

Article

Patterns of Mekong Mollusc Biodiversity: Identification of Emerging Threats and Importance to Management and Livelihoods in a Region of Globally Significant Biodiversity and Endemism

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Abstract: The Lower Mekong Basin (LMB) is a key biodiversity hotspot. To facilitate conservation and management, we examine mollusc biodiversity patterns and distribution along LMB's longitudinal gradients, identify environmental drivers, and discuss the importance of these drivers to management. Cluster analysis, redundancy analysis (RDA), and variation partitioning were conducted using mollusc data collected from 63 sampling sites. Results indicated that species diversity is dominated by gastropods (61%) and bivalves (39%) and feeding trait diversity by scrapers (52%) and filter-collectors (37%). Only 48 species (49%) out of 98 taxa have been assessed by the International Union for Conservation of Nature (IUCN) including a growing number of invasive species. The lack of complete, up-to-date information highlights the need for more research on both native and alien species. Cluster analysis revealed a clear mollusc biodiversity structure along the LMB's longitudinal segments. Diversity was lowest in upstream tributaries, increased in upstream main channels, and was highest in downstream channels and the Mekong delta, the exception being the observed high gastropod abundance in Chi-Mun river mouth and Luang Prabang areas. The RDA and variation partitioning demonstrated that combined physical–chemical and climatic conditions are the key drivers of biodiversity patterns. Given the potential spread of invasive alien species and increasing anthropogenic impacts, further ecological research, regular monitoring, and adaptive management are needed to sustain mollusc biodiversity and associated ecosystem services, which contribute to food security, nutrition, and livelihoods in the LMB.

Keywords: climatic factor; river physical–chemical condition; functional feeding groups; conservation status; river management; macroinvertebrates communities; bivalves; gastropods

1. Introduction

Molluscs are a key component of freshwater ecosystems, contributing to bioturbation and filtration in freshwater lotic and lentic environments [1–3]. Living molluscs and their dead shells can enhance food availability and provide physical structure for other organisms [4]. Ecologically, molluscs play an important role in interacting with other freshwater fauna to stabilize the food web [5], and economically, they provide a source of protein and income [6,7].

Mollusc biodiversity and structural patterns are noticeably influenced by physical–chemical conditions, nutrient availability, and food web dynamics in ecosystems [3]. In tropical and sub-tropical regions, pollution and disturbance, due to agricultural intensification, transportation, and aquaculture, have negatively affected mollusc biodiversity [8,9]. Moreover, changes in water flow and sediment types due to anthropogenic influences have also affected mollusc distribution and abundance [10,11]. Climatic conditions and land cover types can also drive mollusc biodiversity [12,13]. Changes in climatic conditions have been reported to affect mollusc body growth [12]. During a period of very low temperature and humidity, or very high temperature, hibernation and aestivation are likely to occur in many mollusc species. In this regard, a comprehensive understanding of the relationships between mollusc communities and their environmental conditions is an important insight to support biodiversity conservation and ecosystem management.

The Lower Mekong Basin (LMB) is a biodiversity hotspot supporting a large number of mollusc species [1,14,15]. Among 179 mollusc species known in the LMB, 116 species are endemic [14,16], and two major groups of molluscs, Gastropoda and Bivalvia, dominate [16,17]. Gastropods in the LMB, in particular in Cambodia, Laos, and Thailand, possess the highest diversity (~140 species) and endemism (111 species) in the world [14]. The LMB also supports a very high level of endemism of bivalves although there are no accurate species counts [6]. Two major groups of molluscs, Bivalvia and Gastropoda, occur in an array of habitat types in the LMB. However, biodiversity patterns of these molluscs and factors driving these patterns in the LMB have not received a high level of attention compared to those in other regions of the world [6]. Most of the existing studies in this basin are taxonomic studies [15,18–22] while, to our knowledge, there are no studies on mollusc biodiversity patterns, drivers, and conservation implications at a large spatial scale.

In this study, we examine mollusc biodiversity patterns and the key factors driving these patterns. We ask the following research questions: (1) How is mollusc biodiversity organized along the longitudinal gradients of the basin? (2) Are there any differences in mollusc biodiversity (i.e., taxonomic richness, abundance, diversity, and functional feeding groups) between different sections (sub-spatial scales) of the LMB? (3) What are the key drivers of the diversity patterns in the LMB? Recent studies suggest that physical–chemical conditions of habitats [3,8], climatic conditions [12,23], and land cover types [13,24] greatly influence the diversity and distribution of macroinvertebrates including molluscs. Here, therefore, we investigate the relative importance of three factors (physical–chemical, climatic, and land cover) to determine which is/are the main driver(s) of mollusc diversity and distribution patterns in the LMB. We then examine the importance of each driver to biodiversity conservation and management.

2. Materials and Methods

2.1. Mollusc Collection and Physical–Chemical Measurements

From 2004 to 2008, molluscs and along with other benthos were sampled at 63 sampling sites in the LMB (main channels and tributaries) [25] (Figure 1). The sampling was conducted once a year

in the dry season (March). From each sampling site, the mollusc samples were collected at three locations (such as near the left and right banks and in the middle of the rivers) from the benthic zone. After the collecting and preserving processes, molluscs were brought to the laboratory and identified to the lowest taxonomic levels possible using the Mekong River Commission (MRC) key book [26]. Physical–chemical variables, including geographical coordinates and altitude, river width and depth, water temperature and conductivity, dissolved oxygen, pH, and Secchi depth were also measured and collected. We refer to Sor [17] and Sor et al. [13] for further detailed information on the field data collection methods.

