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Spatial organization of macroinvertebrate assemblages in the Lower Mekong Basin

Ratha Sor[a,b,c,*], Pieter Boets[b,d], Ratha Chea[a], Peter L.M. Goethals[b], Sovan Lek[a]

[a] Laboratoire Evolution & Diversité Biologique, UMR 5174, Université Paul Sabatier – Toulouse III, 118 route de Narbonne, 31062 Toulouse cédex 4, France
[b] Laboratory of Environmental Toxicology and Aquatic Ecology, Ghent University, Campus Coupure building F, Coupure links 653, B9000 Ghent, Belgium
[c] Department of Biology, Faculty of Science, Royal University of Phnom Penh,Russian Boulevard, 12000, Phnom Penh, Cambodia
[d] Provincial Centre of Environmental Research, Godshuizenlaan 95, 9000 Ghent, Belgium

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ABSTRACT

In this study, we investigated patterns of spatial variation in macroinvertebrate assemblages in the Lower Mekong Basin (LMB) and examined their relationship with environmental factors. Cluster analysis was used to group macroinvertebrate samples and Linear Discriminant Analysis was performed to discriminate the major factors associated with the macroinvertebrate assemblages. Four clusters could be distinguished based on the dissimilarity between macroinvertebrate assemblages. The assemblages related to the tributaries and the upstream parts (cluster II) were characterized by a lower richness, abundance, diversity and a lower number of indicator taxa compared to the assemblage found downstream in the Mekong delta (cluster I). Aquatic insects and their indicator taxa (e.g. *Caenodes* sp., *Dipseudopsis* sp. and Gomphidae sp.), preferring a high-altitude environment with a high dissolved oxygen concentration and a high density of wood/shrub and evergreen forests, were the most predominant group in the assemblages occupying the tributaries and the upstream parts (cluster IIa). The assemblage found in the delta, consisting largely of molluscs and a moderate richness and abundance of worms, crustaceans and dipteran insects, was mainly represented by *Corbicula leviuscula* and *C. moreletiana* (molluscs), *Namalycastis longicirris* and *Chaetogaster langi* (worms), *Corophium minutum* and *Grandidierella lignorum* (crustaceans), and *Cricotopus* sp. and *Clinotanypus* sp. (dipteran insects). This assemblage was associated with a large watershed surface area, deep and wide rivers and a high water temperature. The intermediate assemblage (cluster IIb1) in-between could be discriminated based on land cover types including inundated, wetland and agricultural land, and was represented most by molluscs. Strikingly, the assemblage occupying the upstream parts (cluster IIa), which is related to intensified agriculture and a moderate conductivity, was characterized by a higher macroinvertebrate diversity compared to the mountainous and less impacted tributaries. This could mean that the natural stress is high in these systems for some taxa, leading to a lower overall taxonomic richness and abundance. Nevertheless, the number of taxa and the diversity of macroinvertebrates remained relatively high across the basin, especially in the delta assemblage. Therefore, the LMB deserves a particular attention for conservation.

1. Introduction

Tropical regions are remarkably rich in biodiversity (Sodhi et al., 2004), with 16 out of the 25 terrestrial biodiversity hotspots of the world being located in the tropical zone (Myers et al., 2000). Southeast Asia has a unique geological history (Sodhi et al., 2004), and can be separated into four biodiversity hotspot regions: The Philippines, Sundaland, Wallacea and Indo-Burma (Mittermeier et al., 1999). Through Indo-Burma, the Mekong River, which is the longest river in Southeast Asia, flows from its source in the Tibetan plateau to the South China Sea (Zalinge et al., 2003). This river harbours diverse biotic communities and is the breeding area of numerous endemic, threatened and endangered species. The aquatic and terrestrial communities of the Mekong form a biologically important food web that supports a high biodiversity (Sodhi et al., 2004). Moreover, it is an economically important region, since aquatic fauna such as fish (~1200 species, Rainboth, 1996), molluscs, crustaceans and insects, are all highly dependent on this basin as a breeding ground (Davidson et al., 2006; Zalinge and Thuok, 1998).

Macroinvertebrates are a key component of freshwater ecosystems (Bogan, 2008; Palmer et al., 1997). In river systems, macroinvertebrate communities are differently organized and structured along environ-

* Corresponding author at: Laboratoire Evolution & Diversité Biologique, UMR 5174, Université Paul Sabatier – Toulouse III, 118 route de Narbonne, 31062 Toulouse cédex 4, France.
E-mail address: sorsim.ratha@gmail.com (R. Sor).

