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Investigating the Contribution of Freshwater Molluscs to Nutrient Recycling in Tropical Wetlands

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Abstract: Tropical wetlands are highly productive, but the contribution of benthic invertebrate consumers to nutrient cycling in these systems has been poorly characterized. Freshwater molluscs, which include apple snails, thiarid and viviparid grazers, unionid mussels and small corbiculid clams, often comprise the greatest proportion of invertebrate biomass in these systems and cycle nutrients, namely nitrogen (N) and phosphorus (P), through their excretion, biodeposition and bioturbation. In this study, examine the importance of freshwater molluscs in the nutrient recycling in tropical wetlands by conducting a structured review of existing information on consumer-mediated nutrient cycling along with developing an allometric and temperature-based excretion model based on metabolic theory and ecological stoichiometry. Four functional groups have been parameterized using representative body sizes of individual species, biomass of the assemblage, and excretion N:P ratio, with areal rates being calculated for a typical water temperature in tropical wetlands (28 °C). The assemblage was estimated to release approximately 55.4 mg N m^{-2} d^{-1} and 9.3 mg P m^{-2} d^{-1}, which amounts to about 62% and 78% of the autotrophic nutrient demand, respectively. Every 4 °C increase in the temperature resulted in an increase in areal excretion of 32% showing that the warming effect could enhance nutrient recycling through molluscs. Apple snails grazed the nutrients from macrophytes and released them in a dissolved form, while filter-feeding bivalves transported nutrients suspended in the water column and deposited them in sediments. These results demonstrate the important role played by molluscs in regulating the nutrient cycles in wetlands such that their invasion or reduction would impact the state of the system.

Keywords: Freshwater Molluscs; Nutrient Recycling; Tropical Wetlands; Consumer-Driven Nutrient Dynamics; Ecological Stoichiometry; Excretion; Ecosystem Functioning; Wetland Management.

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I. Introduction

Despite occupying only a tiny fraction of the Earth's land surface area, wetlands play a disproportionately large role in shaping regional hydrology, carbon sequestration, and the cycling of nitrogen (N) and phosphorus (P) from catchments to rivers and coasts. Tropical wetlands are comprised of riverine floodplains, seasonally flooded marshes, rice paddy complexes, peat swamps, ox-bow lakes, and low-elevation reservoirs. These wetlands are distinguished by warm conditions year-round, biologically intensive environments, and pronounced seasonal flood pulses. Such conditions facilitate rapid decomposition and nutrient turnover, such that the rate of nutrient cycling may be as important as the magnitude of the nutrient store. Identifying the organisms responsible for such processes is thus fundamental to understanding wetland productivity and resilience to human disturbance. Historically, nutrient balances in wetlands were considered to involve abiotic processes, including sedimentation and sorption to iron and aluminum oxides, and biotic processes such as nitrification, denitrification, and mineralization. In the past two decades, nevertheless, significant number of publications have reported that animals play an important role in nutrient transformation. By feeding on organisms, producing waste products, and dying and decaying, animals change nutrient forms, distribute them, and alter their ratios, making them available to primary producers (Vanni, 2002). In places where there is plenty of animal biomass, nutrients released via the recycling process can cover a major part of the nutrient demand of algae and macrophytes, especially when the external loading is low, or nutrients are trapped within organic matter (Vanni, 2002).

Freshwater molluscs are one of the most promising groups for an efficient consumer impact on nutrient cycling. The filtration rate in bivalves is extremely high; they filter huge amounts of water, filter out

phytoplankton and suspended organic matter and create a lot of nutrient-enriched faeces and pseudofaeces on the sediment surface. Burrowing bivalves can also mix and oxygenate sediments, thus impacting the activity of benthic microbes and solute exchange between sediments and water (Vaughn & Hakenkamp, 2001). Gastropods graze on periphyton, macrophytes, and detritus and excrete dissolved ammonium and phosphate as products of nutrient digestion. Field investigations have shown that even one species of very numerous snails can control the nitrogen and carbon flow in a productive freshwater system, as a result of the high biomass of the community, not individual metabolism (Hall et al., 2003).