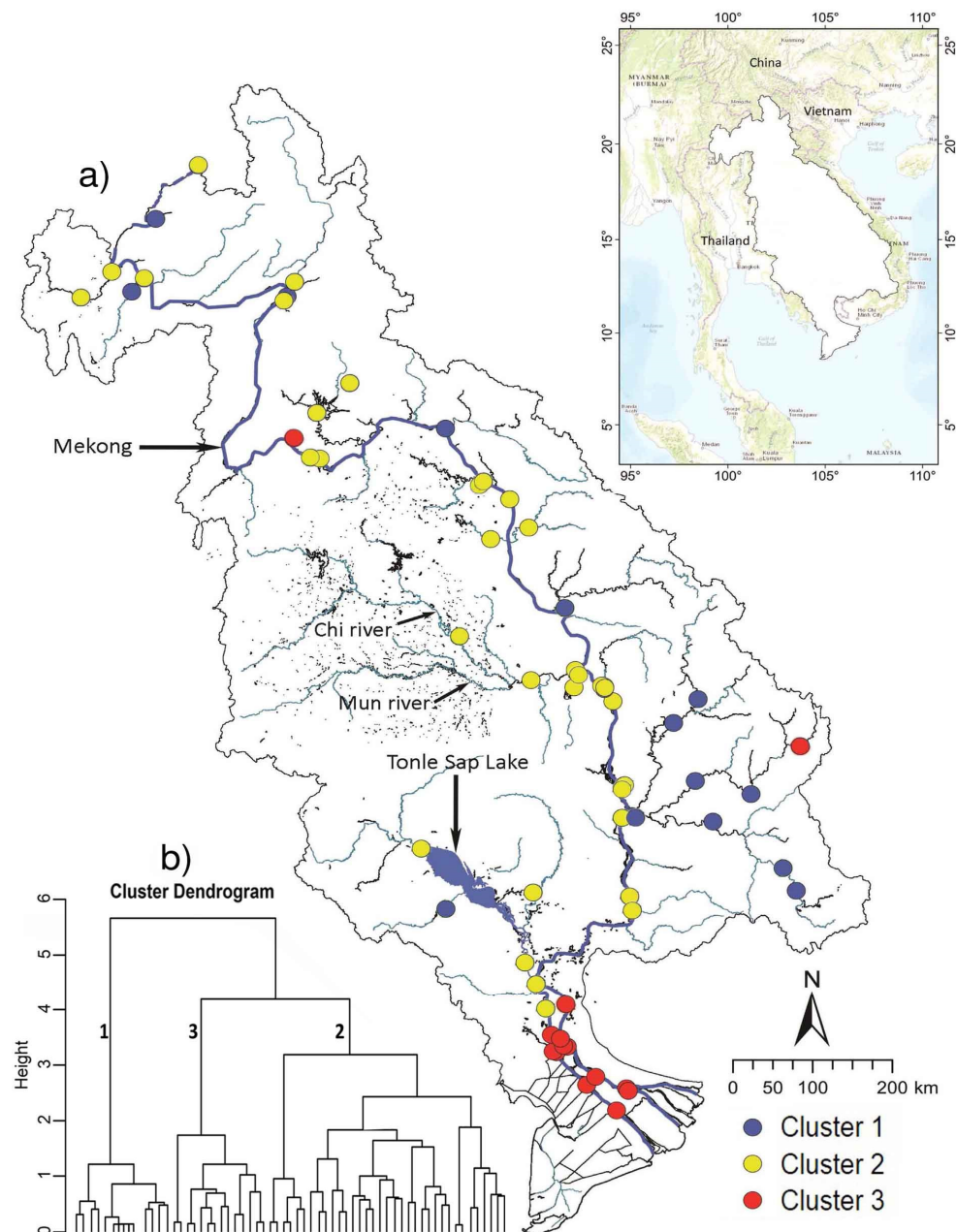


Figure 1. The sampling sites belonging to each cluster projected on the map (a) and the dendrogram showing the three distinct clusters using mollusc data collected from 63 sampling sites from the Lower Mekong Basin (b). See Results (Section 3) for details.

2.2. Land Cover Data

At each sampling site, surface area and land cover data were calculated using a Geographic Information System (ArcGIS 10.4, ESRI). Geographical data (ArcGIS shapefiles) of the LMB (land cover types, river networks, basin boundaries, and sub-catchments derived from topographical maps in 2003) were provided by the MRC, available at <https://portal.mrcmekong.org/land-cover/land-cover-types>.

2.3. Climatic Data

Bioclimatic data (19 variables) were derived from the WordClim database, available at <http://www.worldclim.org>, describing climatic conditions for the period 1950–2000 with a spatial resolution of about 1 km². The mean value of the mentioned period from each sampling site coordinate (as the centre point of the 1 km² grid) was used for the analysis.

2.4. Data Treatment and Analysis

In this study, we examined community spatial variability and environmental variables across sampling sites in the LMB. Median values from biological and environmental data were used to represent each sampling. The median values were used due to unequal sampling efforts [27]; that is, unequal and different number of samples at each site during the 5-year sampling period.

Mollusc biodiversity was first summarized based on the number of classes, families, genera, species, functional feeding groups (FFGs), and their IUCN (International Union for Conservation of Nature) conservation status using the IUCN Red List of Threatened Species website: <https://www.iucnredlist.org>. Then, mollusc community abundance data from the 63 sampling sites (site-by-species) were grouped into different clusters, based on the Bray–Curtis dissimilarity distance of their community, using the Ward's hierarchical clustering method [28]. Each cluster is a group of sampling sites that are characterized by taxonomic similarity, and therefore sampling sites with similar mollusc community composition are grouped into the same cluster [29]. To analyse the spatial variation of mollusc biodiversity, their taxonomic and functional richness, abundance, and diversity index were compared between the clusters (i.e., defined by the Ward's clustering method), using either a one-way analysis of variance (ANOVA) for normal distributed data or a Kruskal–Wallis test for the not-normal distributed data. Both tests were carried out using the *kruskal.test()* and *aov()* functions of the *stats* package [30]. *p* values < 0.05 were considered statistically significant.