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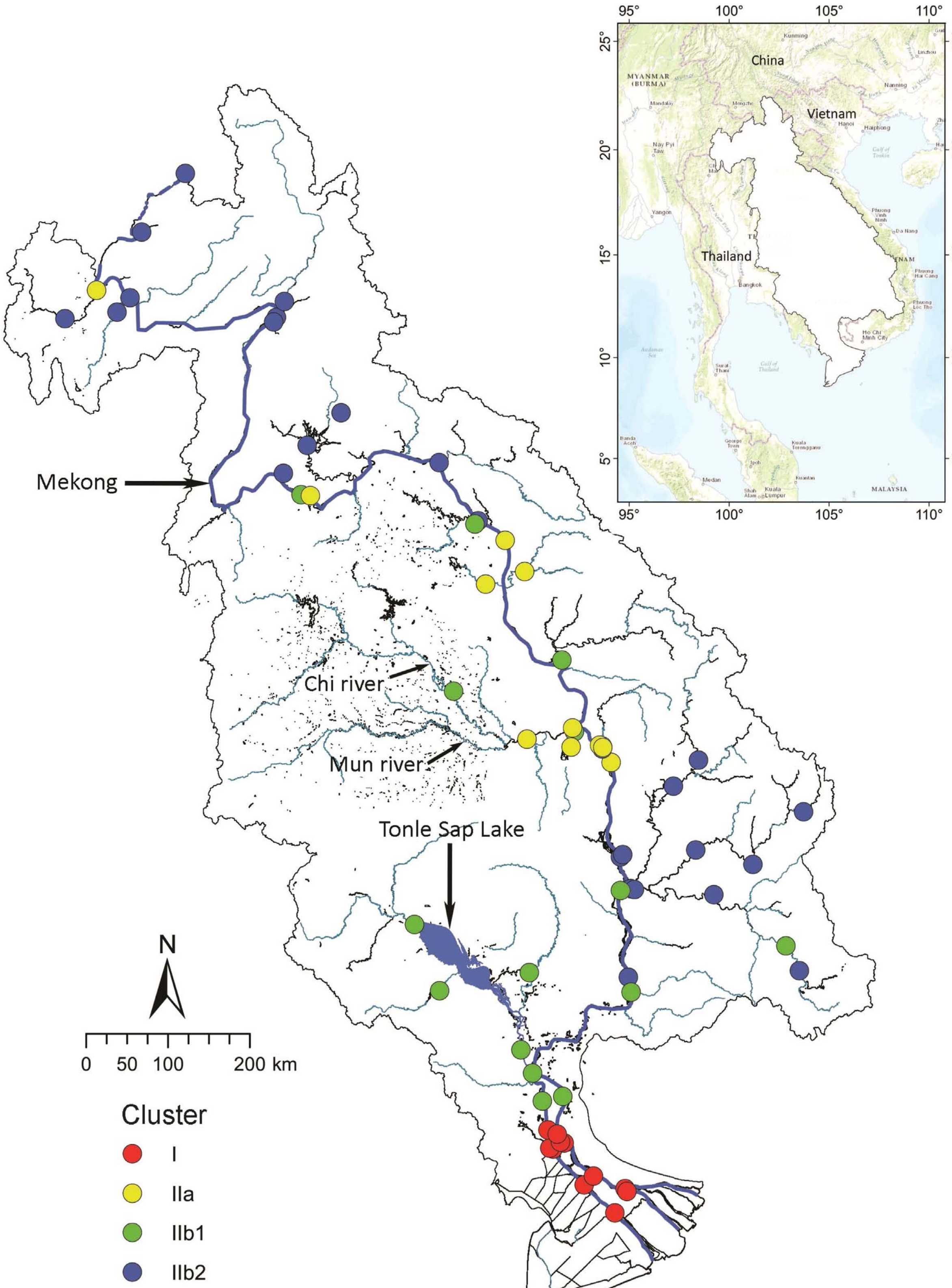

Fig. 1. Sampling sites and the four clusters, representing four macroinvertebrate assemblages, based on the cluster analysis.

mental gradients. Many studies have shown that in the upstream regions, the invertebrate communities are mainly characterized by a high abundance of insects (e.g. Ephemeroptera, Odonata and Trichoptera) (Arab et al., 2009; Collier and Lill, 2008; Jiang et al., 2013), whereas the downstream communities are characterized by a high abundance of molluscs, crustaceans and worms (Arscott et al., 2005;

Collier and Lill, 2008; Pérez-Quintero, 2011). This spatial variation in macroinvertebrate community composition is influenced by trophic variables, e.g. trophic level or food sources (Cai et al., 2012; Nicola et al., 2010); water chemistry, e.g. dissolved oxygen, water conductivity, pH (Al-Shami et al., 2013; Heino, 2009; Kumar and Khan, 2013) and physical river conditions, e.g. river depth, river width, size of catchment area and characteristics of land cover (Allan, 2004; Beisel et al., 1998; Chadwick et al., 2006; Cortes et al., 2013).

The Lower Mekong Basin (LMB) is characterized by a long and large floodplain (Eastham et al., 2008) and is known for its high biodiversity (Sodhi et al., 2004). However, the knowledge of macroinvertebrates in the LMB is limited. Given that this river basin is being impacted by various anthropogenic disturbances such as agricultural activities, aquaculture, urbanization and mining (Köhler et al., 2012; Nhan et al., 2007; Sodhi et al., 2004), there is an urgent need to understand the patterns of spatial organization and community structure of macroinvertebrates in this basin and their relation to environmental factors. Up to date, only a few studies have been published on the basin, e.g. community structure and composition of littoral invertebrates in the Mekong delta (Wilby et al., 2006), the diversity and distribution of crustaceans and molluscs in the Indo-Burma region (Cumberlidge et al., 2011; Köhler et al., 2012), and the assessment of water quality using physicochemical variables and benthic macroinvertebrates in the Chi river in Thailand (Kudthalang and Thanee, 2010). Yet, no attempt has been made to examine the spatial patterns of macroinvertebrate assemblages and their relation to key environmental variables at a large scale.

The objectives of the present study were i) to investigate patterns of spatial variation in macroinvertebrate assemblages in the Lower Mekong Basin, ii) to analyse the variability of macroinvertebrate composition among the assemblages, and to determine their key indicator taxa (the most representative taxa) for particular assemblages, and iii) to identify the important environmental variables that are associated with the macroinvertebrate assemblages in the basin. We expected that physical conditions of habitats, compared to other measured variables, have a strong correlation to the composition and diversity of macroinvertebrate assemblages.