In tropical Asia, an invasive species Pomacea canaliculata (golden apple snail) serves as an excellent example of mollusc effect on wetland nutrient cycling. A survey of Thai wetlands has shown that locations with high snail biomass had no aquatic vegetation, increased nutrient concentrations, and increased biomass of phytoplankton, and calculations of nutrients grazed by snails were enough to explain the increase in phytoplankton biomass (Carlsson et al., 2004). Native molluscs, like the apple snails of the genus Pila, thiarids and viviparids, and unionids, including Lamellidens and Parreysia, are common in South and Southeast Asian wetlands but are rarely measured for nutrient contributions. However, freshwater biodiversity, including molluscs, is declining at a higher rate compared to terrestrial biodiversity due to habitat degradation, water flow modifications, pollutants and invasive species (Dudgeon et al., 2006).

Loss of biodiversity in freshwater ecosystems leads directly to the loss of functions of those ecosystems. The loss of the assemblage of mollusks will lead to changes in nutrient processes (Vaughn, 2010). Communities of filter-feeding mussels were found to modify nutrient limitations and the structure of communities of benthic algae, forming biogeochemical hot spots in nutrient-limiting environments (Atkinson et al., 2013). Tropical wetlands face high risk of damage because 30-90% of the world's wetlands are already damaged and modified, and climate change poses additional threats in terms of hydrology and increased temperatures (Junk et al., 2013). In spite of that, studies on nutrient cycling via molluscs are mostly conducted in temperate rivers and lakes, while the tropical wetlands are neglected, although the latter are characterized by higher temperature and thus higher metabolic rates. This gap is filled in the current study through an examination of the role of freshwater molluscs in nutrient cycling within tropical wetlands. This is accomplished by combining a systematic review of the literature concerning N and P cycles mediated by molluscs with a mechanistic modelling framework to quantify the rate of areal excretion of these organisms in various tropical functional groups. The study is consistent with the ecosystem approach of Aquatic Ecosystems and Environmental Frontiers, which considers the relationship between biota, biogeochemical processes, and water quality.

Objectives

1. To synthesise the processes of recycling of nitrogen and phosphorus by freshwater molluscs in tropical wetlands via excretion, biodeposition, grazing, and bioturbation.
2. To quantify the rate of nutrient excretion by the main functional groups of tropical molluscs and compare these values with the typical demand of nutrients in an autotrophic organism.
3. To explore how body size, assemblage biomass, and temperature influence the rate of nutrient recycling by molluscs.
4. To provide recommendations for the integration of molluscs in the management and conservation of tropical wetlands.

Structure of the article: Section I (Introduction) introduces the context, research gap, and objectives of this study; Section II (Methods) outlines the synthesis approach and the method for the calculation of the rates of nutrient excretion; Section III (Results) provides the results of calculations; Section IV (Discussion) discusses these results and their implications in the context of tropical wetland ecosystems; Section V (Conclusion) concludes the paper.

II. Methods

Study Framework and Literature Synthesis

A two-step approach was used for the analysis. In the first step, peer-reviewed literature on animal-mediated nutrient cycles, freshwater molluscs and their ecology, and the ecology of wetlands was analyzed to determine the key pathways by which the molluscs affect the N and P cycles, and the required scaling relationships for quantitative estimation. The studies included those which (i) dealt with nutrient excretion, biodeposition or nutrient storage by freshwater molluscs or other aquatic consumers, (ii) studied the ecosystem effects of nutrient dynamics driven by the consumers, or (iii) provided information on the state of tropical and global wetlands and threats to them. Specific focus was made on those studies which provided links between individual physiology and ecosystem processes and on those dealing with dominant biomass species (Hall et al., 2003; Carlsson et al., 2004; Atkinson et al., 2013).

In this analysis, four functional groups of molluscs have been identified which are prevalent in tropical wetlands of South and Southeast Asia and which vary in their modes of feeding, body sizes, and their positioning within the wetlands. The four functional groups include (1) large herbivorous apple snails (Pomacea spp. and Pila spp.) that graze on the macrophytes; (2) small to medium sized thiarid and viviparid snails grazing on the periphyton and detritus; (3) large long-lived filter feeders such as unionid mussels (Lamellidens and Parreysia spp.); and (4) small fast-growing filter and deposit feeders such as *Corbicula spp.*

Tropical Wetland Context

The study is conducted in shallow, warm, seasonally flooded wetlands that are characteristic of tropical South and Southeast Asia, namely floodplains, ox-bow lakes, tanks, reservoirs, and wetlands in a rice-field landscape. The following characteristics of the systems under consideration are important for molluscs to mediate nutrient cycling in them. The water temperature usually varies from about 22 to 34 °C, with the annual average value equal to 28 °C; therefore, the rates of metabolism in ectotherms stay high all year round. The depth of the water varies greatly during the monsoon and dry seasons, resulting in periods of expansion and shrinking of the aquatic environment (Junk et al., 2013). The presence of macrophytes is widespread, and the sediments contain a lot of organic matter, which serves as food for the grazing and deposit-feeding molluscs. Anthropogenic loading with nutrients occurs frequently, and many wetlands are invaded by alien species, among which the apple snails, introduced for food and aquaculture, are included (Carlsson et al., 2004; Dudgeon et al., 2006).