Redundancy analysis (RDA, [28]) was used to gain a comprehensive understanding of factors driving biodiversity patterns. The community data were Hellinger-transformed before conducting the RDA, while the environmental variables were normalized using the zero minimum because the value of each variable highly varies from one to another (different measuring scales) [31]. In this normalization approach, the normalized values are based on the standard deviation of each variable while at the same time keeping the range of all variables constant. The strength of each variable in explaining the mollusc communities is depicted by the length of its arrow in the ordination map; the longer the arrow length, the stronger the correlation/association will be [28]. Forward selection of the RDA model was then performed to retain only the most significant environmental variables. To identify which types of environmental variables (i.e., physical–chemical vs. land cover types vs. climatic variables) is/are the main driver(s) of biodiversity patterns, variation partitioning [28] was performed using the community transformed data and the most significant environmental variables yielded by the RDA forward selection. All statistical analyses were performed in R statistical programming language [30].

3. Results

3.1. Overall Biodiversity and Conservation Status

From 9645 individuals, 98 taxa belonging to 21 families, 8 orders/clades, and 2 classes were identified in the dataset. Among all taxa, only 69 taxa were identified to species level, while the remaining (29 taxa) were identified to genus or family or higher classification levels. The class Bivalvia

(38 taxa) comprised the orders Arcoida (2), Mytiloida (2), Unionida (18), and Veneroida (16); whereas the class Gastropoda (60 taxa) comprised the clades Caenogastropoda (52) and Hygrophila (3), the orders Heterostrophia (1) and Neritimorpha (2), and 2 taxa of unknown identifiable order.

The most common families were Unionidae (18%), followed by Corbiculidae (14%), Viviparidae (12%), Stenothyridae (11%) and Pomatiopsidae (8%). The species *Corbicula tenuis* was the most frequently observed (65% of all sites) across the LMB, followed by *Stenothyra koratensis holosculpta* (29%), *Corbicula lamarckiana* (27%), and *Limnoperna siamensis* (24%), whereas *Corbicula leviuscula* was the most abundant species (17% of the total abundance), followed by *Limnoperna siamensis* (13%), *Corbicula tenuis* (12%), *Corbicula lamarckiana* (9%), and *Stenothyra koratensis holosculpta* (7%).

Among all taxa, the functional feeding groups scrapers, filter-collectors, and gatherer-collectors represented 52% (51 taxa), 37% (37), and 5% (5), respectively. Forty-eight of the 69 identified species had been assessed based on the IUCN Red List: Data Deficient (DD, 10 species), Least Concern (LC, 37), and one Near Threatened (NT) species, *Pachydrobiella brevis*. Moreover, five species are alien to the LMB, four of which (i.e., *Angulyagra polyzonata*, *Corbicula fluminea*, *Sermyla riqueti*, *Sinotaia aeruginosa*) are native to the river basin in China and/or Hong Kong, Korea, and one of which (*Neritina rubida*) is native to Madagascar and French Polynesia [32]. For further details on all taxonomic information, see Supplementary Table S1.

3.2. Community Variation

Three regional clusters were identified based on biodiversity patterns using mollusc community dissimilarity (Bray–Curtis) and hierarchical analysis (Figure 1a). Cluster 1 was made up mainly from sites located in the 3S (Sesan, Sekong, Srepok) rivers in northeastern Cambodia and Vietnam; Cluster 2, from sites in Mun, Chi, and Tonle Sap River basins, and also sites along the main channel of the Cambodian Mekong; and Cluster 3, mainly from sites in the Mekong delta (Figure 1b).

A significant difference between clusters and a generally increasing trend in richness, abundance, and diversity from Cluster 1 (the tributaries) to Cluster 3 (Mekong delta) was observed for most of the computed metrics (Figures 2 and 3; Table 1). An exception to this trend was found for gastropod and scraper abundance, which was the highest in the upstream main channel (Figures 3 and 4), i.e., Chi-Mun river mouth and Luang Prabang, where the confluence of the Mekong and Nam Khan rivers occurs, and the lowest in the tributaries (Table 1).

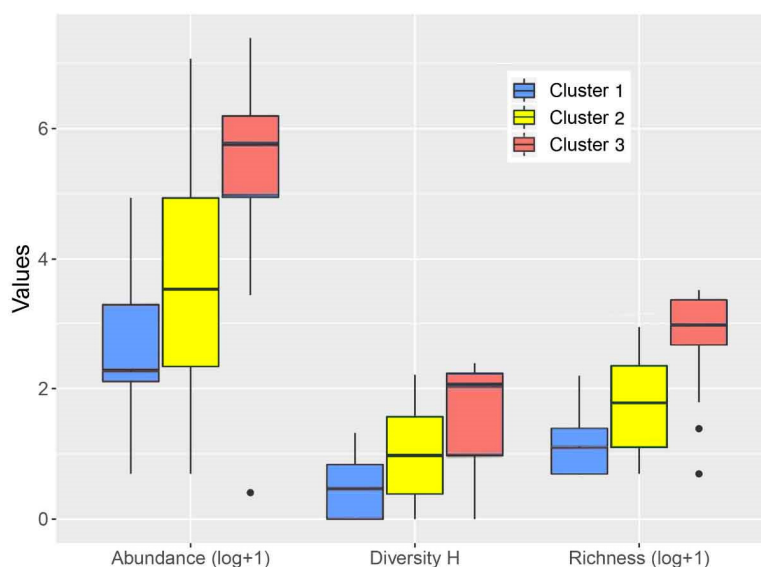


Figure 2. Box-and-whisker plots of values for taxonomic abundance (TA), and taxonomic richness (TR) and Shannon–Wiener’s diversity (H) of mollusc assemblages in each cluster. Rectangles delineate the first and third quartiles, dark bars are the medians, and the dots are outliers.

