



Ecosystem links: Anthropogenic activities, environmental variables, and macrophytes structure snail preferences in man-made waterbodies

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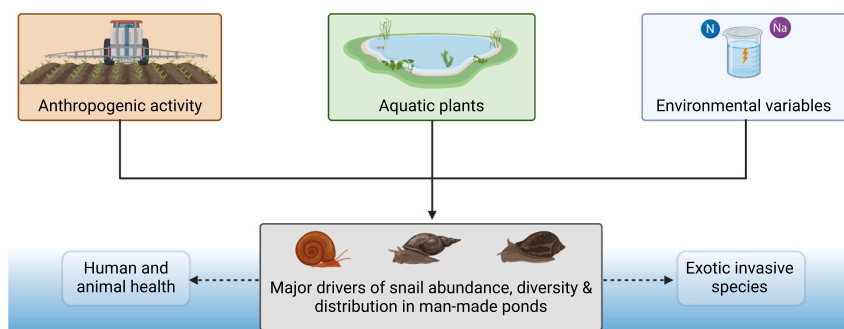
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HIGHLIGHTS

- Examined the complex relationship among snail diversity, trematode infection prevalence, and ecological context in man-made ponds
- Ecosystem state is largely influenced by surrounding land use.
- Ecosystem state and macrophytes structure freshwater snails distribution and abundance

GRAPHICAL ABSTRACT



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ABSTRACT

Freshwater snails act as obligate intermediate hosts for trematode parasites that cause trematodiasis threatening public and veterinary health, and biodiversity conservation. While interest in snail control for trematodiasis has re-emerged, their ecology remains poorly understood. We examined the relationship between ecosystem indicators – such as environmental variables, macroinvertebrates, macrophytes, and land use – and their correlation with snail abundance, diversity, and infection prevalence in 19 man-made ponds in eastern Zimbabwe. In total, 926 freshwater snails from 10 species were collected, with 547 individuals belonging to five schistosome-competent species: *Bulinus tropicus*, *Bulinus truncatus*, *Bulinus globosus*, *Bulinus forskalii*, and *Biomphalaria pfeifferi*.

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The remaining 379 snails comprised *Radix natalensis*, *Gyraulus* sp., and the exotic invasive species *Melanoides tuberculata*, *Pseudosuccinea columella*, and *Physella acuta*. Six cercarial types – mammalian schistosomes, avian schistosomes, longifurcate pharyngeates, echinostomes, amphistomes, and xiphidiocercariae – were isolated from 104 out of 926 snails (11.2 %). PCR revealed a significantly higher infection rate, with 70.2 % of snails testing positive for trematodes. Snail taxon diversity and infection rate significantly varied across land use types, with the lowest values observed in the commercial tobacco farm section, highlighting the potential adverse effects of agriculture on biodiversity. Ponds with extensive *Lagarosiphon major* (oxygen weed) coverage appeared to facilitate the presence and abundance of *P. acuta* and *P. columella*. Schistosome-competent snails such as *B. truncatus* and *B. tropicus* seemed to favor shallow water depths and more eutrophic sites characterized by high levels of nitrates, phytoplankton biomass, turbidity, and phycocyanin. These ponds were predominantly associated with the emergent macrophyte *Cladium mariscus*, revealing a potential association with important intermediate snail hosts. In conclusion, our study emphasizes the complex interplay among environmental factors, macrophyte composition, land use, and the abundance, diversity, and infection prevalence of freshwater snails, offering insights into potential strategies for targeted snail control and disease management in man-made waterbodies.

1. Introduction

Ecological disturbances in aquatic environments, such as biodiversity loss, chemical pollution, climate change, and the introduction of non-native species, are associated with increases in infectious disease risks (Mahon et al., 2024). Additionally, activities such as deforestation, human settlement, and agricultural projects have been linked to a rise in parasitic diseases (Ellwanger et al., 2020; Gyasi et al., 2019; Johansen et al., 2023; Kibret, 2018; Sokolow et al., 2017). These interventions increase disease transmission through various mechanisms, including changes in water quality or salinity (Lin et al., 2022; Sow et al., 2002), alterations in aquatic community structure (McAllister et al., 2001), and the introduction of new (sometimes invasive) species (Habib et al., 2021; Zhang et al., 2022), all of which can reflect a ‘poor ecosystem state’. Additionally, the creation of permanent water bodies - often an anthropogenic response to climate-change-related water scarcity - further disrupts hydrological regimes (Leo et al., 2020; Tortajada et al., 2012). This leads to the creation or expansion of habitats conducive to disease vectors such as dipterans and snails, thereby putting numerous communities at risk of disease (Kyei-Baafour et al., 2020; Sokolow et al., 2017).

Snail-borne trematodiasis are prevalent neglected tropical diseases in sub-Saharan Africa, caused by parasitic trematode flatworms infecting humans and animals (Díaz et al., 2023; Gyapong and Boatın, 2016). Schistosomiasis, the most common trematodiasis in Africa, significantly impacts social and economic development, with over 90 % of global cases concentrated in sub-Saharan Africa (Hotez et al., 2014; Lai et al., 2015; Steinmann et al., 2006; WHO, 2020). Advances in managing schistosomiasis morbidity have been made through large-scale administration of praziquantel, but this drug only treats mature infections and does not prevent reinfection (Kokaliaris et al., 2022; Pica-Mattoccia and Cioli, 2004; Sokolow et al., 2017). Consequently, the disease persists and intensifies, particularly in regions relying on open waterbodies for water and sanitation (Hunter et al., 1982; Sokolow et al., 2017). Thus, mass chemotherapy should be complemented with sustainable vector control, improved water supply, and proper sanitation adapted to the local environment (Sokolow et al., 2016).

Trematode parasites require freshwater snails as first intermediate hosts in their complex lifecycle (Toledo and Fried, 2014). Controlling snail abundance - primarily through molluscicides but also via environmental modifications - effectively reduces schistosomiasis spread (King et al., 2015; Rollinson et al., 2013). While molluscicides are expected to play a significant role in future elimination schemes, currently used molluscicides are usually not eco-friendly, harming many other aquatic lifeforms and persisting in the environment (Dai et al., 2008; Keighley et al., 2021; Yang et al., 2020).

It is therefore essential to comprehensively understand local aquatic ecosystems and integrate sustainable snail control efforts in local environmental management regimes. There are a variety of ecological

factors influencing freshwater snail distribution and infection prevalence, which in turn may affect disease epidemiology. Local conditions such as temperature, water quality, macrophyte cover, and various biodiversity components can directly impact vector snail distribution and life history, ultimately influencing parasite transmission (Becker et al., 2020; Halstead et al., 2018; Kalinda et al., 2017; Malan et al., 2009).

The intricate relationships between snail diversity, trematode infection prevalence, and their ecological context remains a critical yet understudied area in fundamental and applied freshwater ecology. Despite significant progress to date, most insights have come from controlled laboratory experiments (Brodersen and Madsen, 2003; Kalinda et al., 2018). Due to the limited ecological relevance of such experiments, gaps regarding the specific influences of ecological variables such as land use practices and ecosystem state on the prevalence and diversity of trematode infections in natural snail populations persist.