2. Materials and methods

2.1. Study area

The Mekong River Basin (MRB) is divided into the Upper Mekong Basin (UMB) and the Lower Mekong Basin (LMB). The UMB on the Tibetan plateau in China is composed of narrow, deep gorges and small, short tributaries, whereas the LMB stretches from Yunnan province in South China to the delta in Vietnam and covers approximately 70% of the total length of the MRB (Eastham et al., 2008). The LMB consists of a large floodplain and long, broad tributaries and it drains more than 76% of the Mekong basin. The climate of the LMB is dominated by a tropical monsoon rainfall system, which is characterized by a dry (November − April) and a wet (May − October) season generated by the northeast monsoon and the southwest monsoon, respectively. The most intensive rainfall falls from July to September, while the lowest precipitation is observed between January and April (Adamson et al., 2009). The annual rainfall of the LMB varies from 1000–1600 mm in the driest regions to 2000–3000 mm in the wettest regions (Hoanh et al., 2003). A higher precipitation is found in the eastern mountainous regions of Laos and in northeast Thailand (Eastham et al., 2008).

The largest floodplain water body of the LMB is the Tonle Sap Lake (TSL) in Cambodia (Adamson et al., 2009), which is the largest freshwater lake in Southeast Asia (Sarkkula et al., 2003). The TSL is connected to the Mekong through the Tonle Sap River, and thus creating an exceptional hydrological cycle. In the wet season, the TSL receives an excess water from the Mekong River and expands its surface area from 2500 km^2 to 15,000 km^2. In the dry season when the rain ceases and water levels drop in the Mekong, a reverse flow occurs; the drained water from the TSL flows to the Mekong delta (Arias et al., 2011). The Mekong delta is characterized by a number of man-made canals, which are mostly used for domestic and agricultural activities (Kummu et al., 2008).

2.2. Data collection and processing

Benthic macroinvertebrates were sampled at 60 sampling sites along the main channel of the LMB and its tributaries by the Mekong River Commission (MRC) (Fig. 1). This sampling was carried out once a year in March during the dry season from 2004 to 2008. At each sampling site, macroinvertebrates were sampled from three locations in the benthic zone: near the left and right banks, and in the middle of the rivers. At each location, a minimum of three samples (where inter-sample variability is low, e.g. tributaries) and a maximum of five samples (where inter-sample variability is higher, e.g. the main channel and the delta) were collected using a Petersen grab sampler which has a sampling area of 0.025 m^2. With the grab sampler, four sub-samples were taken and pooled to give a single sampling unit covering a total area of 0.1 m^2. In total, between nine (3 samples × 3 locations) and fifteen (5 samples × 3 locations) pooled samples were collected at each sampling site. Each pooled sample was rinsed using a sieve (300 μm mesh size). In the field, the samples were sorted and then preserved by adding 10% formaldehyde to obtain a final concentration of about 5%. In the laboratory, they were identified to the lowest taxonomic level possible and counted using a compound microscope (40–1200 magnification) or a dissecting microscope (16–56 magnification). Macroinvertebrate abundance data per sampling unit was averaged across all samples (between 9 and 15 samples) collected from each sampling site.

At the sampling sites, geographic coordinates and altitude were determined with a GPS (Garmin GPS 12XL). River width was measured in the field using a Newcon Optik LRB 7 × 50 laser rangefinder. Other physical-chemical variables were measured at the three locations where macroinvertebrates were sampled. River depth was measured using a line metre. With a handheld water quality probe (YSI 556MP5), water temperature, dissolved oxygen, pH and water conductivity were measured at the surface (0.1–0.5 m) and at a depth of 3.5 m or at a maximum depth of the river (wherever less than 3.5 m) and then the average value was recorded for each location. Water transparency was measured with a Secchi disc by lowering it into the water and recording the depth at which it was no longer visible. The physical-chemical data of each sampling site was represented by the average value across the three sampling locations. The surface area and land cover data of watersheds drained at each sampling site were determined using a Geographic Information System (ArcGIS 10.4, ESRI). Geographic data (ArcGIS shapefiles) about the LMB (land cover types, river networks, basin boundaries and subcatchments derived from topographical maps) was provided by the MRC.

In total, 108 samples were collected from the 60 sampling sites. In 2008, 3 sampling sites were sampled further away from their original sampling coordinates, and thus we considered them as different sampling sites (see Supporting Information Appendix S1). Therefore, a total of 63 sampling sites were taken into account in the present study. Because of unequal sampling efforts (i.e. unequal and different number of samples at each site during the 5-year sampling period) and missing values of environmental variables, we used median values from the collected data to represent each site in our analysis, as suggested by McCluskey and Lalkhen (2007). More precisely, for the sites (49 sites) which were sampled only one time during the 5-year sampling period (see Appendix S1), the one sample collected from each site was used as the representative sample. The remaining 14 sites contained two samples (11 sites), three samples (2 sites) and four samples (1 site). From these 14 sites, the median values were used to represent the corresponding sites.