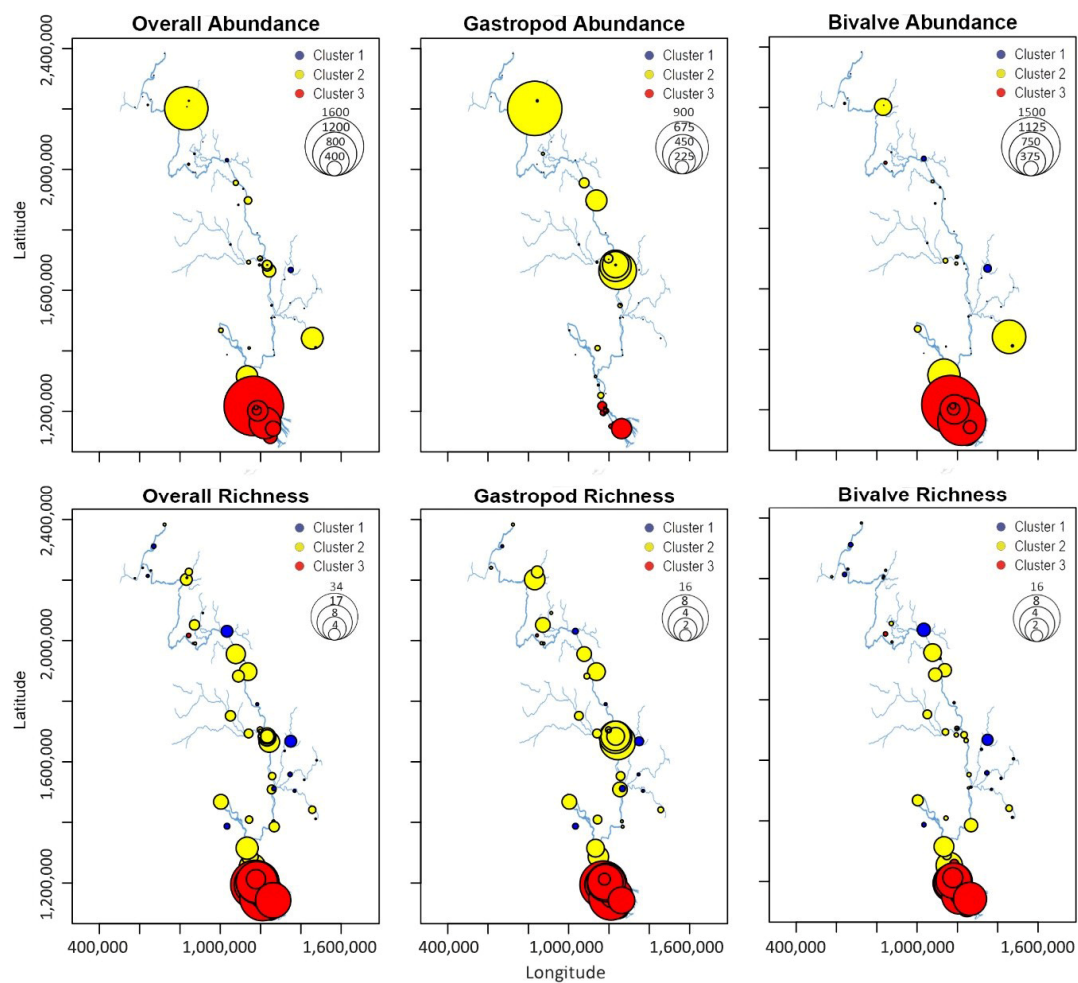


Figure 3. Abundance and richness distribution of overall mollusc communities, gastropods and bivalves in the Lower Mekong Basin.

Table 1. Median, mean, and standard deviation values for different metrics measured in each cluster.

	Cluster 1			Cluster 2			Cluster 3			
Metrics	Tributaries			Upstream Main Channel			Delta			p-Value
Taxonomic Richness	2.0	2.9	2.4	5	6.3	4.7	18.5	18.7	10.6	0.0000
Taxonomic Abundance	8.8	26.2	39.6	33.5	130	235.6	316	406.1	417.4	0.0004
Shannon Diversity H	0.5	0.5	0.4	1	1	0.7	2.1	1.6	0.8	0.0011
Sub-group richness										
Gastropods	1	0.9	1	3	3.6	3.2	8	7.8	5.3	0.0001
Bivalves	1	1.9	1.6	2	2.7	2.8	11.5	10.9	5.4	0.0000
Sub-group abundance										
Gastropods	0.8	1.4	1.6	10	69.4	164	36.8	43.9	49.3	0.0002
Bivalves	7.5	24.8	38.7	11.5	60.6	139.3	238.5	362.2	403.7	0.0002

Table 1. Cont.