To address these gaps, our study explored whether the ecosystem state of man-made ponds affected various aspects of freshwater snails, including their abundance, diversity, and infection status. In this context, we define poor ecosystem state based on one or a combination of the following indicators: i. poor water quality, characterized by low dissolved oxygen levels (essential for aquatic organisms), high conductivity (often harmful to aquatic organisms), and nutrient overload (such as nitrogen and phosphorus, known to cause eutrophication, algal blooms, and oxygen-depleted environments) (Bashir et al., 2020); and ii. biodiversity loss, characterized by a reduced richness of macrophytes and macroinvertebrates, including snails, and an increased abundance of invasive species (Bashir et al., 2020; Collier et al., 2016).

Our study therefore hinged on three primary research questions and their respective hypotheses. First, we hypothesized that environmental variables would indeed show variation across the ponds, influenced by inputs from surrounding land use activities. We anticipated, for instance, that ponds located near farming areas would exhibit higher nutrient loads and conductivity due to agricultural run-off (Nhiwatiwa et al., 2017), compared to ponds within wildlife conservation areas.

Secondly, we explored a cascading effect of environmental variables on the composition of macroinvertebrate and macrophyte communities. We expected, for example, that eutrophic water bodies would harbor a low abundance and diversity of macroinvertebrates and macrophytes due to the adverse effects of excess nutrients (Peng et al., 2023). Similarly, elevated conductivity levels and anoxic conditions are associated with reduced macroinvertebrate richness (Dalu and Chauke, 2019), which we anticipated to observe.

Finally, we investigated whether the ecosystem state, as reflected by environmental variables and/or macroinvertebrate and macrophyte community composition, would influence freshwater snail metrics, including abundance, diversity, and infection status. We anticipated lower snail abundance and diversity in ponds with poorer ecosystem states, as water quality stress tends to favor resilient species, leading to

reduced overall diversity and abundance (Bae and Park, 2020). Additionally, richer macrophyte communities create more habitat for macroinvertebrates (Chibsa et al., 2022) for which we postulated would in turn would support snail communities and thus snail-borne parasites, while low macrophyte diversity would only support few snail species and thus lower diversity of snail-borne parasites.

2. Methods

2.1. Study area and sampling design

Our study was conducted at the Imire Rhino and Wildlife Conservancy and the adjacent Mhakwe villages (Fig. 1), situated in the Wedza district of Zimbabwe, approximately 70 km from the capital city Harare. The region features a temperate highland tropical climate with an average annual rainfall of about 675 mm and an average temperature of 21.5 °C. This area was chosen due to its reported second-highest prevalence of schistosomiasis in the country (Midzi et al., 2014) and its history of potential parasite-related animal mortalities, offering an opportunity to investigate snail-borne parasites in relation to environmental conditions.

The study encompassed 19 ponds representing a gradient in land use categories. These included five distinct areas, four within the

conservancy and one in the villages outside the conservancy (Fig. 1). The conservancy comprises three fenced sections – Chiwawe, the Middle section, and Lodge section – primarily dedicated to nature conservation and tourism (herein also referred to as protected area). The fourth section is a commercial tobacco farm managed by the conservancy and devoid of wildlife. Additionally, three sites in the surrounding villages outside Imire were sampled. These village sites are primarily used for cattle drinking, fishing, irrigation, and household activities. Sampling was conducted following the warm wet season in March 2022. A sampling site was established as an 8-m stretch along the shoreline, centered at a designated GPS coordinate, extending 3 m from the shoreline into the pond. All sampling activities, including the collection of snails, macroinvertebrates, macrophytes, and water samples for determining environmental pond variables, were conducted within this defined transect (details provided below).

2.2. Environmental pond variables

The GPS coordinates for each site were recorded using a Garmin GPSMAP® 60CSx. The site's maximal depth and area were estimated using a calibrated depth stick, while the dam's surface area was estimated using the ArcGIS application (Supplementary Table S1). On-site land use was assessed based on the location of the man-made ponds,

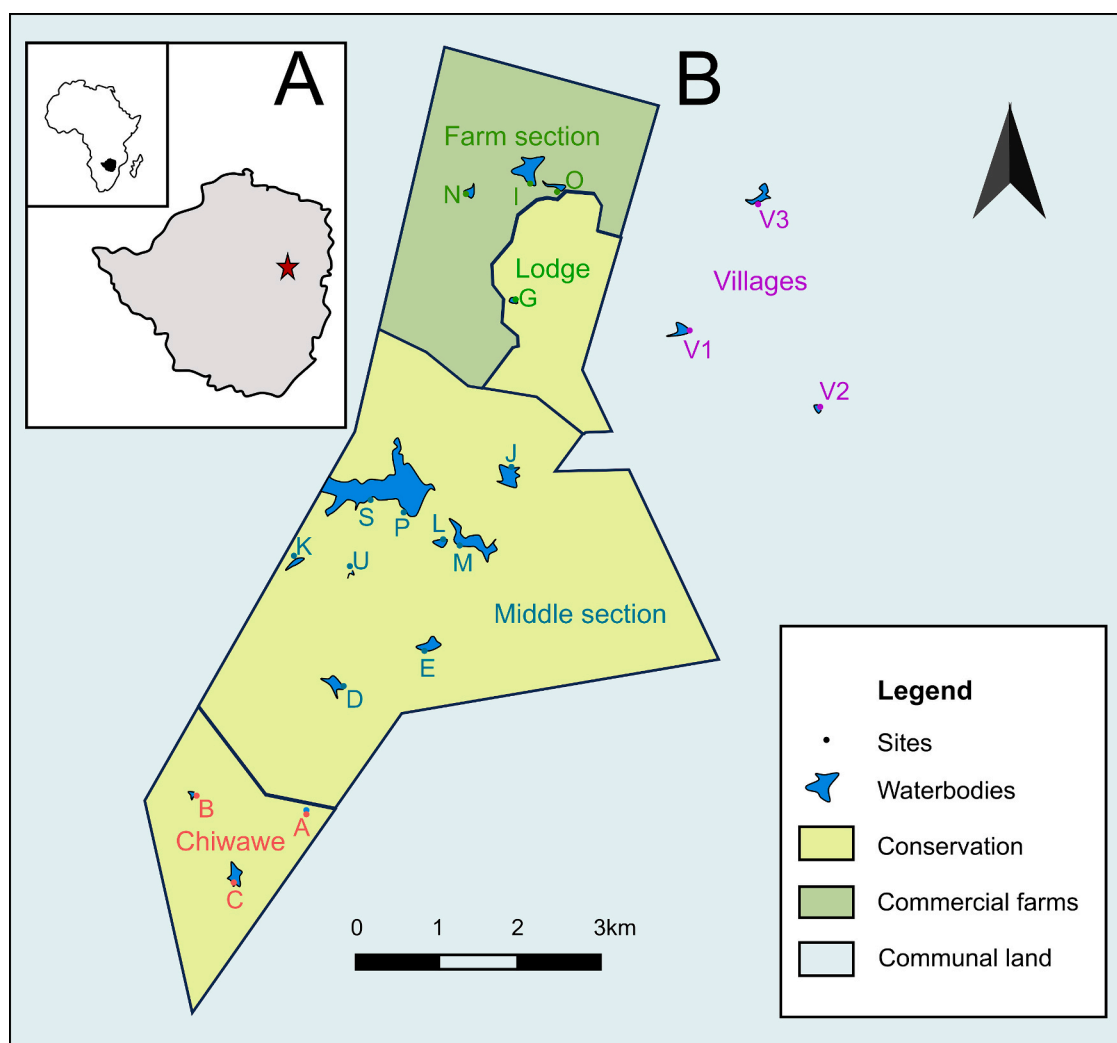


Fig. 1. Map of the study area depicting the 19 investigated ponds (A) position of the study area in Zimbabwe (shaded black) on the map of Africa and the location of the study region (shown as a red star) on the map of Zimbabwe. (B) Map of Imire and surroundings showing the sampled sites. The colors indicate the different land use types according to the legend inset. The borders of Imire and the different sections within are indicated by black lines.

which was categorized into three designations: conservation, communal land, and commercial farms (Fig. 1).