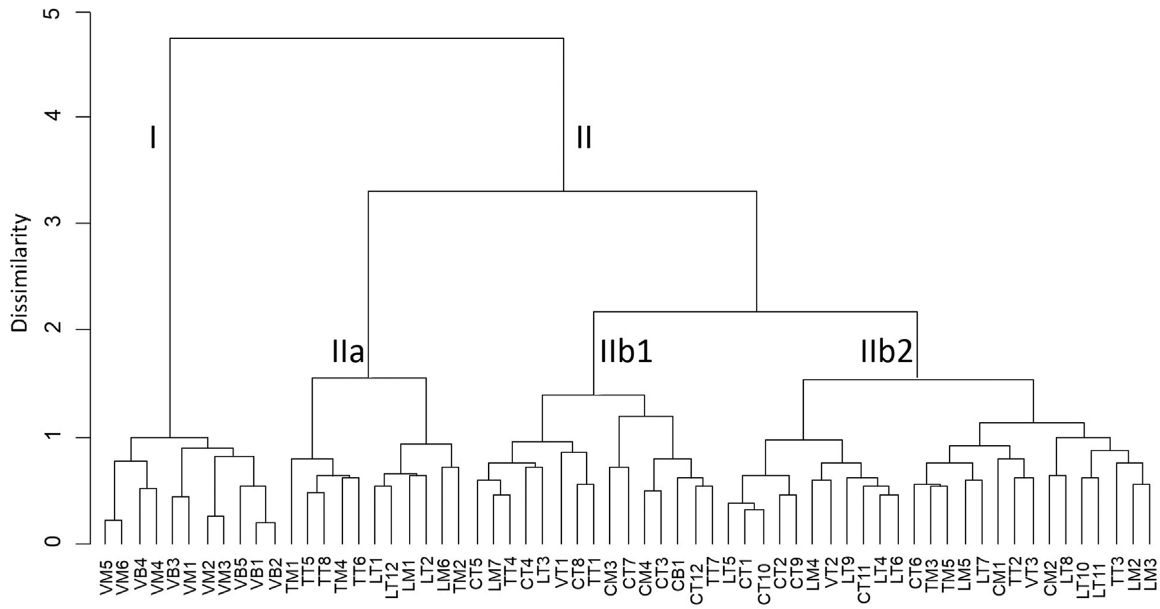

Fig. 2. Dendrogram showing sites belonging to the four clusters, representing four macroinvertebrate assemblages, based on the Bray-Curtis dissimilarity and Ward's hierarchical clustering method.

2.3. Data analysis

We used Ward's hierarchical clustering method to group the 63 sampling sites into different clusters. The Bray-Curtis dissimilarity distance (Legendre and Legendre, 2012) of macroinvertebrate samples between sites was calculated using the Hellinger transformation in the package "vegan" of R (Rao, 1995). Macroinvertebrate richness, abundance, Shannon-Wiener diversity were used to analyse the variability in macroinvertebrate assemblage composition among the different clusters. An "assemblage" of macroinvertebrates refers to different taxonomic groups (i.e. annelids, crustaceans, insects and molluscs) living in a given geographic area (e.g. a defined cluster) (Fauth et al., 1996). The indicator taxa of macroinvertebrate assemblages in the defined clusters were determined using the Indicator Value (IndVal, Dufrene and Legendre, 1997) with the package "labdsv" of R (Roberts, 2013). The Indicator Value of a taxon is an index ranging from 0 to 1, indicating the least to the most important taxa occurring in a group of sites. A value of 1 is obtained when every individual of the taxon is found only in the group and when it occurs in all sites of that group. A high number of taxa with significant Indicator Values may provide information on the habitat they prefer to share. Taxa having Indicator Values with a p-value ≤ 0.01 were retained as the most important taxa representing the assemblage in each cluster (consisting of a group of sites).

Significant differences in macroinvertebrate assemblage composition (i.e. richness, abundance, diversity) and in environmental conditions among different clusters were tested using a one-way ANOVA or a Kruskal-Wallis test. One-way ANOVA was applied when residuals of the models were normal (Shapiro-Wilk test, $p > 0.05$, and homoscedastic (Bartlett's test, $p > 0.05$)); otherwise, the non-parametric test (Kruskal-Wallis) was used. To evaluate the differences between clusters, multiple pair-wise comparisons were conducted using a Kruskal-Wallis test.

Linear Discriminant Analysis (LDA) was performed, using the package "ade4" of R (Chessel, 2006), to assess which measured environmental variables best accounted for the differences in macroinvertebrate assemblage composition among clusters grouped by the hierarchical clustering. Before performing the LDA, environmental variables were tested for multivariate homogeneity of within-group covariance (Borcard et al., 2011). The contribution of each variable to the discrimination between clusters was represented by the standardized factorial coefficient, projected as an arrow on the LDA plot. Cross-validation was used to evaluate the predictive performance of the LDA model. The overall quality of the model and the reliability of the prediction for the member of each cluster were evaluated by Cohen's Kappa Statistic (Kappa). All statistical analyses were performed in R (R Core Team, 2013).

3. Results

3.1. Macroinvertebrate diversity

Two hundred and ninety-nine macroinvertebrate taxa accounting for a total of 21,810 individuals were identified; of which, 131 taxa (44%) were insects, 98 (33%) were molluscs, 38 (13%) were crustaceans and 32 (10%) were annelids. The most commonly found insect orders were Diptera (37 taxa), Ephemeroptera (32), Odonata (22) and Trichoptera (20). For molluscs, most taxa belonged to the order Unionida (18), Veneroida (15) and Caenogastropoda (50); whereas for crustaceans, most taxa belonged to the order Decapoda (18) and Amphipoda (9). Annelids were mainly represented by the order Haplotaxida (15). Shannon diversity of macroinvertebrates at each site ranged from 0.8 to 3.3.

3.2. Macroinvertebrate assemblages and indicator taxa

Based on the Bray-Curtis dissimilarity and the hierarchical analysis, the 63 sites were grouped into four clusters (Fig. 2). Cluster I consisted of 11 sites located in the Mekong delta in Vietnam; cluster IIa, of 11 upstream sites in Laos and Thailand; cluster IIb1, of 15 sites mostly in middle part in Cambodia, a few sites in Laos and Thailand, and 1 site in Vietnam; and cluster IIb2, of 26 sites mostly located in the tributaries of the LMB (Fig. 1). The number of sampling sites and environmental variables characterizing each cluster are shown in Table 1.