	Cluster 1			Cluster 2			Cluster 3				
Metrics	Tributaries			Upstream Main Channel			Delta			<i>p</i> -Value	
FFG richness											
SC	0.5	0.9	1	2	3.2	3	7.5	6.7	4.3	0.0002	
FC	1	1.9	1.4	2	2.6	2.8	11.5	10.6	5.3	0.0000	
GC	0	0.1	0.3	0	0.2	0.5	0.5	0.6	0.7	0.0179	
FFG abundance											
SC	0.3	1.2	1.5	9	67.5	162	26.5	40.6	49.4	0.0004	
FC	7.5	24.8	38.7	10.5	60.2	139.1	238.5	361.3	404.2	0.0002	
GC	0	0.1	0.1	0	1.7	5.4	0.3	1.7	2.7	0.0274	
FFG diversity H											
SC	0	0.2	0.4	0.5	0.5	0.6	1.3	1.2	0.8	0.0009	
FC	0	0.2	0.3	0.03	0.4	0.6	1.7	1.3	0.7	0.0002	
GC	0	0	0	0	0	0.1	0	0.1	0.1	0.1685	

The functional feeding groups (FFGs) observed are scraper (SC), filter-collector (FC), and gatherer-collector (GC).

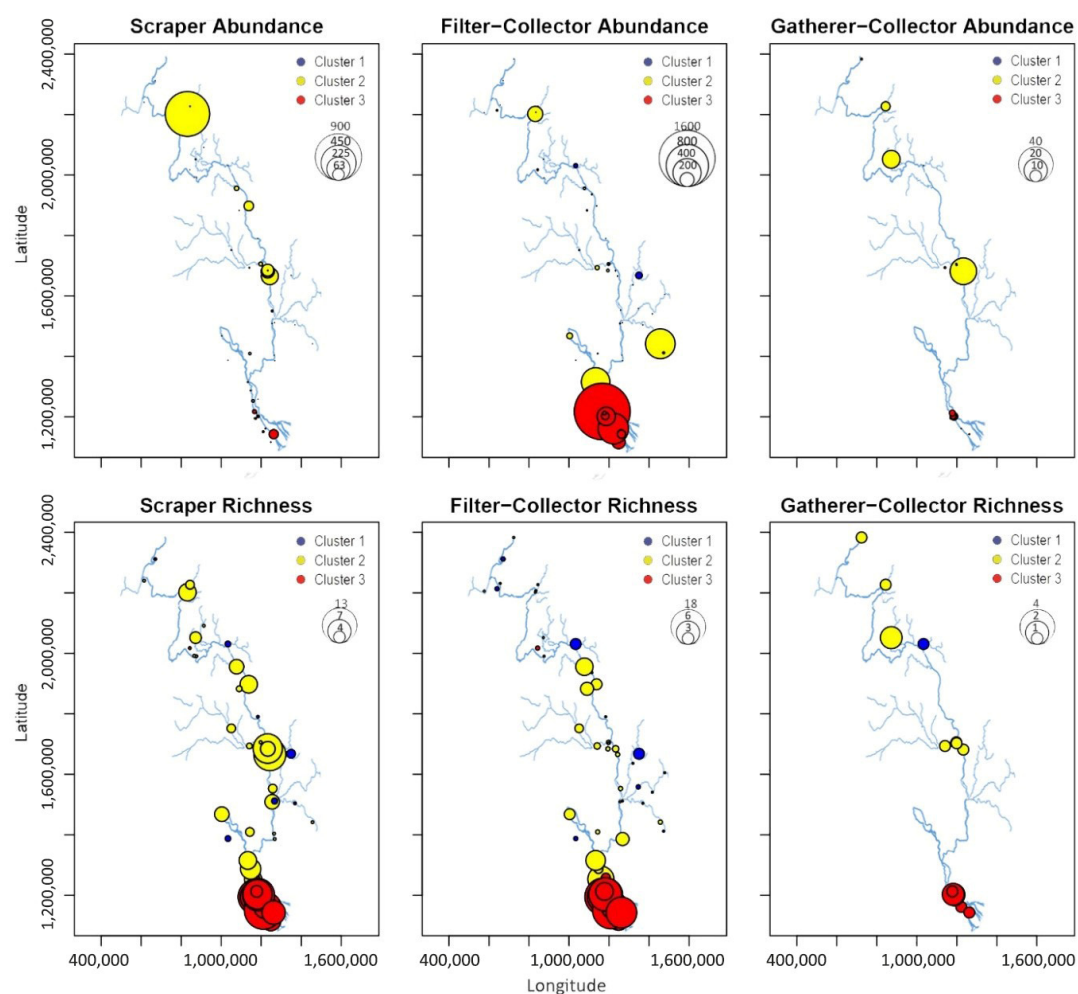


Figure 4. Abundance and richness distribution of mollusc functional feeding group communities in the Lower Mekong Basin.

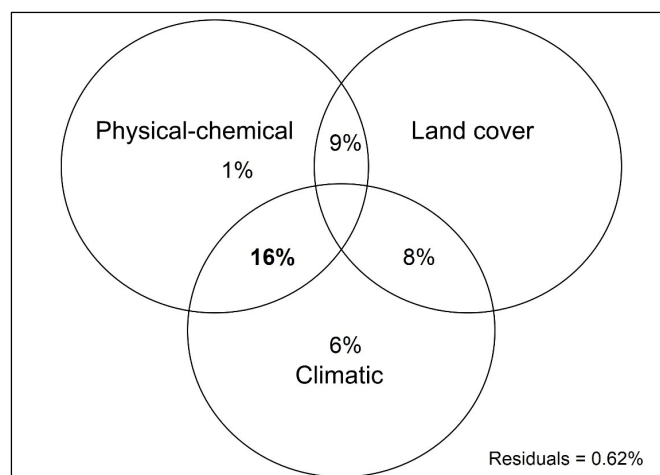


Figure 6. Venn diagram of variation partitioning showing the pure and combined effects of physical–chemical factors, climatic factors, and land cover types (values < 1 are not shown) on mollusc communities.