Several physical and chemical water variables, such as pH, temperature (°C), conductivity (µS/cm), salinity (PSU), oxygen concentration and saturation (% and mg/L), total suspended solids (mg/L), and total dissolved solids (mg/L), were measured in situ using a HANNA Instruments® HI9829 multiparameter probe. Ten 1-L samples were collected from multiple locations within each sampling site to create an integrated 10-L sample, which was homogenized to represent the entire site for downstream analysis of turbidity (NTU), chlorophyll-a, and phycocyanin concentrations (µg/L) using a Turner® AquaFluor fluorometer. Additionally, a 500-ml subsample from the 10-L sample was filtered using a 64 µm zooplankton net, stored cold for transport, and further analyzed in the field laboratory for water quality using a spectrophotometer (HACH DR/2010, Colorado). Standard methods (Hach Chemical Company, 2007) were followed for the analysis of sulphates (mg/L), total phosphorus (mg/L), reactive phosphorus (mg/L), nitrates (mg/L), nitrites (mg/L), total nitrogen (mg/L), ammonia (mg/L), chemical oxygen demand (mg/L), calcium (mg/L), and magnesium (mg/L) (Supplementary Table S1).

2.3. Snail community structure

Time and space restricted snail sampling was conducted by the same researchers at each site to ensure uniformity. Following the sampling protocols outlined in the studies by Carolus et al. (2019) and Mudavanhu et al. (2024), sampling at each site lasted 30 min, with 25 min dedicated to kick-netting and 5 min allocated for sorting the collected material. Nets with 1 mm mesh size mounted on 2-m-long handles were used to accommodate depth variations, sampling to a maximum depth of 2 m. When large rocks or logs obstructed netting, snails were hand-picked, although this method was rarely applied and only in small sections of the transect (sites E, J and O). We meticulously sampled from the substratum to the surface, encompassing all key mesohabitats, including substratum, rocks, logs, suspended debris, and macrophytes proportional to their occurrence. This approach enabled us to capture the full diversity of snail communities while upholding a consistent sampling effort across all sites.

All collected snail specimens were counted and identified to species level based on classification keys (Brown, 1994; Mandahl-Barth, 1962). A previous study (Mudavanhu et al., 2024) conducted in August 2021 morphologically and molecularly identified snail and trematode communities in the same ponds sampled here. Therefore, snail identification in the current study benefited from the molecular analysis of the precursor study to address the complexities associated with morphology-based identification of freshwater snails.

2.4. Determining snail infections

Following overnight storage in darkness, snails were exposed to bright light and indirect sunlight, an experimental setup known to trigger the emergence of cercariae from their intermediate host termed “shedding experiment”. During this experiment, we transferred individual snails to multi-well plates filled with bottled water. Emerging cercariae were identified at the family level according to appropriate keys (Appleton and Miranda, 2015; Frandsen and Christensen, 1984). Shedding snails were stored individually, while individuals that did not release cercariae (uninfected or prepatent infection) were pooled together per species per site in 80 % ethanol for transportation and later molecular analysis. During the prepatent infection phase inside the snail, trematodes occupy the mantle, digestive, and/or reproductive organs (Lafferty and Kuris, 2009), and since shedding snails were already isolated no cross-contamination was anticipated in pooled snail collections. To effectively preserve snail and parasite DNA while removing any external trematode larvae, we implemented a serial washing protocol using both water and ethanol, with ethanol renewed

12 h and one week later.

Cercariae recovered during the shedding experiment were stored in 80 % ethanol in a separate tube labelled to match the individual snail of origin and transferred to the University of Leuven and the Royal Museum for Central Africa in Belgium for digitalization and molecular identification.

During the preparation of snail tissue for DNA extraction, the soft tissue was extracted from the shell using a sterile needle inserted into the shell apex. Excess ethanol was removed from the isolated tissue using absorbent paper to prevent interference with downstream molecular procedures and to minimize the risk of genetic contamination, particularly in pooled snail samples. The E.Z.N.A.® Mollusc DNA Kit (OMEGA Bio-Tek, Norcross, GA, USA) was utilized following the manufacturer's protocol to extract DNA from the whole snail tissue, resulting in 150 µL of DNA extract. Subsequently, their infections were analyzed using multiplex rapid diagnostic polymerase chain reaction (RD-PCR) techniques, as outlined by Schols et al. (2019) and Carolus et al. (2019). The infection RD-PCR assays were designed to detect infections caused by all trematodes, and a marker targeting *Schistosoma* spp. or *Fasciola* spp. in snail DNA extracts. Hence, infection prevalence could be determined for the respective taxonomic levels (i.e., all trematodes, schistosomes and fasciolids). Samples positive for *Schistosoma* spp. were identified to species level based on differential amplicon size, using the *Schistosoma* RD-PCR according to Schols et al. (2019).

2.5. Macroinvertebrate and macrophyte community structure

Macroinvertebrates were collected using a 250 µm mesh net during a 10-minute sweep at each site. To ensure representativeness, the sampling effort was adjusted based on the proportional coverage of mesohabitats (i.e., bottom, submerged vegetation, floating vegetation, water column) at each site. The sweep time was then allocated proportionally to each habitat, ensuring that areas with abundant macroinvertebrates, such as vegetated ones, received more sampling effort than open water, where densities tend to be lower. All collected macroinvertebrate specimens were sorted and stored in 80 % ethanol in the field, transported back to the field laboratory and classified to family level using multiple identification keys (Day et al., 2003; de Moor et al., 2003a, 2003b; Stals and de Moor, 2007).

Two researchers visually estimated the percentage cover of submerged, emergent, and floating vegetation within the predefined 8x3m site, consistent with the area used for snail and macroinvertebrate sampling. Cover was estimated in increments of 5 %, and the average values from both assessments were used. We acknowledge the inherent challenges of visually estimating submerged vegetation, particularly due to potential interference from factors like water turbidity and the overshadowing effects of surface vegetation. To mitigate these challenges, initial estimates were further supplemented by passive observations during the 25-minute snail survey and the 10-minute macroinvertebrate sampling, allowing us to verify or adjust our initial estimates of submerged vegetation. All estimates represent horizontal coverage which is consistent with the scope of this study. All observed macrophyte taxa were identified to species level based on Cook (2004) and Gerber et al. (2004).

2.6. Data analysis

Data were analyzed to address the three research questions set forward in this study. First, we investigated whether environmental variables differed across the ponds in the study area. To assess variation among sites in physical and chemical variables, we performed Principal Component Analysis (PCA) using the `prcomp` function from the `stats` package (R Core Team, 2021). The resulting biplot was constructed using the `ggbiplot` function from the `ggbiplot` package (Kassambara and Mundt, 2020).

Next, we explored whether the variation in environmental variables

had a cascading effect on the composition of macroinvertebrate and macrophyte communities. We began by examining similarities in macroinvertebrate and macrophyte communities among sites using Nonmetric Multi-Dimensional Scaling (NMDS) and hierarchical cluster analysis. NMDS was performed using the metaMDS function from the vegan package (Oksanen et al., 2022) with Chord's distance for macroinvertebrates and Bray-Curtis distance for macrophytes. Cluster analysis was conducted using the hclust function from the stats package (R Core Team, 2021), with the same distance measures and with unweighted average linkage agglomerative clustering (UPGMA) as the clustering method. We then proceeded to test the association between macroinvertebrate and macrophyte communities and environmental variables using redundancy analysis (RDA) using the function rda from the vegan package (Oksanen et al., 2022).