The four clusters, which were later in the text considered as four different assemblages, had a significant difference in macroinvertebrate richness (Kruskal-Wallis $H = 27.7$, $p < 0.001$), abundance (Kruskal-Wallis $H = 23.7$, $p < 0.001$) and Shannon diversity (Kruskal-Wallis $H = 11.7$, $p < 0.01$) (Fig. 3, Table 1). The highest macroinvertebrate richness, abundance and diversity were found for assemblage I, followed by assemblage IIa and IIb1. The lowest macroinvertebrate richness, abundance and diversity were found for assemblage IIb2 (Fig. 3A and B, Table 1). Molluscs represented the highest proportion of

Table 1
Mean value (and standard deviation) for richness, abundance and Shannon diversity of macroinvertebrate assemblage and for environmental variables in each cluster.

	Cluster [n]							
Variable (unit)	I [11]		IIa [11]		IIb1 [15]		IIb2 [26]	
Assemblage composition								
Richness*	54	(13)$^{-\text{IIa},-\text{IIb1,2}}$	23	(11)	18	(7)	16	(9)
Abundance*	955	(526)$^{-\text{IIa},-\text{IIb1,2}}$	251	(184)	233	(204)	193	(286)
Diversity*	2.7	(0.7)$^{-\text{IIa},-\text{IIb1,2}}$	2.1	(0.5)	2.0	(0.5)	1.9	(0.4)
Physical-chemical								
Altitude (m)*	6.6	(1.8)$^{-\text{IIa},-\text{IIb2}}$	136	(77)	63	(67)$^{-\text{IIb2}}$	207	(1539)
River width (m)*	1057	(468)$^{-\text{IIa},-\text{IIb1,2}}$	413	(372)	349	(412)	339	(375)
River depth (m)*	11.5	(3.5)$^{-\text{IIa},-\text{IIb1,2}}$	5.0	(3.3)$^{-\text{IIb2}}$	5.0	(4.3)$^{-\text{IIb2}}$	2.5	(1.7)
Secchi depth (m)*	0.6	(0.2)$^{-\text{IIb2}}$	0.8	(0.4)	0.7	(0.5)	1.0	(0.7)
WT (°C)*	29.6	(0.5)$^{-\text{IIa},-\text{IIb2}}$	26.0	(2.1)$^{-\text{IIb1}}$	28.9	(1.6)$^{-\text{IIb2}}$	26.4	(3.7)
DO (mg/L)*	6.2	(1.2)$^{-\text{IIa},-\text{IIb2}}$	7.9	(0.5)$^{-\text{IIb1}}$	6.1	(1.7)$^{-\text{IIb2}}$	7.7	(0.7)
pH	7.8	(0.4)	7.6	(0.6)	7.5	(0.3)	7.6	(0.5)
WC (mS/m)*	17.8	(1.4)$^{-\text{IIa},-\text{IIb2}}$	22.8	(6.0)$^{-\text{IIb1}}$	13.5	(6.4)$^{-\text{IIb2}}$	14.2	(9.8)
SAW (km^2)*	764,797	(4714)$^{-\text{IIa},-\text{IIb1,2}}$	180,454	(202,943)	187,351	(276,932)	123,341	(196,952)
Land cover (%)								
Agricultural land*	25.77	(0.29)$^{-\text{IIb2}}$	24.56	(26.7)	28.14	(24.82)$^{-\text{IIb2}}$	11.68	(12.71)
Bamboo*	0.47	(0)	0.17	(0.22)$^{-\text{IIb2}}$	0.61	(1.37)	2.14	(3.6)
Crops	5.48	(0.03)	5.53	(3.71)	3.97	(3.09)$^{-\text{IIb2}}$	8.59	(7.62)
Deciduous forests	10.02	(0.13)	15.1	(26.54)	20.55	(18.28)$^{-\text{IIb2}}$	9.01	(15.44)
Evergreen forests*	14.07	(0.06)	10.03	(5.5)$^{-\text{IIb2}}$	14.07	(10.52)	20.35	(15.62)
Glacier	0.1	(0)	0.11	(0.14)	0.04	(0.08)	0.08	(0.14)
Grassland	11.6	(0.06)	11.55	(13.89)	5.96	(7.32)	10.76	(13.22)
Inundated*	0.39	(0.01)$^{-\text{IIa},-\text{IIb2}}$	0	$^{-\text{IIb1}}$	0.5	(0.96)$^{-\text{IIb2}}$	0	
Mix_evg.dec	8.99	(0.05)	12.82	(11.64)	9.68	(6.49)	8.79	(7.9)
Plantations*	0.17	(0)	0.03	(0.07)	0.2	(0.35)	0.17	(0.3)
Regrowth*	0.88	(0.01)	0.31	(0.3)$^{-\text{IIb2}}$	0.98	(1.1)	1.25	(1.58)
Rocks*	0.6	(0)	1.46	(3.34)$^{-\text{IIb1,2}}$	0.23	(0.31)	0.4	(0.54)
Urban areas*	0.08	(0)	0.51	(1.49)$^{-\text{IIb1,2}}$	0.07	(0.06)	0.07	(0.11)
Water surface*	1.18	(0.01)$^{-\text{IIb2}}$	0.82	(1.57)	1.18	(1.26)$^{-\text{IIb2}}$	0.42	(0.87)
Wetland*	0.07	(0.01)	0.02	(0.02)	0.09	(0.18)$^{-\text{IIb2}}$	0.01	(0.02)
Wood- & shrub-land*	17.23	(0.07)	14.05	(10.68)$^{-\text{IIb2}}$	12.5	(7.91)$^{-\text{IIb2}}$	24.38	(15.76)

WT: water temperature, DO: dissolved oxygen, WC: water conductivity, SAW: the surface area of watersheds, Mix_evg. dec: mixed evergreen and deciduous forests. The number of samples [n] in each cluster is indicated between square brackets. * indicates ANOVA and Kruskal-Wallis Test for significant differences among clusters at $p < 0.05$. Superscripts (IIa, IIb1, IIb2) indicate significant pair-wise comparisons between the corresponding cluster (each column) and superscript-labeled clusters (i.e. IIa, IIb1, IIb2) at $p < 0.05$.

richness and abundance for assemblage I and IIb1. For assemblage IIa and IIb2, insects represented the highest proportion, followed by molluscs. Crustaceans and annelids made up the lowest proportion of richness and abundance for assemblage IIa, IIb1 and IIb2, but they represented a higher proportion compared to insects for assemblage I (Fig. 3C and D).