4. Discussion

4.1. Mollusc Biodiversity, Conservation Status, and Threats

Mollusc biodiversity in the LMB has not been well-studied. Existing information is restricted to taxonomy, distribution, and general macroinvertebrate patterns. More information is needed on species, family, and order diversity; species functional feeding groups; and conservation status. Here, we fill this gap and thus improve the existing knowledge, focusing on mollusc biodiversity patterns and the key environmental drivers of these patterns [6,13,20,21].

At the species level, five species including *Corbicula leviuscula*, *Corbicula tenuis*, *Corbicula lamarckiana*, *Limnoperna siamensis*, and *Stenothyra koratensis holosculpta* were dominant, as reflected by their widespread distribution and high abundance [13,33]. Therefore, they are the key species representing mollusc communities in the LMB. Other Near Threatened (i.e., *Pachydrobiella brevis*) and less common species (e.g., *Clea scalarina*, *Hyriopsis (Limnoscapha) desowitzi*, *Adamietta housei*) may be more vulnerable to environmental changes including climate change and threats from alien species.

At a higher taxonomic level, the mollusc communities in the LMB are mainly characterized by two common families of bivalves (Unionidae and Corbiculidae) and three families of gastropods (Viviparidae, Pomatiopsidae, and Stenothyridae). The sampling design used in this study (e.g., much of the river course of the LMB were not sampled, e.g., Cambodian–Lao and Lao–Thai borders, the Tonle Sap and its tributaries, etc.) may affect the resulted diversity of this study. The other caveat for the study is that it was conducted only in March in the dry season. Some species belonging to Corbiculidae are highly abundant in dry season when there is less precipitation and higher temperature, while others such as *Pila* spp. (e.g., *Pila virescens*) are more abundant in the wet season with more precipitation and lower temperature [34]. Regarding the dominant family Unionidae found in this study, its members mainly occur in both forested and grassy riparian zones [1,35], whereas Corbiculidae has various reproductive strategies and spreading abilities [22]. These life strategies and biological traits may explain their wide distribution across the basin. However, the two families were more abundant in terms of biomass and richness downstream, which indicated their preferred habitats (e.g., large rivers with slow water flow) similar to that found by previous studies [36,37]. The commonness of these families could be also due to their wide distribution in both freshwater and estuary habitats and good dispersal strategies [14]. Among the five common families, Unionidae, Viviparidae, and Pomatiopsidae were more diverse in terms of their member genera. However, some genera of the three families were found at only one sampling site (e.g., *Hyriopsis*, *Scabies*, *Uniandra*, *Anulotaia*, *Lacunopsis*). The remaining two families Corbiculidae and Stenothyridae are entirely dominated by the genera *Corbicula* and *Stenothyra*,

respectively. Because of their high diversity, widespread distribution, and varied reproductive strategies, these families are less likely impacted by habitat invasion and competition from the other species [22,38,39]. Regarding the less common families, most of them were found with only 1 occurrence of 1 individual, e.g., *Clea scalarina* (Buccinoidae), *Adamietta housei* (Pachychilidae), and *Lymnaea swinhoei* (Lymnaeidae) or 2 occurrences of 2 individuals, e.g., *Neritina violacea* (Neritidae), *Cochliopa riograndensis* (Cochliopidae), and *Neoradina prasongi* (Thiaridae). These species' distributions and abundances have not been assessed from the LMB, and therefore their population statuses are unknown [32]. Some exceptions were for *Adamietta housei*, of which 28 individuals were recorded from two stations in Thailand (Sri-Aroon, 2007), and for *C. scalarina*, of which 8 specimen-based occurrences are recorded in the Global Biodiversity Information Facility (GBIF) database [40]. In this regard, further studies on these species are needed because they already appear rare and may be more vulnerable to environmental change, high anthropogenic stress, climate change, or ecological alteration [32].

Compared to other basins, the species richness occurrence range reported in the LMB (14–58 species) [6] is relatively similar to that in other tropical river basins such as Yangtze, Pearl, Huaihe, and the Southeast rivers in China (8–158 species) [41]. However, studies dating back to the 2000s (e.g., Bogan, 2008; Strong et al., 2008) reported that the LMB supports the most diverse freshwater mollusc species (140 gastropod and 39 bivalve species) in the world and highest level of endemism, second after the Mobile Bay Basin in the southeastern United States (271 bivalve and 118 gastropod species) [1,14]. Our study, which does not cover the entirety of the Tonle Sap, Mun, and Chi basins, in the mid-reaches of the Mekong near the border between Cambodia, Laos, and Thailand (e.g., Kong Island) that are thought to be hotspots of pomatiopsids and stenothyrids [42,43], also reports a higher maximum species richness of bivalves per site (16 species) than that reported from European river basins (10 species) [44], and a higher total number of gastropod taxa (60 taxa) than those in Northern Australia Monsoonal wetlands (~56 taxa), Lower Uruguay River and Rio de la Plata, Argentina–Uruguay–Brazil (~54), Western lowland forest of Guinea and Ivory Coast (~28), and Zrmanja river basin in Croatia (~16) [14]. In this regard, and given the fact that much of the river course of the LMB (e.g., the Cambodian Tonle Sap Lake and River and its main tributaries such as Sangke, Pursat Stung Sen, and Chinith Rivers) has not been investigated, the LMB still appears to be the hotspot area for molluscs, as illustrated by Köhler et al. [6]. The main channels (the Mekong and Bassac) most likely support a higher mollusc species diversity than that indicated in Köhler et al. [6]. This can be due to the fact that the highest species richness of the present study (34 taxa/site) is recorded along these main channels and that another 20 additional species (see Quang et al. [45]), which are different from the recorded species of the present study, have been also reported from the main channels and its tributaries in the delta [45]. This suggests that the main channels downstream of the LMB and its tributaries deserve a re-assessment as mollusc biodiversity hotspots.