Nutrient uptake requirements of primary producers in such environments are high and are fulfilled through both external additions, sediment release, and internal recycling by microorganisms and animals. Molluscs usually form the largest biomass of benthic invertebrates since their calcareous shell offers protection from predators, and they can withstand low oxygen conditions which prevail in tropical marshes due to warm water and organic matter abundance. The above-mentioned properties are the basis for considering molluscs as candidates for key nutrient recyclers in tropical wetlands, and consequently the selection of functional groups and parameters provided below.

Excretion Model

Nutrient excretion was estimated based on the metabolic theory of ecology together with ecological stoichiometry, which has been demonstrated to predict N and P excretion by aquatic animals across more than ten thousand measurements globally (Vanni & McIntyre, 2016). In accordance with this theoretical background, the individual excretion rate is proportional to body mass to the power approximately equal to 0.75 and exponentially dependent on temperature; therefore, the mass-specific excretion rate decreases with the increasing body size. The mass-specific excretion rate of ammonium-N (E_N, μmol N g^{-1} dry tissue mass h^{-1}) for each functional group was estimated as:

$$E_N = a \times M^{-0.25} \times \exp[0.0693 \times (T - 20)] \quad (1)$$

In equation (1) where a is the mass-specific excretion rate of a 1 g (dry tissue mass) individual at 20 °C, set at 2.5 μmol N g^{-1} h^{-1}, M is the representative individual dry tissue mass (g), T refers to temperature of water (°C), and the coefficient 0.0693 is the coefficient that corresponds to doubling the metabolic rate per 10 °C (Q_{10} = 2). The choice of a was based on the value falling into the usual range of freshwater invertebrates that were primary consumers (Vanni & McIntyre, 2016; Atkinson et al., 2017).

The Phosphate-P excretion (E_P) value was calculated using the formula E_N divided by the molar ratio of N:P excretion per functional group. The ratios used for this were 12 for apple snails, 14 for thiarid and viviparid grazers, 20 for unionid mussels, and 10 for corbiculid clams, due to differences in diet quality and body stoichiometry found in the literature on consumer-driven nutrient dynamics (Vanni, 2002; Strayer, 2014; Atkinson et al., 2017). Flux values were obtained from mass-specific rates multiplied by assemblage biomass (g dry tissue mass m^{-2}), 24 hours per day, and by the atomic mass of N (14.007) or P (30.974), then divided by 1000.

Scenario Parameters

The reference scenario was set up to be that of a relatively productive, molluscan-rich tropical wetland with a water temperature of 28 °C. The representative individual dry tissue weights of the four species considered in the study were 1.5 g for apple snails, 0.3 g for thiarids and viviparids, 4.0 g for unionid mussels and 0.15 g for corbiculid clams. Assemblage biomass values were 12, 5, 15 and 6 g dry tissue mass m^{-2} for each species, respectively. This gave a total value of 38 g m^{-2}. These figures fall within the range that dense communities of molluscs can achieve in a productive freshwater ecosystem (Hall et al., 2003; Atkinson et al., 2013; Vaughn, 2018). In order to put the flux estimates into perspective, they were compared to an illustrative autotrophic nutrient demand of 90 mg N m^{-2} d^{-1} and 12 mg P m^{-2} d^{-1} for combined macrophyte, periphyton and phytoplankton growth in a productive tropical wetland.

Sensitivity Analysis

For determining the effects of biomass and temperature, areal N and P excretion was determined for a general community of organisms of average body mass 1.0 g and excretion N:P ratio of 15 within a biomass gradient ranging from 0 to 60 g dry tissue mass per square meter at temperatures 24, 28 and 32 °C.

This temperature range corresponds to cool, warm seasons and future warming for monsoonal wetlands. All calculations were done using the Python programming language, and the same equations were used for both the reference case and sensitivity analysis.