Finally, on the third research question of whether the ecosystem state would influence freshwater snail variables, including abundance, diversity, and infection status, we began by examining similarities in snail community composition among sites by performing NMDS and hierarchical cluster analysis using Chord distance and UPGMA clustering. The association between Hellinger-transformed snail community composition and environmental variables was tested with redundancy analysis (RDA) (Oksanen et al., 2022). The significance of the RDA was assessed using permutation F-test statistics from anova.cca (step = 1000), and the resulting triplots were generated using the function triplot in the vegan package.

To determine how snail community characteristics (diversity, abundance, infection rates) correlate with water quality variables, macroinvertebrates and macrophytes, we used multiple (generalized) linear mixed models. For the response variable snail diversity, we used linear mixed models (LMM), while for count data (richness and abundance) and proportional data (PCR-based infection rate), we applied generalized linear mixed models (GLMM) with Poisson and binomial distributions, respectively. Explanatory variables included water quality variables, richness, diversity of macroinvertebrates and macrophytes, and macrophyte cover. We included a random factor for the part of the study area nested in conservation status (protected/unprotected). Ponds located in the Chiwawe, Lodge, and Middle sections were considered protected areas, while ponds in the farmed and village sections were classified as unprotected areas. Differences in mean snail abundance were tested across the different sections and land use types using pairwise comparisons of estimated marginal means (emmeans) with Tukey's adjustment for multiple comparisons. Differences in snail richness and infection rate were each tested with the Wilcoxon test with a Bonferroni correction for multiple testing.

We examined all models for overdispersion and incorporated an additional dispersion parameter when necessary. In generalized linear models, we used a quasipoisson approach for count data and a quasibinomial for infection prevalence. For generalized mixed linear models, we addressed overdispersion by including a random effect at the observation level. The best model was selected based on AIC values. Linear mixed models were fitted with the lmer function, and generalized linear mixed models with the glmer function, both from the lme4 package (Bates et al., 2015).

All data were analyzed using RStudio® v2021.09.0 Build 351 (RStudio Team, 2021). The significance level for statistical tests was set at $\alpha = 0.05$. Graphs generated in R were exported to Microsoft PowerPoint® to improve layout and readability using the export package (Wenseleers and Vanderlaan, 2016).

3. Results

3.1. Environmental pond variables

A total of 23 environmental variables were recorded across the 19 sampled ponds (Supplementary Table S1). Mean values and standard deviations for all environmental variables are provided in

Supplementary Table S2. Principal component analysis (PCA) was conducted to visualize the variation in environmental variables across all sites (Fig. 2). The first two principal components accounted for 35.8 % of the variance in physicochemical variables between sites, with PC1 explaining 21.1 % and PC2 explaining 14.7 %. The variables carrying the most weight for PC1 were total dissolved solids (TDS), total suspended solids (TSS), and turbidity. PC2 was predominantly associated with calcium and magnesium. Three out of four sites that were located in proximity of the farm (Farm section and Lodge section) appeared more on the left side of the PCA plot, indicating an association with higher total dissolved solids, conductivity levels and submerged vegetation cover (Fig. 2). In contrast, sites appearing more on the right side are typically more eutrophic with high nitrate levels, high phytoplankton biomass and higher turbidity and cyanobacteria. These sites are mostly located in the conservation sections. Several variables also showed high correlations with each other, as reflected by the angles in the correlation plot and more in detail in the correlation matrix (Supplementary Fig. S1).

3.2. Macroinvertebrates in relation to environmental pond variables

A total of 41 families of macroinvertebrates were identified, with individual counts per site ranging from 24 to 471, family richness ranging from 9 to 26, and Shannon diversity ranging from 1.148 to 2.586 (Supplementary Table S3). Linear models did not reveal any significant differences in richness and diversity across the different parts of the study area. However, we observed that mean Shannon diversity was highest in the Chiwawe and Middle sections, while it was lowest in the farm and lodge sections. Cluster analysis performed to determine the distribution of macroinvertebrates across the study area did not reveal distinct groups based on the macroinvertebrate community, and the dispersion of sites across the plot did not appear to correlate with the different sections of the study area (Supplementary Fig. S2). Redundancy analysis using forward selection suggested that salinity and depth were important predictors of macroinvertebrate community composition (ANOVA, $F_{2,16} = 2.59$; $p = 0.001$). Baetidae were associated with higher salinities, whereas Chironomidae were more associated with deeper ponds and Belostomidae preferred more shallow ponds.

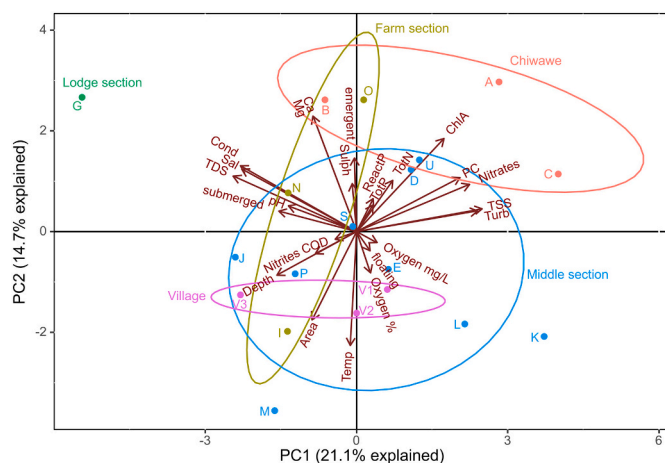


Fig. 2. PCA correlation biplot visualizing the association among sites based on physicochemical water variables and macrophyte cover. The scores (points) represent the 19 different sites, with variables shown as arrows. Colored circles indicate sites belonging to the same section. Abbreviations stand for total dissolved solids (TDS), total suspended solids (TSS), turbidity (Turb), conductivity (Cond), salinity (Sal), sulphates (Sulph), calcium (Ca), magnesium (Mg), temperature (Temp), phycocyanin (PC), chlorophyll *a* (ChlA), total nitrogen (TotN), total phosphorus (TotP), reactive phosphorus (ReactP), and chemical oxygen demand (COD).

3.3. Macrophytes in relation to environmental pond variables

A total of 21 macrophyte species were identified, and species richness and relative abundance were used to calculate Shannon diversity, while macrophyte cover was estimated for emergent, submerged and floating aquatic plants as displayed in Supplementary Table S4. Shannon diversity ranged from 0.86 (Chiwawe) to 1.81 (Villages). Submerged vegetation exhibited a cover range of 0 (two sites in Chiwawe, one site in Farm, and two sites in Middle section) to 90 % (one site in Lodge section), with a mean of 30 ± 30 %. Emergent vegetation ranged between 10 % (two sites in Middle section) and 60 % (one site in Middle section), with an average cover of 31 ± 15 %, and floating vegetation cover varied from 0 % (one site in Middle section) to 70 % (one site in Villages), with a mean cover of 15 ± 16 %. On the NMDS plot, sites exhibit a discernible separation along the horizontal axis (Fig. 3). Two main clusters of sites appeared. The first, green coloured cluster includes the Farm, Lodge, and upper Middle section sites with *Lagarosiphon* sp. dominance. These are mostly sites in the farm's vicinity, characterized by higher levels of total dissolved solids and conductivity. The second, black cluster contains Chiwawe and Middle section ponds with *Cladium mariscus* dominance. These ponds are characterized by more eutrophic conditions (Fig. 2). The red cluster comprises *Nymphaea caerulea* and *Stuckenia pectinata* abundant sites and the blue cluster is mostly characterized by *Typha capensis*.