Despite the high biodiversity of molluscs and their importance for the ecosystems as well as the livelihoods of local people in the region [6,46], this resource is facing critical threats. Overharvesting, habitat degradation (e.g., land use change), and changes of water regime are among the major factors negatively impacting mollusc biodiversity [34]. These impacts have already been observed in the rivers of North America [47,48]. Other anthropogenic disturbances, e.g., agricultural wastes such as chemical fertilizers, herbicides and pesticides, and household wastes, are also a great threat, leading to the decline of molluscs and other biodiversity. Alien invasive species are the other emerging threat; they compete, alter the habits of the native species [49]. Although there is limited research on alien mollusc species in the LMB, which reflects the necessity of up-to-date assessment, several of them have already become established in the LMB, as in the case of this study (i.e., *Angulyagra polyzonata*, *Corbicula fluminea*, *Sermyla riqueti*, *Sinotaia aeruginosa*, and *Neritina rubida*) [32]. Many more alien species are suspected to occur in the LMB. In this Anthropocene epoch, the current impact of climate change in the LMB can facilitate the spread of alien species. Since the LMB is a transboundary river in which its channel is inter-connected to other neighbouring ecosystems, the species most likely move (e.g., via water flow) or are transported in and out of the LMB when facing the on-going climate change

and the current anthropogenic activities. Limited or regulated flow in the LMB, due to hydropower development, also has a negative effect on the species turnover (i.e., the presence of rare species in the community) in the LMB [13,50], and this indeed benefits alien species as they are considered to have high ability to compete and adapt to different environmental changes. All of these factors consequently and inevitably will have strong negative impacts on the native mollusc and other biodiversity in the LMB.

4.2. Environmental Gradients as Drivers of Mollusc Diversity

Environmental gradient is the key factor driving biodiversity patterns in lotic ecosystems [51,52]. Here we found that environmental heterogeneity of the LMB, compared to other factors, had a greater influence on mollusc biodiversity patterns. The overall mollusc community, sub-groups, and FFG diversity, by means of richness, abundance, and Shannon diversity H' , increased following the longitudinal gradients of the LMB. This result is different from the finding of Köhler et al. [6], who reported mollusc species richness was the highest in the main channel and large floodplain tributaries (e.g., Mun and Chi rivers) of the LMB upstream. The difference could be due to the fact that the study of Köhler et al. [6] counted the species richness at the catchment scale while this study measured the diversity at a sampling site scale and did not include a large portion of the Mun, Chi, and Tonle Sap Lake basins. Nonetheless, we found that mollusc communities at the site-specific scale are less diverse in the tributaries and the mainstream upper channels but more diverse in the delta (lower floodplains) downstream.

Tributary rivers such as the 3S river system (Cluster 1) of the LMB are smaller, narrower, and shallower than the main channels and the downstream. Moreover, they are covered by a large proportion of forests or evergreen forests (Figure 5). These conditions are mostly preferred by insect shredders [13] but not molluscs because such conditions constrain the abundance of phytoplankton and reduce organic materials produced via photosynthesis in the water, due to limited penetration of solar radiation [13,53]. Therefore, in these tributary rivers, the consumption outpaces the production and thus limits the diversity of molluscs, in particular the collectors. Only some mollusc scrapers prefer these habitats.

Mollusc diversity increases in the main channels of the basin (except for the delta) (Figure 2). The habitats of mollusc communities in this cluster mainly located at/nearby the main channels and in key large sub-river basins such the Chi, Mun, and Tonle Sap rivers [15]. The structure of these river habitats is characterized by a large floodplain, varied aquatic plants, different rock sizes and riffles, and deciduous forests. These conditions lead to a higher production than the consumption, and so play an important role in supplying organic matter (e.g., periphyton and other autochthonous), which is preferred by mollusc scrapers (snails) [34,54]. Therefore, it is not surprising that the highest gastropod and scraper abundance were found in Cluster 2.

We found the highest diversity of molluscs in the downstream of the LMB (Cluster 3). The Mekong delta is the mouth of the Mekong basin with a large flux of particulate materials. The large watershed and large and open rivers in the delta support diverse, abundant mollusc populations/communities. This is because the high flux of particulate materials and high temperature, due to solar radiation, provide the most suitable conditions for phytoplankton [53,55], and as a result, phytoplankton feeders and filter/gatherer molluscs proliferate. These findings also support previous study results in other tropical regions such as the Guadiana River basin (SW Iberian Peninsula) [36] and Southern Brazil wetlands [56].

Drivers contributing to biodiversity patterns are more than just simple or single factor. Shared contribution of drivers is often reported to shape biodiversity in the river systems [57–59]. As we found in this study, the combined contribution of physical-chemical and climatic conditions explained a larger proportion of variation of mollusc biodiversity, compared to single and other combined factors (Figure 6). Climatic variables such as the annual mean temperature (bio1), maximal temperature of warmest month (bio5), temperature annual range (bio7), precipitation seasonality

(bio15), and precipitation of driest quarter (bio17) were the key factors driving the patterns of mollusc biodiversity. These variables are interrelated with the physical–chemical and land cover conditions. High temperature at some degree can lead to decreased dissolved oxygen and increased electrical conductivity [13,60], whereas the precipitation depends on the forest land cover and vice versa [61]. Precipitation affects the seasonal water flow and thus the movement of nutrients along the longitudinal segments of the rivers and flood-pulse regime (e.g., the Tonle Sap) [52,62]. For instance, higher temperatures (climatic factor), coupled with higher nutrients inputs (physical–chemical factors) in the Delta, lead to higher mollusc diversity. All of these combined factors and interrelations are therefore the main drivers shaping the biodiversity patterns of the LMB biota including the molluscs.