III. Results

Functional-Group Contributions to Nutrient Recycling

Table 1 shows the predicted contributions by the four mollusc groups to nutrient recycling under the reference case. The highest mass-specific N excretion occurred in small bodied corbiculid clams and thiarid and viviparid grazers (6.99 µmol N g^{-1} h^{-1}), while the lowest N excretion rate was observed in large unionid mussels (3.08 µmol N g^{-1} h^{-1}). This is due to the decrease in mass-specific metabolic processes with an increase in body size. Although apple snails and unionid mussels had the lowest mass-specific excretion rate, they contributed significantly to the areal N excretion (15.9 and 15.5 mg N m^{-2} d^{-1}), because of their large biomass.

Table 1: Modeled Nutrient Excretion by Major Mollusc Functional Groups in a Tropical Wetland Reference Scenario (28 °C)

Functional Group	Individual Mass (g DM)	Biomass (g DM m^{-2})	Mass-Specific N Excretion (µmol N g^{-1} h^{-1})	N flux (mg N m^{-2} d^{-1})	P flux (mg P m^{-2} d^{-1})	Excretion N:P (Molar)	Share of N / P Demand (%)
Apple Snails (Pomacea, Pila)	1.50	12	3.93	15.9	2.92	12	18 / 24
Thiarid and Viviparid Grazers	0.30	5	5.88	9.9	1.56	14	11 / 13
Unionid Mussels (Lamellidens, Parreysia)	4.00	15	3.08	15.5	1.72	20	17 / 14
Corbiculid Clams (Corbicula)	0.15	6	6.99	14.1	3.12	10	16 / 26
Total Assemblage	**—**	**38**	**—**	**55.4**	**9.32**	**13**	**62 / 78**

DM = dry tissue mass. Shares are relative to an illustrative autotrophic demand of 90 mg N m^{-2} d^{-1} and 12 mg P m^{-2} d^{-1}. Values are calculated with the excretion model described in Section II.

Table 1 provides an overview of the representative body mass, biomass, mass-specific excretion rate, areal N and P excretion rates, excretion stoichiometry, and relative contribution to the illustrative demand for nutrients by primary producers.

Together, the mollusc community contributed to 55.4 mg N m^{-2} d^{-1} and 9.3 mg P m^{-2} d^{-1}, representing 62% and 78%, respectively, of the illustrative autotrophic N and P demands. The relative contribution to P recycling was higher than to N recycling because apple snails and corbiculid clams excrete nutrients with relatively low N:P ratios. Together, apple snails and corbiculid clams accounted for nearly half of the total P excretion rate (6.0 mg P m^{-2} d^{-1}), while unionid mussels, with the highest excretion N:P ratios, provided N and P in relatively higher proportions. Overall, the molar N:P of excreted nutrients from the reference scenario was approximately 13, lower than the Redfield ratio of 16, implying that molluscs tend to alleviate P rather than N limitations in these ecosystems.

Influence of Biomass and Temperature

In figure 1, the excretion rate of areal N and P was plotted against mollusk biomass at three different water temperatures. The excretion rates were found to increase linearly with respect to biomass for a fixed temperature, and therefore, the population density has been found to be the controlling factor on ecosystem function of the molluscs. At 28 °C, the fluxes of 40 g m^{-2} assemblages were found to be 58.5 mg N m^{-2} d^{-1} and 8.6 mg P m^{-2} d^{-1}. When the temperature is increased from 24 to 28 °C and from 28 to 32 °C, the areal fluxes increased by 32% each time: from 44.4 to 58.5 to 77.2 mg N m^{-2} d^{-1}, and from 6.5 to 8.6 to 11.4 mg P m^{-2} d^{-1}.