Redundancy analysis on the entire macrophyte community revealed that depth was associated with certain plant species (ANOVA, $F_{2,15} = 2.88$; $p = 0.001$). For instance, deeper ponds were mostly associated with oxygen weed (*Lagarosiphon major*). The PCA plot (Fig. 2) further revealed that submerged vegetation cover (which includes *Lagarosiphon major*) was associated with sites in proximity of the farm, being less eutrophic and showing higher levels of total dissolved solids and conductivity.

3.4. Freshwater snails in relation to environmental pond variables

A total of 926 freshwater snails, representing 10 species, were collected from the study area. Among these, 547 individuals (59.1 %) belonged to five schistosome-competent species: *Bulinus tropicus* (28.4 %; $n = 263$), *Bulinus truncatus* (14.1 %; $n = 131$), *Bulinus globosus* (8.2 %; $n = 76$), *Bulinus forskalii* (0.5 %; $n = 5$), and *Biomphalaria pfeifferi* (7.8 %;

$n = 72$). The remaining 379 individuals (40.9 %) consisted of five other species: *Radix natalensis* (15.8 %; $n = 146$), *Gyraulus* sp. (1.3 %; $n = 12$), and the exotic invasive species *Melanoides tuberculata* (0.3 %; $n = 3$), *Pseudosuccinea columella* (4.3 %; $n = 40$), and *Physella acuta* (19.2 %; $n = 178$).

Snail abundance significantly varied throughout the sections ($F_{(4, 14)} = 4.972$, $p = 0.0105$; Fig. 4). The highest mean abundance of snails was recorded in the village ponds, while the lowest mean abundance was observed in Chiwawe and the Farm section. The Tukey HSD test revealed significant differences in snail abundance between the village sites, which accounted for 41.3 % of all snail counts, and the Chiwawe ($p = 0.046$), Farm ($p = 0.009$), and Middle sections ($p = 0.014$). However, pairwise comparisons using estimated marginal means revealed only a significantly higher snail abundance in the villages compared to the Middle section ($p = 0.02$, Fig. 4). The different sections had a significantly different Shannon diversity (ANOVA: $F_{(4, 14)} = 3.18$, $p = 0.047$). The highest diversity was observed in the Middle section and villages, while the lowest diversity was recorded in the Farm section and Chiwawe (Fig. 5). However, Tukey HSD and Wilcoxon tests revealed only a significantly higher snail diversity in the Middle section compared to Chiwawe (Tukey: $p = 0.048$; Wilcoxon: $p < 0.01$). Supplementary Table S5 provides detailed data per site for snail variables, including individual species counts, total snail count, and diversity.

Sites that appeared left on the PCA ordination, were mostly sites in the farm's vicinity characterized by high conductivity and low snail abundances dominated by exotic invasive snail species (Fig. 2). Sites that appeared on the right of the PCA ordination were more associated with eutrophic conditions and had high abundances of planorbid snails (Fig. 2). This separation of sites based on snail species was also reflected in the snail community NMDS plot (Supplementary Fig. S3). Redundancy analysis further revealed that depth was an important predictor of snail community composition (ANOVA, $F_{2,16} = 4.45$; $p = 0.001$, Supplementary Fig. S4). *Physella acuta* was associated with deeper ponds, while *B. tropicus* and *B. truncatus* were associated with more shallow ponds.

3.5. Snail infection prevalence in relation to environmental pond variables

Through shedding experiments, six cercarial morphotypes were identified (Supplementary Fig. S5). These included *Schistosoma* cercariae from a single *B. truncatus* snail at site V2 (village). Longifurcate pharyngeate distome subtype cercariae were found in 43 snails, including *B. tropicus*, *B. truncatus*, *B. globosus*, and *B. pfeifferi*. Avian schistosomes were released from two *B. truncatus*. Echinostome-type

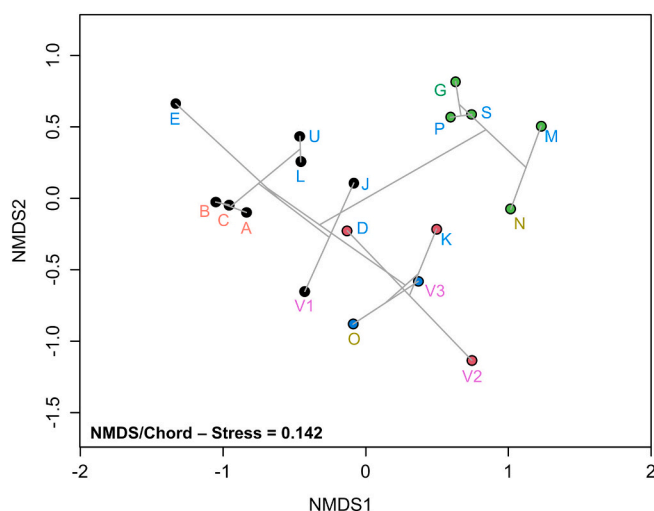


Fig. 3. Macrophyte NMDS plot with scores (circles) representing 18 sites (Site I omitted due to incomplete data). Grey lines represent the clustering dendrogram, and colors of the circles represent the clusters they belong to based on UPGMA clustering. Colors of the site names indicate the section the site belongs to (blue: Middle section, red: Chiwawe, purple: Village, green: Lodge section; light green: Farm section).

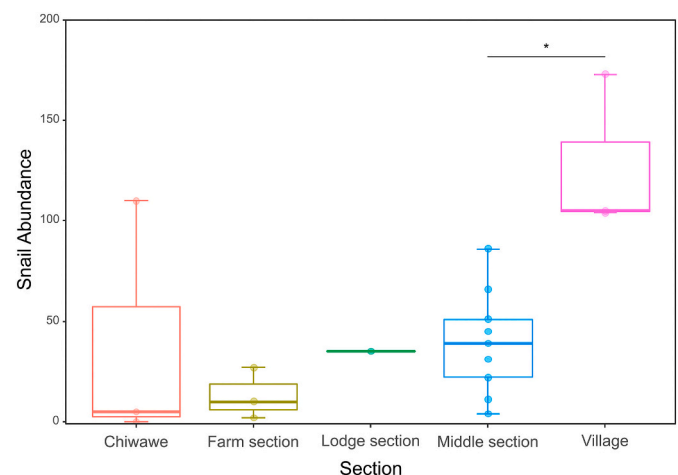


Fig. 4. Boxplots showing snail abundance per section of the study area. Significant differences between sections based on pairwise comparisons using estimated marginal means are indicated by a line with asterisks.