The four assemblages were represented by a different number of indicator taxa: 53, 14, 2 and 2 taxa, for assemblage I, IIa, IIb1 and IIb2, respectively. Molluscs, crustaceans and annelids represented a relatively high number of indicator taxa compared to insects for assemblage I. The assemblage IIa was mostly represented by insects, while assemblages IIb1 and IIb2 were represented by two different indicator taxa. The detailed information on indicator taxa for each assemblage is provided in Table 2.

3.3. Relationship between macroinvertebrate assemblages and environmental variables

Most of the environmental variables showed significant differences between the four macroinvertebrate assemblages. The detailed information on the environmental differences between the assemblages is provided in Table 1. The results of the LDA used to discriminate the macroinvertebrate assemblages based on the physical-chemical and land cover types are shown in Fig. 4. The factorial axes 1, 2 and 3 respectively explained 65.7%, 23.1% and 11.2% of the total variance of the data. The global performance of the LDA was high (Kappa = 0.86). The predictive reliability (Kappa) for assemblage I, IIa, IIb1 and IIb2 was 0.90, 0.84, 0.80 and 0.90, respectively. Along axis 1, assemblage I was situated opposite to assemblage IIa and IIb2. Assemblage I was positively correlated with the surface area of watershed, river depth, river width and water temperature, but negatively associated with altitude and dissolved oxygen. Whereas assemblage IIa was positively correlated with water conductivity and urban areas, and assemblage IIb2 was positively linked to high altitude, dissolved oxygen, Secchi depth, wood-/shrub-land and evergreen forests. Based on axis 1 and 3, assemblage IIb1 was positively linked to inundated, wetland and agricultural areas (Fig. 4A–D).

4. Discussion

4.1. Spatial variation in macroinvertebrate assemblages and habitat characteristics

Macroinvertebrate assemblages can vary substantially according to habitat characteristics, particularly with large variations in habitat types and resources (Costa and Melo, 2008; Ilg et al., 2008; Vaughn and Hakenkamp, 2001). The combination of environmental factors such as water velocity, river depth, organic material load, watershed and substratum structure, together with the high amount of food resources and different water quality conditions found in the LMB (Chea et al., 2016), are responsible for determining macroinvertebrate assemblages (Al-Shami et al., 2013; Beisel et al., 1998; Lamouroux et al., 2014; Lorenz and Feld, 2013; Pan et al., 2014). Moreover, macroinvertebrate assemblages are also structured by different land cover characteristics, e.g. agricultural land, wood-/shrub-land and urban areas (Allan, 2004; Cortes et al., 2011, 2013). Therefore, these physical-chemical variables and land cover types are likely the main factors determining the spatial organization and composition of macroinvertebrate assemblages in this