4.3. Management Implications

The LMB is a biodiversity hotspot supporting one of the most diverse mollusc communities in the world. Appropriate planning and management of the basin are vital for protecting molluscs, which depend on healthy aquatic habitats and support people's livelihoods. In the basin, molluscs are an important ecosystem element as they can change the biotic diversity in the basin, due to their high among-site taxonomic and FFG variation (i.e., high beta diversity) across the LMB [33]. Moreover, molluscs are considered as ecosystem engineers, especially gastropods and bivalves, by means of shell production [63]. Architectural complexity and heterogeneity in the benthic environments, as the results of shell aggregation, are important in determining other species' colonization success and composition within the habitat. This is because the complexity and heterogeneity routinely modify the resources available to other aquatic organisms. For instance, the shell cavity of a gastropod can be a microhabitat of other organisms (e.g., crabs), where they can avoid temperature extremes, hydrodynamic forces, or predation. All of these processes can therefore positively influence the whole basin (or landscape-) level species richness.

In the context of ecosystem services, molluscs are an excellent water filtering organism. Bivalves can filter out large amounts of phytoplankton, bacteria, and organic materials and can also absorb pollutants such as heavy metals [1,46]. In terms of provisioning services, molluscs play a key role in food web dynamics as they are the food sources of various organisms (fish, turtles, rodents, birds etc.). Moreover, molluscs are the source of protein intake for the local people sharing the LMB. In some regions, e.g., the Tonle Sap Lake in Cambodia, they are the second most important fisheries after fish [34], from which local people can generate significant income.

Anthropogenic disturbance is changing and degrading the LMB. Modification of rivers' flow (e.g., artificial island created along the rivers, ports development), degradation of habitats (e.g., forest clearance, erosion, agricultural and industrial wastes), and hydropower development are contributing causes to biodiversity changes and river alteration. For instance, the current development of the hydropower dam in the Lower Sesan 2 leading to the creation of large reservoir could create favourable conditions for some invasive species including *Pomacea* spp. to thrive as they can tolerate a high nutrient load in the reservoir. The environmental changes induced by dams can also alter the distribution of some native pomatiopsid and stenothyrid species, which are the intermediate hosts of paragonimiasis and schistosomiasis [64,65]. These parasitic worms, which can infect local people, are thought to benefit from the regulation and modification of the Mekong and its tributaries. Moreover, as discussed earlier, the LMB is already home to several invasive species. In addition to the five reported alien species in this study, the golden apple snail (*Pomacea canaliculata*) is also of great threat to biodiversity [59], in particular to native mollusc species. For instance, the golden apple snail can outcompete the food resources and available habitats of the native snails (e.g., *Pila* spp.). The golden apple snail is a globally well-known invasive species, wide-spread and highly adaptable to different environments. Overharvest is another potential threat, especially in the Tonle Sap Lake and Mekong Delta, which can affect the overall food web, reducing food available for higher tropic level organisms [34]. All of these factors consequently impact the biodiversity sustainability and thus raise a global concern for the long-term persistence of Mekong molluscs and their availability as a food resource in the basin.

Given the factors driving the mollusc biodiversity, the LMB resources require a higher attention for management and conservation planning such as habitat/resource protection and enhancement and resource use coordination between competing users. Good conservation efforts and effective management of the basin and its sub-catchment, e.g., Mun, Chi, and Tonle Sap River basins, and the Mekong Delta (where numerous mollusc taxa and species indicators occupy [13]), will enhance biodiversity and maintain the system integrity, functions, and services and consequently contribute to food security, employment, and socioeconomics of the people sharing this important river ecosystem.

5. Conclusions

In this study, we revealed that main channel and large tributary mollusc biodiversity in the LMB is dominated by gastropods and bivalves, consisting mainly of scrapers and collectors. Among the 98 taxa, 48 species (49%) have already been assessed in the IUCN RedList, one of which is Near Threatened, 10 are Data Deficients, and 5 Aliens. This suggests a need for a more up-to-date assessment of the species and existing and potential threats, including new alien species, by setting up regular monitoring on aquatic invertebrates including the molluscs and environmental DNA. Regarding their biodiversity patterns, this study showed mollusc diversity structured along environmental gradients of the river. Their diversity increases from the upstream tributaries to the upper main channels and then to the Mekong delta, except for the high abundances of gastropod and scraper found in the upstream. Combined physical–chemical and climatic conditions, such as river width, river depth, surface area of watersheds (physical–chemical), and temperature, temperature annual range, and precipitation (climatic), are the key drivers of the observed patterns. Other important variables such the nutrient and sediment loads, and micro/meso habitat types should be considered in the analysis as well in further studies. Nevertheless, given high levels of endemism, lack of relevant and up-to-date data, potential invasion, and anthropogenic impacts, further ecological research, regular evaluation, management planning, and legislative support are needed to sustain mollusc biodiversity and associated ecosystem services, especially in the context of people’s livelihood in the LMB and global change.

Supplementary Materials: The following are available online at <http://www.mdpi.com/2073-4441/12/9/2619/s1>, Table S1: Taxonomic information on the mollusc taxa and their IUCN category, functional feeding group, occurrence, and abundance.

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