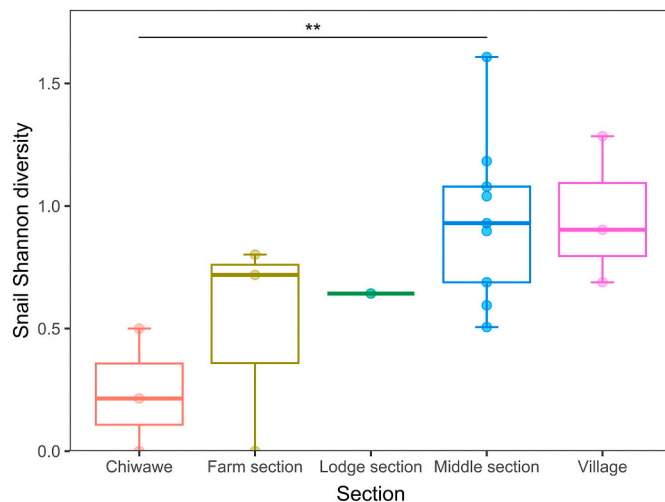


Fig. 5. Boxplots showing snail Shannon diversity per section of the study area. Significant differences between sections based on Wilcoxon tests are indicated by a line with asterisks.

cercariae were released from 13 snails, including *B. tropicus* and *B. pfeifferi*. Xiphidiocercariae-type cercariae were recovered from 13 *B. tropicus* snails, while amphistome-type cercariae were released from five snails, including *B. tropicus*, *B. truncatus*, and *B. forskalii*. In total, cercariae were isolated from 104 out of 926 snails (11.2 %). Infection prevalence based on shedding experiments per site is detailed in Supplementary Table S6. Among the 547 schistosoma-competent snails, 88 were producing cercariae (16.1 %). *Bulinus tropicus* exhibited the highest overall infection prevalence (76 out of 263, 28.9 %), followed by *B. forskalii* (1 out of 5, 20.0 %). The infection prevalence was 16 out of 168 (9.5 %) for *R. natalensis*, 9 out of 131 (6.9 %) for *B. truncatus*, and 2 out of 72 (2.8 %) for *B. pfeifferi*. No cercariae were recovered from *P. acuta*, *P. columella*, *M. tuberculata*, and *Gyraulus* sp. during shedding experiments. Wilcoxon tests did not reveal any significantly different shedding rates across the sections but did reveal a significantly higher proportion of shedding snails in village as a land use category compared to farm as a land use category (Supplementary Fig. S6).

Infection prevalence based on molecular assessment with PCR, revealed that 70.20 % (351/500) out of the extracted snails were infected with trematodes, ranging between 8.33 % (Lodge section, site G) and 100 % (Middle section, site D and L). The overall infection prevalence among schistosoma-competent snails, determined through RD-PCR, was 74.7 %. Snail species with the highest infection prevalence were *B. forskalii* (100 %), *B. tropicus* (93.4 %), and *B. truncatus* (82.5 %). *Bulinus globosus* had an infection prevalence of 46.7 %, and *B. pfeifferi* of 37.1 %. Notably, three (potentially) medically relevant infections were identified. Two *B. globosus* snails in the village area were infected with schistosomes. One snail was infected with *S. matthei* (site V2) and the other one was coinfecting with *S. haematobium* and *S. matthei* (site V1), as revealed by the diagnostic PCR. Additionally, one *R. natalensis* snail in the conservation area (site E) was infected with *Fasciola* sp., later identified as *Fasciola gigantica* through COI barcoding. Wilcoxon tests revealed a significantly higher proportion of infected snails, as detected by PCR, in conservation vs farm land use categories, which persisted at the section level between the middle section and the farm section ($p < 0.05$, Supplementary Fig. S7).

3.6. Macroinvertebrates and macrophytes in relation to freshwater snails

Specific snail species were found to co-occur with various macroinvertebrate families, as demonstrated by the distance triplot of macroinvertebrates and snails, which incorporates forward selection for macroinvertebrate groups (Supplementary Fig. S8). Notably, sites with

high abundances of *B. tropicus* and *P. acuta* also exhibited high abundances of macroinvertebrates from the Belostomatidae and Ecnomidae families, respectively. No significant relationship was found between the abundance and diversity of macroinvertebrates and snail diversity, abundance, or infection rates.

There were significant associations between macrophyte cover and both snail counts and richness. Submerged vegetation cover positively correlated with lymnaeid and physid richness ($\chi^2_{(1, N=19)} = 4.01$, $p = 0.045$; Supplementary Fig. S9) and abundance ($\chi^2_{(1, N=19)} = 6.38$, $p = 0.012$; Supplementary Fig. S10). Since two aquatic plant species, *L. major* and *C. mariscus*, influenced the structure of the studied ponds (Fig. 3), they were included in the redundancy analysis to examine their associations with snail variables. The resulting RDA (Fig. 6) significantly indicates that *B. tropicus* is associated with the presence of *C. mariscus*, while both *P. columella* and *P. acuta* are most associated with *L. major*, further supported by similar patterns in Supplementary Fig. S9 & S10 (ANOVA, $F_{2,14} = 2.18$; $p = 0.031$).

4. Discussion

Understanding ecological drivers of snail distribution patterns is imperative to achieve a comprehensive and sustainable strategy for controlling snail-borne diseases. Therefore, our investigation explored the impact of the ecological state of man-made ponds on the abundance, diversity, and infection status of freshwater snails in Zimbabwe's Wedza district. We anticipated that proximate anthropogenic or conservation activities would drive environmental variables across the studied ponds, cascading down to macrophyte and macroinvertebrate communities, including freshwater snails.

4.1. Environmental variables across the study area

Overall, ponds in the study area exhibited decent water quality, evidenced by near-neutral pH levels, moderate dissolved oxygen, and balanced nutrient levels in contrast to other water systems in Zimbabwe e.g., Manyame River catchment (Kibena et al., 2014; Muhoyi et al., 2022) and Chiredzi-Runde River catchment (Nhiwatiwa et al., 2017). However, various ponds located in the vicinity of the agricultural area, denoted as G, I, O, and N, showed relatively high levels of TDS and conductivity (Fig. 2). These findings are most likely attributable to the intense and proximate tobacco farming, a high input intensive crop leading to agricultural pollutant runoff, significantly influencing the concentration of dissolved solids and water conductivity (Lecours et al., 2012). Moreover, magnesium and calcium are vital minerals for the tobacco plant and are therefore frequently applied to the farms (Gonese,

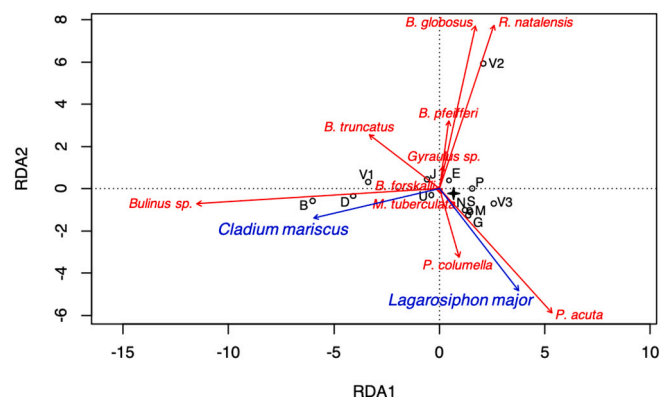


Fig. 6. Distance triplot of the redundancy analysis. Sites (scores: black circles) are plotted in relation to the snail community of each site (response variables: red arrows) and macrophyte variables *Cladium mariscus* and *Lagarosiphon major* (explanatory variables: blue arrows). The black star indicates sites K, O, L, and C that were positioned too closely to be displayed clearly.

2001; Li et al., 2023). Consequently, the ponds near tobacco farms also exhibited increased magnesium and calcium levels.