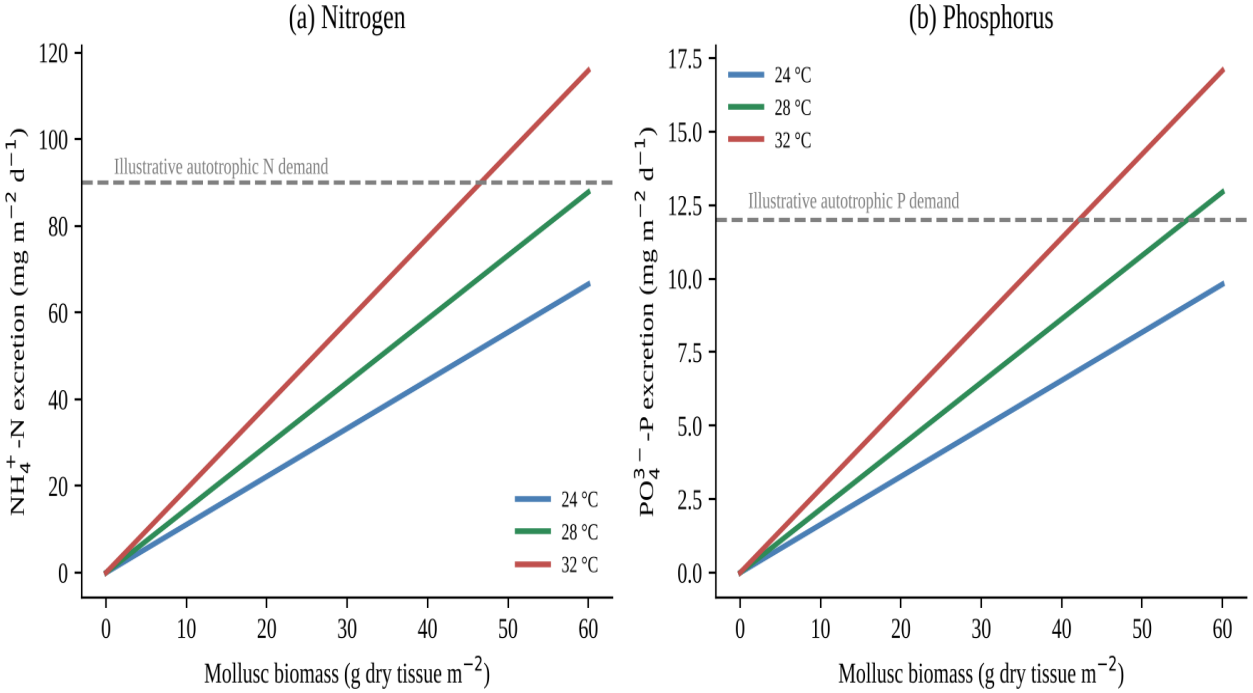


Figure 1: Modeled Areal Excretion of (a) Ammonium-Nitrogen and (b) Phosphate-Phosphorus by Freshwater Molluscs Across a Biomass Gradient at 24, 28 and 32 °C

Figure 1 depicts the linear increase in the rate of nutrient excretion by the assemblage of molluscs as a function of the assemblage biomass and the steep increase in this parameter in response to water temperature. The dotted lines represent the illustrative autotrophic demand for nitrogen and phosphorus, which was used for benchmarking purposes, and this is the demand that becomes easier to fulfill with the increase in the temperature of the wetland.

As follows from the sensitivity analysis, the biomass of molluscs necessary for them to fulfill the illustrative autotrophic demand decreases with increasing temperature. For instance, at 32 °C, the generic assemblage provided for the illustrative demand for phosphorus at around 42 g m^{-2} of its biomass, while at 24 °C, the biomass of molluscs would have to be at around 73 g m^{-2}.

Mechanistic Pathways Identified in the Synthesis

This synthesis has revealed four distinct but interconnected pathways by which molluscs affect nutrient recycling in wetlands. Firstly, nutrient excretion turns nutrients obtained from food sources into a dissolved inorganic state for easy uptake by phytoplankton and macrophytes (Vanni, 2002; Vanni & McIntyre, 2016). Secondly, filtering of bivalves brings suspended particles into the sediment where fecal and pseudofaecal materials are deposited, shifting nutrients from the water column to the benthic habitat and encouraging benthic microbial activities (Vaughn & Hakenkamp, 2001; Strayer, 2014). Thirdly, grazing snails help move nutrients from relatively slower pools of macrophyte tissues to dissolved pools where nutrients might benefit phytoplanktons more than rooted plants (Carlsson et al., 2004). Lastly, molluscs hold large amounts of nitrogen, phosphorus, and carbon in their bodies and shells that provide long-term storage of nutrients and slowly release these stored nutrients after death (Strayer, 2014; Vaughn, 2018). Thus, the above-mentioned processes control both the amount of nutrient cycling and its destinations.

IV. Discussion

These results show that freshwater molluscs may significantly contribute to nutrient cycling in tropical wetlands. Modeled excretion fluxes exceeded 50% of the assumed nitrogen requirement and 75% of the assumed phosphorus requirement of the system. These results are consistent with those found in previous studies, suggesting the significance of nutrient recycling by consumers in supporting aquatic productivity, especially when animal biomass is abundant (Vanni, 2002; Atkinson et al., 2017). Such findings were also confirmed in other studies which showed that dominant snail populations are the primary producers of ammonium ions in aquatic environments (Hall et al., 2003). These modelling results, however, should be field-tested prior to their broader application.