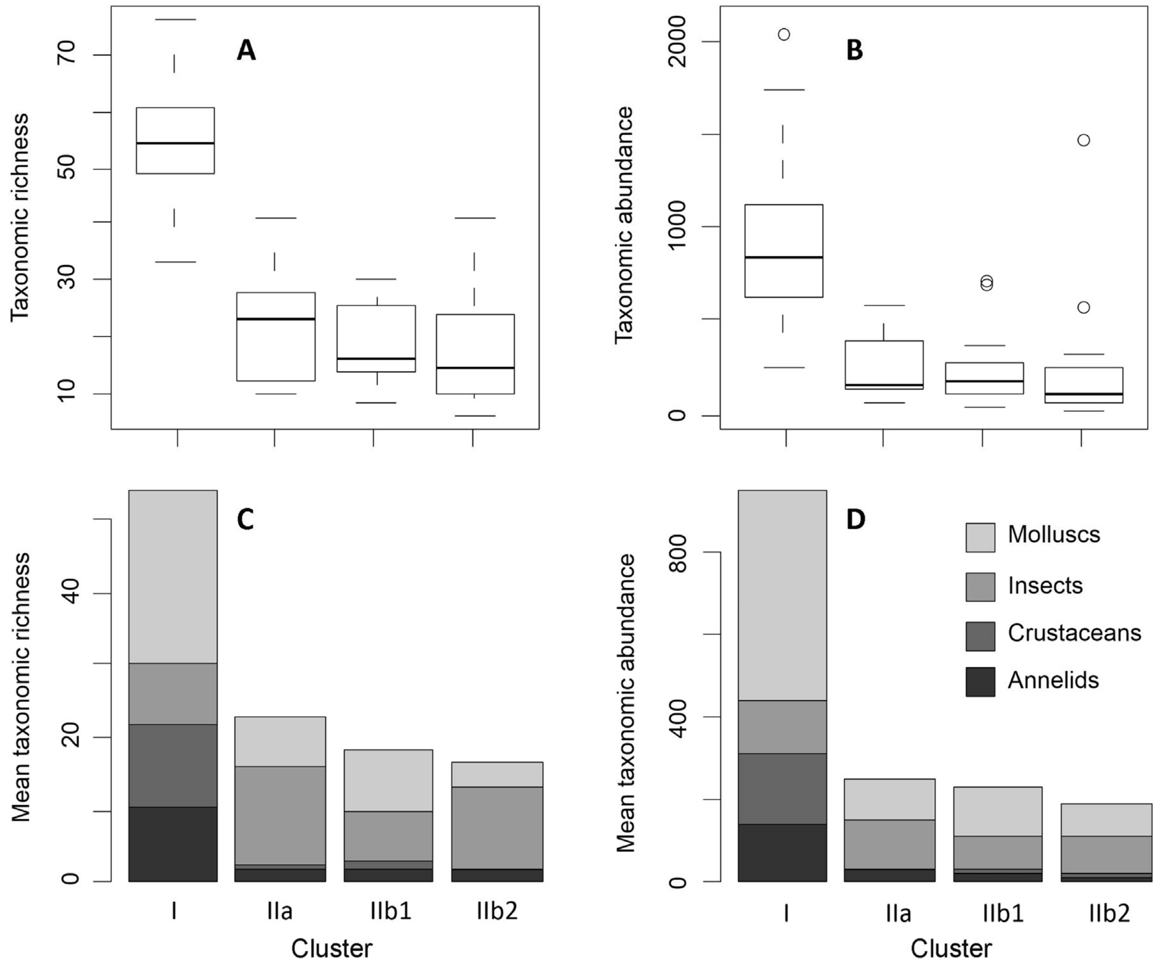

Fig. 3. Box and whisker plots of richness (A) and abundance (B) of macroinvertebrate assemblage in each cluster and its proportion of mean richness (C) and abundance (D) consisting of different taxonomic groups of macroinvertebrates.

large floodplain river.

The spatial organization of macroinvertebrate assemblages is mainly related to the relationship between habitat conditions and life-history traits at different spatial scales or along the longitudinal gradients of rivers (Collier and Lill, 2008; Tonkin et al., 2012). In this regard, key physical-chemical variables and land cover types can act as environmental filters, which allow the most suited taxonomic groups of macroinvertebrates to be present in each assemblage (Menezes et al., 2010). We found a higher insect richness and abundance for assemblage IIb2, which is mostly related to the tributaries and some sites of the main channel at the upstream parts. This assemblage is represented only by one insect and one annelid indicator taxon, which were widely distributed in the assemblage. This result suggests that natural stress in the mountainous and tributary system is probably too high for some taxa to occur (Feld and Hering, 2007). The fact that this assemblage was dominated by insects agrees with the expectation that insect orders mainly inhabit mountainous and shaded habitat regions (Ferrington, 2008; Heino, 2009; Suhaila and Che Salmah, 2014). The presence of evergreen forests, bamboo, crops and woody debris may provide food resources and egg deposition sites for many insect taxa (Medhurst et al., 2010; Sweeney, 1993). Clear water and a high level of dissolved oxygen found in high altitude streams characterize the tributaries, which are preferred by insect taxa (Collier and Lill, 2008; Dobson et al., 2002; Królak and Korycińska, 2008). Moreover, sampling sites in this assemblage are comparable to the Holarctic region where Diptera are more abundant (Ferrington, 2008), and are characterized by the increasing latitude where most Ephemeroptera occur (Pearson and Boyero, 2009).

Macroinvertebrate assemblage IIa was mainly related to the upstream sites situated along the main channel and some tributaries. In this assemblage, insects were also the dominant group in terms of richness, abundance and indicator taxa (7 out of 14 taxa, Table 2). However, annelid and mollusc indicator taxa were also found in this assemblage. A high water conductivity (22.8 ± 6 mS/m), resulting from anthropogenic disturbance (e.g. runoff from the surrounding agricultural areas and the discharge of urban wastewaters), could be one of the factors responsible for the community composition found, as it has been demonstrated that conductivity has a strong impact on macroinvertebrate diversity (Kumar and Khan, 2013; Lods-Crozet et al., 2001). The high contribution of insects to this assemblage could be explained by a high level of dissolved oxygen present at some sites (Table 1), as indicated in previous studies (Dobson et al., 2002; Królak and Korycińska, 2008), while disturbance-tolerant taxa of Oligochaeta and Gastropoda may be well adapted at sites having a high water conductivity (Feld and Hering, 2007; Wang et al., 2012). Moreover, the main channel generally provides a higher variation in habitats and a higher nutrient and sediment load, which are also favourable for annelids and molluscs (Haag and Warren-Jr., 1998).

In-between the upstream and downstream parts of the river basin, the macroinvertebrate assemblage was dominated by molluscs, followed by insects. Characteristics of sites in the mid-reaches such as rock and deciduous forests play an important role in supplying organic matter, which is preferred by snails (grazers) and insect collectors and shredders (Thorp and Delong, 1994). Many sites belonging to this assemblage that are located around the Tonle Sap Lake, Cambodia, are characterized by inundated, agricultural land and wetland (Fig. 4C and

Table 2
List of indicator taxa (and their indicator values, IndVal) of macroinvertebrate assemblage in each cluster.