Conversely, it was observed that sites A and C from the Chiwawe section displayed comparatively elevated nitrate, phytoplankton and turbidity levels (Fig. 2). Increased nitrate levels are often linked to high microalgae biomass (He et al., 2023) while cyanobacteria have the ability to fix free nitrogen (Massey and Davis, 2023). Importantly, the Chiwawe section, where these relatively more eutrophic ponds are located, is limited in size relative to mammalian pressure and therefore particularly vulnerable to disturbance by large mammals, which may in turn alter nitrate levels through sediment resuspension and urinary nitrogen (Holtmeier, 2015).

4.2. Environmental variables and their influence on biotic variables

Macroinvertebrates are often used as indicators of water quality (Bird, 2010; Gabriels et al., 2010). Typically, higher macroinvertebrate abundance and diversity are expected at sites with good water quality. However, our study did not find a clear association between environmental variables and macroinvertebrate abundance and diversity. Baetidae or mayflies, were mostly associated with ponds with high salinity levels yet this taxon is normally considered sensitive to elevated TDS and salinity (Gabriels et al., 2010). However, tolerance levels can sometimes be species specific (Kefford et al., 2005). Therefore, the lack of species level identifications could explain the observed pattern.

Macrophytes can also be important indicator species for ecosystem states in the aquatic environment (Chibsa et al., 2022). We noted a significant association between environmental variables and submerged vegetation cover. Sites near the farm showed higher levels of total dissolved solids and conductivity and a higher coverage of the submerged macrophyte, *Lagarosiphon major* (commonly known as African curly-leaved waterweed or oxygen weed). *Lagarosiphon major* has a broad environmental tolerance, vegetative reproduction and high relative growth rate contributing to its invasive success worldwide (Sutherland, 2004). It forms dense mats just below the water surface (DiTomaso et al., 2013), which can lead to unintended fish kills due to oxygen depletion, hinder recreational activities such as boating, swimming, and angling, and obstruct hydroelectric and irrigation systems (DiTomaso et al., 2013; Matthews et al., 2012). Strong wave action can exacerbate the situation by dislodging weed mats and depositing rotting vegetation elsewhere, ultimately reducing the ecosystem services provided by man-made reservoirs (DiTomaso et al., 2013). From a biodiversity perspective, the dense mats formed by *L. major* block sunlight penetration to the lakebed, which is detrimental to aquatic invertebrates (DiTomaso et al., 2013). Therefore, ponds characterized by the abundance of *L. major* should be monitored and considered for integrated management practices to improve their ecosystem state. Local management can assess the suitability of *L. major* removal to improve pond ecosystem quality and recycling as either crop fertilizer on the tobacco farm or, once dried, as livestock feed (Rohr et al., 2023). Both applications have been shown to be financially viable with high benefit-to-cost ratios (Rohr et al., 2023).

4.3. Snail community composition across land use categories

Our study investigated the abundance, diversity, and distribution of freshwater snails in ponds located in and around a biodiversity conservation area and its adjacent human-influenced zones. We examined three types of land use: conserved areas, human settlements, and farm sections representing increasing levels of anthropogenic interference around the ponds.

In alignment with the previous study by Mudavanhu et al. (2024), conducted during the drier season of August 2021 in the same ponds, we found the same ten snail species: *Bulinus tropicus*, *B. truncatus*, *B. globosus*, *B. forskalii*, *Biomphalaria pfeifferi*, *Radix natalensis*, *Gyraulus* sp., and the exotic invasive species *Melanoides tuberculata*, *Pseudosuccinea columella*, and *Physella acuta*. Our study revealed significant

differences in the abundance of these snail species across the three land use categories. Villages had the highest abundance and diversity of snails, consistent with previous studies (Lange et al., 2013; Mereta et al., 2019; Oso and Odaibo, 2021). An explanation for this heightened abundance could be anthropogenic activities taking place in the villages such as settlement, fishing, farming, land drainage, grazing, and recreational water use (Lange et al., 2013; Mereta et al., 2019; Oso and Odaibo, 2021). These activities impact water chemistry through sediment resuspension and pollution, creating favorable conditions for snails. Schistosome-competent snails were particularly abundant in villages, as also observed by Lange et al. (2013). Both *Bulinus* spp. and *Biomphalaria* spp. thrive in disturbed habitats, exploiting resources such as plastic waste for egg-laying and tolerating oxygen-depleted, polluted conditions (Stothard et al., 2017).

Conversely, the commercial farm section was dominated by invasive species like *P. acuta* and *P. columella*. Only one schistosome-competent individual snail was found in this area. Despite both the village and farm sections practicing agriculture, differences in intensity led to distinct outcomes. Commercial tobacco farming in Zimbabwe involves the use of various agrochemicals, including insecticides and herbicides, which may create an environment that supports resilient invasive snails like *P. acuta* and *P. columella*. Studies such as Hoover et al. (2020) have shown that insecticides like chlorpyrifos can promote schistosome-competent snails by reducing competition and predation. However, we observed almost no schistosome-competent snails in the farm section, suggesting that the intensity and potential overuse of these agrochemicals may not only eliminate macroinvertebrates but also negatively impact schistosome-competent snails. This selective pressure could explain the dominance of invasive species like *P. acuta*, which thrive in degraded habitats. Additionally, herbicide use may have favored the growth of resilient submerged vegetation, such as *Lagarosiphon major*, further contributing to the proliferation of these invasive snails (see sections below).

In total, six cercarial types were isolated from 104 out of 926 snails (11.2 %) during shedding experiments. Molecular assessment using PCR, a more sensitive method than shedding experiments (Born-Torrijos et al., 2014; Schols et al., 2019), revealed that 70.2 % (351 out of 500) of the extracted snails were infected with trematodes. Notably, four medically relevant trematodes were identified for the first time in or near the Imire conservancy in the Wedza district. Two *B. globosus* snails in the village area were infected with schistosomes: one with *S. matthei* and the other co-infected with *S. haematobium* and *S. matthei*, as revealed by RD-PCR. Additionally, one *R. natalensis* snail in the conservation area was infected with *Fasciola gigantica*, determined through COI barcoding while five bulinid specimens released amphistome-type cercariae. The discovery of amphistomes, schistosomes, and fasciolids in the current study adds to the eight trematode species reported by (Mudavanhu et al., 2024), bringing the total to 12 species recovered from Wedza.

Higher proportions of shedding snails were observed in villages compared to farm sections (Supplementary Fig. S6), likely due to the presence of more final hosts (e.g., humans and livestock) frequently visiting the village ponds. In contrast, the studied ponds in the farm section exclusively support irrigation activities and are devoid of livestock or human settlements. Similarly, there was a significantly higher proportion of infected snails, as detected by PCR, in conservation areas compared to farm areas (Supplementary Fig. S7), reflecting the greater presence of final hosts in conservation zones. Snail communities could also have played a role in infection proportions as the farm section only had two dominant snail species, *P. acuta* and *P. columella*, whereas various ponds across the conservation area harbored a greater diversity of snails. *Physella acuta* was previously shown to harbor little to no infections (Mudavanhu et al., 2024). However, *P. columella* has been shown to transmit trematodes at unusually high rates (Carolus et al., 2019; Schols et al., 2021). Combined, these results suggest that the presence of final hosts is a better predictor of the proportion of infected

snails than the snail community, yet compatible snail hosts must be present too.

4.4. Snail community structure and infection rate in relation to environmental variables

The intricate relationship between abiotic environmental conditions and the structure of snail communities has been extensively studied, highlighting the pivotal role of factors such as depth, pH, chlorophyll-a, and TDS in shaping aquatic communities - findings that align with our study (Maes et al., 2021; Min et al., 2022; Tabo et al., 2022; Zhou et al., 2024).