One of the main conclusions drawn here is that biomass determines the effect on nutrient fluxes at the ecosystem level much better than excretion rates of the animals individually. Smaller-sized clams and snails had higher mass-specific excretion, while larger apple snails and unionid mussels produced similar or even higher areal excretion fluxes due to their high biomass. This is consistent with previously obtained results that significant nutrient release from mollusc populations depends mostly on biomass rather than physiological performance (Hall et al., 2003). Nutrient excretion stoichiometry also plays a role in nutrient availability. The modeled community excreted nutrients in an N:P ratio lower than the Redfield ratio, which means more phosphorus was available, and a shift to nitrogen limitation could occur. It is known from earlier studies that mussel clumps have the ability to alter nutrient limitation and benthic algal community (Atkinson et al., 2013; Strayer, 2014). Phosphorus recycling can increase the risk of eutrophication in wetlands rich in nutrients but support production of primary producers in cases of deficiency.

Differences in functionality between gastropod and bivalve molluscs also have an effect on ecological conditions in wetlands. Grazing apple snails contribute to nutrient flow from aquatic plants into dissolved form and can lead to reduction in density of vegetation cover and increase turbidity (Carlsson et al., 2004). Filter-feeding bivalves, on the other hand, remove particles from the water column, decrease turbidity, and move nutrients to the bottom (Vaughn & Hakenkamp, 2001; Vaughn, 2018). Temperature is yet another factor influencing nutrient cycling. The simulation of 4 °C warming increased the areal excretion flux by around one-third, demonstrating strong temperature sensitivity. Nutrient regeneration may be intensified in tropical wetlands under warmer conditions and dry periods due to the accumulation of molluscs in the remaining water basins (Junk et al., 2013). This will result in an increase in algae production and hypoxia; however, the exact consequences should be proven by the field data.

The decreasing numbers of local molluscs will lead to changes in nutrient cycling and the provided ecosystem services. The unionid mussels participate in biofiltration, nutrient retention, and sediment-to-water nutrient fluxes; therefore, the preservation of this species becomes crucial (Dudgeon et al., 2006; Vaughn, 2018). The invasion of new species may cause changes in nutrient flux patterns and ecosystem functioning (Carlsson et al., 2004). In comparison with mobile aquatic consumers, sedentary molluscs may create permanent hotspots of nutrient recycling and retain nutrients in their bodies and shells (Strayer, 2014; Atkinson et al., 2017).

This evidence is in favor of the use of metrics such as population size, biomass, and community structure in wetland conservation and restoration projects. The maintenance of native populations, control of invasive species, and optimal hydrology may improve nutrient cycling and water filtration processes. However, the study is based on generalized scaling equations and parameter values, not on field data. The processes of biodeposition, bioturbation, and nutrient sequestration were not quantified. It is necessary to measure the rates of nutrient excretion, nutrient ratios, and biomass of tropical wetlands for a more accurate validation of modeling predictions.

V. Conclusion

The contribution of freshwater molluscs to nutrient cycling in tropical wetlands has been assessed by linking the synthesis of consumer-driven nutrient cycles with the development of an allometric, temperature-dependent excretion model. These findings demonstrate that molluscs play an important, but underappreciated role in nitrogen and phosphorus cycling. Under the conservative reference conditions at 28°C, the excretion from an assemblage of apple snails, thiarid and viviparid grazers, unionid mussels, and corbiculid clams amounted to approximately 55.4 mg N m^{-2} d^{-1} and 9.3 mg P m^{-2} d^{-1}, which is comparable to 62% and 78% of an example autotrophic requirement. The standing biomass, not the individual physiology, was the principal control on the ecosystem-scale excretion, and the low ratio of N/P in excretions implies that molluscs play an important role in phosphorus provision. Excretion was increased by approximately one third for every 4°C increase in temperature, meaning that both warming and dry season population aggregation will increase excretion. Apple snails, which graze on vegetation, and bivalves, which filter the water, are in opposition. While the herbivorous apple snail can contribute to the release of nutrients tied up in macrophytes, causing turbidity, bivalves contribute to water clarity and nutrient transfer to sediments. Thus, both the reduction in the population of endemic molluscs and the increase in the number of invasive ones could affect the nutrient dynamics, productivity, and water quality of wetlands. This means that wetland management practices should take into account not only the number of molluscs but also their biomass and role. Seasonal measurements of excretion, biodeposition, and nutrient content per species should be taken into account.

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