freshwater gastropods and bivalves to assess changes in faunal composition that have occurred and to provide information that could assist national and provincial efforts to conserve biodiversity in KwaZulu-Natal, as well as in South Africa as a whole (Chapter 5). However, in view of potentially declining species in freshwater ecosystems in KwaZulu-Natal, high species diversity was recorded in organically polluted rivers, supposedly rich in vegetation and dissolved solids. Nevertheless, this study argued that the prevalence of invasive species in highly organic-polluted freshwater ecosystems might have displaced endemic species, while predation and competition favoured invasive species over the survival of endemic species. This study also suggested that the combination of climate change in the form of natural disasters, such as droughts and floods in KwaZulu-Natal, with river pollution, potentially contributed to low mollusc diversity. However, this study noted that our presence - absence data may not directly indicate possible extinction or species decline, as many mollusc families have been excluded from REMP since its establishment over the last decade. Additionally, long-term monitoring of freshwater molluscs on the exact same sites has not been considered over

the last decade, and records data of those sites have not been systematically deposited or donated to museums. Although ongoing samplings by the FBIS team have been closing this gap, this study supports the view that inadequate sampling and the lack of long-term follow-up monitoring programmes may not provide a full spectrum of mollusc species diversity and composition in the province. Nevertheless, this study undoubtedly supports the national mandate to monitor the ecological status of freshwater ecosystems in South Africa.

6.4 Recommendations

Following this multifaceted study, the following recommendations are made:

1. An increase in capacity building, collaboration, and institutional support from academic institutions, natural history museums and funding agencies would be a big boost to the increased study of freshwater molluscs in Africa, and South Africa in particular. This would also contribute to the update of the IUCN Red List status of many freshwater mollusc taxa.
2. It is advocated that public engagement and raising awareness about the existence of natural history collections be considered, so that collaboration amongst the general public, museum researchers and academics may increase. Additionally, increased investment in financial and skills for research using natural history collections would facilitate wider geographical and long-term temporal sampling, taxonomic updates, and data mobilisation and sharing.
3. It is advocated for the inclusion of the higher resolution of mollusc taxa in REMP, data sharing and better management of freshwater ecosystems in KwaZulu-Natal and South Africa as a whole, so that the sustainability and health of these systems can improve. This

is important not only for biodiversity conservation, but most importantly, for rural communities that depend on freshwater ecosystems for their survival.

4. The national programs, such as REMP and FBIS, have the opportunity to identify and include new key biodiversity sites for biomonitoring of biodiversity, emergence of future diseases and climate change.
5. The SASS 5 should consider including more mollusc families on the Scoring sheet, to increase the broader spectrum of mollusc diversity and population composition.
6. Regional trends in anthropogenic activities such as urbanisation, agriculture, industrialisation, damming and sand mining should be regulated, as this will reduce their impacts on river fragmentation and disconnection.
7. It is also vital to combat river pollution, which is not only important to ensure healthy mollusc populations but also to withstand other threats. Establishment of riparian buffers to minimise flooding and runoff within impacted areas, as well as improvements to wastewater treatment and pesticide and fertiliser regulation, may assist the province.
8. Future research should focus on priorities for conservation of endemic freshwater mollusc species to better understand the impact of threats, such as pollution and climate change. A long-term study to follow up on higher resolution of freshwater mollusc taxa at the REMP sites would increase understanding of the state of freshwater malacofauna in the country.

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