We observed a dominance of *B. truncatus* and *B. tropicus* in more eutrophic sites characterized by elevated nitrate levels, phytoplankton biomass, and turbidity (see Section 4.1, Fig. 2). More eutrophic ecosystems tend to be resource-rich, supporting higher snail populations. Conversely, ponds within commercial farm areas, associated with higher TDS, salinity, and conductivity, exhibited low species diversity, primarily dominated by the resilient *P. acuta*.

Using redundancy analysis, we found a significant correlation between snail community assemblage and water depth. *Bulinus tropicus* and *B. truncatus* were negatively associated with depth, whereas *P. acuta* showed a positive association. But this could also be indirectly linked to macrophyte coverage (see Section 4.6). Previous studies have emphasized the importance of water depth in snail distribution (Olkeba et al., 2020; Oloyede et al., 2017), often noting positive associations between shallow pond areas, and the associated increased productivity, and snail abundance (Min et al., 2022). However, contrary to our findings, Olkeba et al. (2020) reported positive relationships between water depth and the occurrence of *B. pfeifferi* and *B. globosus* in Ethiopia, potentially due to different ambient temperature profiles.

No significant association was found between environmental variables and snail infection rates, further supporting the earlier hypothesis whereby final hosts appear to be the major driver of the proportion of infected snails.

4.5. Snail-macroinvertebrate relations

Snails are a subset of macroinvertebrates, and their distribution patterns are expected to mirror those of functionally or phylogenetically similar macroinvertebrates, or groups with similar environmental preferences and tolerance capabilities (Liu et al., 2021). Our study revealed notable co-occurrences among various macroinvertebrate families and snail species. Specifically, ponds with large populations of *B. tropicus* and *P. acuta* also exhibited high abundances of macroinvertebrates from the Belostomatidae (giant water bugs) and Ecnomidae (caddisflies) families, respectively. Belostomatidae specializes in eating snails, which likely explains the positive association observed (Statton and Cothran, 2024) while the co-occurrence of *P. acuta* and Ecnomidae could be explained by their common feeding behavior as occasional collector feeders (Hamid and Md Rawi, 2014; Taylor, 2003).

4.6. The influence of aquatic macrophytes on freshwater snail communities

Aquatic macrophytes are fundamental to aquatic ecosystems, playing a crucial role in community structure and nutrient cycling (Lind et al., 2022). They provide essential food, shelter, and habitats for a wide range of organisms, from microorganisms to large fish (Bornette and Puijalon, 2011; Engelhardt and Ritchie, 2001). Their significance in snail ecology is well-established. While green algae are the primary food source for most snails, decomposing plants also offer a supplementary diet as detritus (El Deeb et al., 2017; Plummer, 2005). Additionally, aquatic plants serve as substrates for snail eggs and create favorable habitats by reducing water velocity and wave action (El Deeb et al., 2017; Plummer, 2005). High river flows can disrupt nutrient and

substrate availability, impacting snail growth and abundance, with life stages vulnerable to being washed downstream at velocities over 0.3 m/s, thereby affecting overall population dynamics (Maes et al., 2021).

In our study, we identified 21 different species of macrophytes across various sites, categorized into submerged, emergent, and floating functional groups. Our findings align with previous research underscoring the importance of aquatic macrophytes in predicting freshwater snail species (Desautels et al., 2022; Haggerty et al., 2020; Rohr et al., 2023). Specifically, redundancy analysis revealed a particular association between *B. tropicus* and *Cladium mariscus*, an emergent macrophyte. Similar associations have been documented in previous studies, such as *B. globosus* with *Cyperus* sp. and *Typha* sp., and *B. tropicus* with *Cyperus* sp. and *Polygonum* sp. (Chingwena et al., 2004; Pfukenyi et al., 2005). Other vegetation types linked to these snails include submerged *Potamogeton* sp. with *B. globosus* and *B. pfeifferi*, and floating *Nymphaea caerulea* with *B. tropicus* (Chingwena et al., 2004; Pfukenyi et al., 2005). Recent studies in Senegal highlight the association between submerged plants, such as *Ceratophyllum* spp., and the presence of snail species *Bulinus* and *Biomphalaria* spp. These plants are known for reducing water flow and providing essential nutrition to snails through the availability of periphyton (Desautels et al., 2022; Haggerty et al., 2020; Rohr et al., 2023).

Furthermore, lymnaeids and physids showed significant associations with submerged vegetation. Specifically, *P. columella* and *P. acuta* were associated with *L. major*. This exemplifies a “cascade of biological invasions” where the invasion success of an aquatic macrophyte promotes the abundance of exotic invasive freshwater snail species (Carolus et al., 2019), facilitated by damming activities that encourage the establishment of *L. major*. In their study, Carolus et al. (2019) reported a significant association between *P. columella* and *Eichhornia crassipes*, a floating water hyacinth species originally from South America that also forms vast mats in Lake Kariba (Zimbabwe and Zambia).

The association between macrophytes and freshwater snails presents opportunities for disease management. For instance, a recent study conducted in Senegal demonstrated that the removal of aquatic macrophytes from water collection points significantly reduced the transmission of schistosomiasis in endemic villages (Rohr et al., 2023). Similar strategies could be implemented in numerous affected countries across sub-Saharan Africa, potentially diminishing the reliance on chemical control methods for snails. Rohr et al. (2023) underscored that vegetation removal had no discernible long-term adverse effects on local water quality or freshwater biodiversity. Additionally, the harvested vegetation offers various ecosystem services to local communities, including animal feed, manure, bioremediation by absorbing excess nutrients from the water body, and the production of charcoal briquettes for household fuel needs (Kwenda et al., 2023; Rohr et al., 2023). Macrophyte removal can, however, cause physicochemical changes in freshwater ecosystems, potentially negatively impacting ecosystem structure and functioning (Misteli et al., 2023; Thiemer et al., 2021; Wojciechowski et al., 2018). It is therefore advised to make a well-informed decision based on more pond-specific research.

5. Conclusions

In conclusion, our study offers valuable insights into the structure of snail communities and the factors driving their ecology. Our findings highlight the association of exotic invasive snail species with submerged macrophytes and agricultural reservoirs, while schistosome-competent snails exhibit a preference for more eutrophic habitats characterized by high emergent macrophyte cover. These environmental factors play a crucial role in shaping the transmission dynamics of snail-borne diseases. Therefore, with careful considerations, removal of associated plants presents potential avenues for snail control and also harnessing ecosystem services through nutrient recapture, compost production, animal feed, and fuel production. These practices have the potential to provide holistic, win-win benefits for local communities, uplifting their

economies while addressing disease transmission. We also advocate for reducing nutrient and pollutant inputs into reservoirs through improved agricultural practices to reduce macrophyte proliferation. This integrated approach mitigates risks for snail-borne diseases while promoting overall ecosystem health and preserving local biodiversity.

CRediT authorship contribution statement

Aspire Mudavanhu: Writing – review & editing, Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Emilie Goossens:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Ruben Schols:** Writing – review & editing, Resources, Investigation, Formal analysis. **Tawanda Manyangadze:** Writing – review & editing. **Tamuka Nhiwatiwa:** Writing – review & editing, Conceptualization. **Pieter Lemmens:** Writing – review & editing, Methodology. **Tine Huyse:** Writing – review & editing, Supervision, Resources, Project administration, Conceptualization. **Luc Brendonck:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2024.176394>.

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