Cluster I	IndVal	p-value
Annelid		
Aeolosoma bengalense	0.52	0.01
Aulodrilus prothecatus	0.67	0.005
Chaetogaster langi	0.85	0.005
Chaetogaster limnaei limnaei	0.6	0.005
Dero pectinata	0.67	0.005
Dero sp.	0.74	0.005
Dero sp.1	1	0.005
Dero sp.2	0.95	0.005
Lumbriculidae sp.	0.6	0.005
Namalycastis longicirris	0.9	0.005
Nectopsyche sp.	0.67	0.005
Orbinia johnsoni	0.52	0.01
Polydora sp.	0.67	0.005
Crustacean		
Corophium minutum	0. 8	0.005
Corophium sp.	0.67	0.005
Cyathura carinata	0.74	0.005
Cyathura truncata	0.57	0.005
Decapoda sp.	0.91	0.005
Eohaustorius sp.	0.6	0.005
Eohaustorius tandeensis	0.67	0.005
Gammarus sp.	0.6	0.005
Grandidierella lignorum	0.78	0.005
Grandidierella vietnamica	1	0.005
Hyale hawaiensis	0.67	0.005
Hyale sp.	0.85	0.005
Kamaka sp.	0.6	0.005
Macrobrachium equidens	0.6	0.005
Melita sp.	0.82	0.005
Palaemon curvirostris	0.6	0.005
Mollusc		
Afropisidium clarkeanum	0.73	0.005
Angulyagra polyzonata	0.6	0.005
Angulyagra sp.	0.9	0.005
Bithynia siamensis	0.67	0.005
Corbicula baudoni	0.87	0.005
Corbicula bocourti	0.74	0.005
Corbicula leviuscula	0.97	0.005
Corbicula moreletiana	0.86	0.005
Corbicula sp.	0.95	0.005
Gastropoda sp.	0.74	0.005
Hyriopsis bialatus	0.64	0.005
Limnoperna siamensis	0.99	0.005
Limnoperna sp.	0.95	0.005
Lymnaea viridis	0.94	0.005
Mekongia swainsoni swainsoni	0.67	0.005
Sinomytilus harmandi	0.9	0.005
Stenothyra annandalei	0.6	0.005
Stenothyra glabrata	0.85	0.005
Trochotaia trochoides	0.52	0.005
Insect		
Arigomphus sp.	0.67	0.005
Cricotopus sp.	1	0.005
Clinotanypus sp.	0.52	0.005
Monocorophium sp.	0.91	0.005
Sigara sp.	0.6	0.005
Cluster IIa	IndVal	p-value
Annelid		
Oligochaeta sp.	0.99	0.005
Polychaeta sp.1	0.6	0.005
Mollusc		
Corbicula sp.	0.88	0.005
Hubendickia sp.	0.6	0.01
Kareliania sp.	0.52	0.01
Scaphula sp.	0.52	0.01
Stenothyra sp.	0.6	0.005
Insect		
Anagenesia sp.	0.67	0.005
Caenoculis sp.	0.52	0.01
Caenodes sp.	0.74	0.005
Choropterpes sp.	0.51	0.005
Dipseudopsis sp.	0.69	0.005
Heterocloeon sp.	0.52	0.01
Micronecta sp.	0.6	0.005
Cluster IIb1	IndVal	p-value
Mollusc		
Filopaludina filopaludina filosa	0.45	0.025
Insect		
Pentagenia sp.	0.62	0.01
Cluster IIb2	IndVal	p-value
Annelid		
Naididae sp.	0.76	0.005
Insect		
Gomphidae sp.	0.56	0.01

D, Table 1). These site specific features could promote the richness and abundance of molluscs found at these sites. Moreover, it is noteworthy that the areas around the Tonle Sap Lake support a high mollusc production (Ngor et al., 2016). Therefore, it is not surprising that molluscs made up the largest proportion of the macroinvertebrate assemblage and that snail species were put forward as indicator species for this assemblage. The tributary sites that are located upstream, characterized by shaded areas and surrounded by large aquatic plants, are likely responsible for the second highest proportion of insect richness and abundance and the presence of an insect indicator taxon.

In the LMB, downstream sites were mainly associated with a large surface area of watersheds, large floodplains, wide and deep rivers. These conditions promote a high nutrient and sediment load from the upstream parts (Blair et al., 2004), which can support many species and a high abundance of macroinvertebrates (Cai et al., 2012; Nicola et al., 2010). Moreover, the high temperature related to the downstream sites may also enhance the richness and abundance of molluscs (Vaughn and Hakenkamp, 2001). High nutrient input and high temperature due to sunlight observed at the downstream delta provide optimal conditions for the phytoplankton community to reach a high abundance (Hecky and Kilham, 1988; Statzner and Higler, 1985; Vannote et al., 1980), which in turn enhance the richness and abundance of phytoplankton feeders such as molluscs (Vaughn and Hakenkamp, 2001). However, although the downstream assemblage was dominated by molluscs, annelids and crustaceans, dipteran insects (14 out of 33 occurring taxa) also made up a relatively high proportion. As a result, each taxonomic group in this assemblage is represented by many indicator taxa. This suggests that the downstream sites, the delta, provide good habitat conditions to support a diverse fauna. The high richness and abundance of all taxonomic groups and the high diversity in this assemblage might be explained 1) by the large surface area of the watershed and the large width and depth of the river, which may provide an optimal nutrient load and different mesohabitats and microhabitats, respectively (Al-Shami et al., 2013; Haag and Warren-Jr., 1998; Jacobsen et al., 1997; Mereta et al., 2012; Sedell et al., 1989), and 2) by a slow water flow, as reflected by the low change in altitude (6.6 ± 1.8 m) of the sampling sites, which may provide good habitat conditions for less-mobile taxa like molluscs, annelids and crustaceans (Castella et al., 1994; Haag and Warren-Jr., 1998).

The compositional and diversity differences found for the four macroinvertebrate assemblages were related to spatial environmental heterogeneity observed from the upstream to the downstream parts of the LMB (Dobson et al., 2002; Heino et al., 2005; Salmah et al., 2014; Wang et al., 2012). This can be explained by the proportion of the

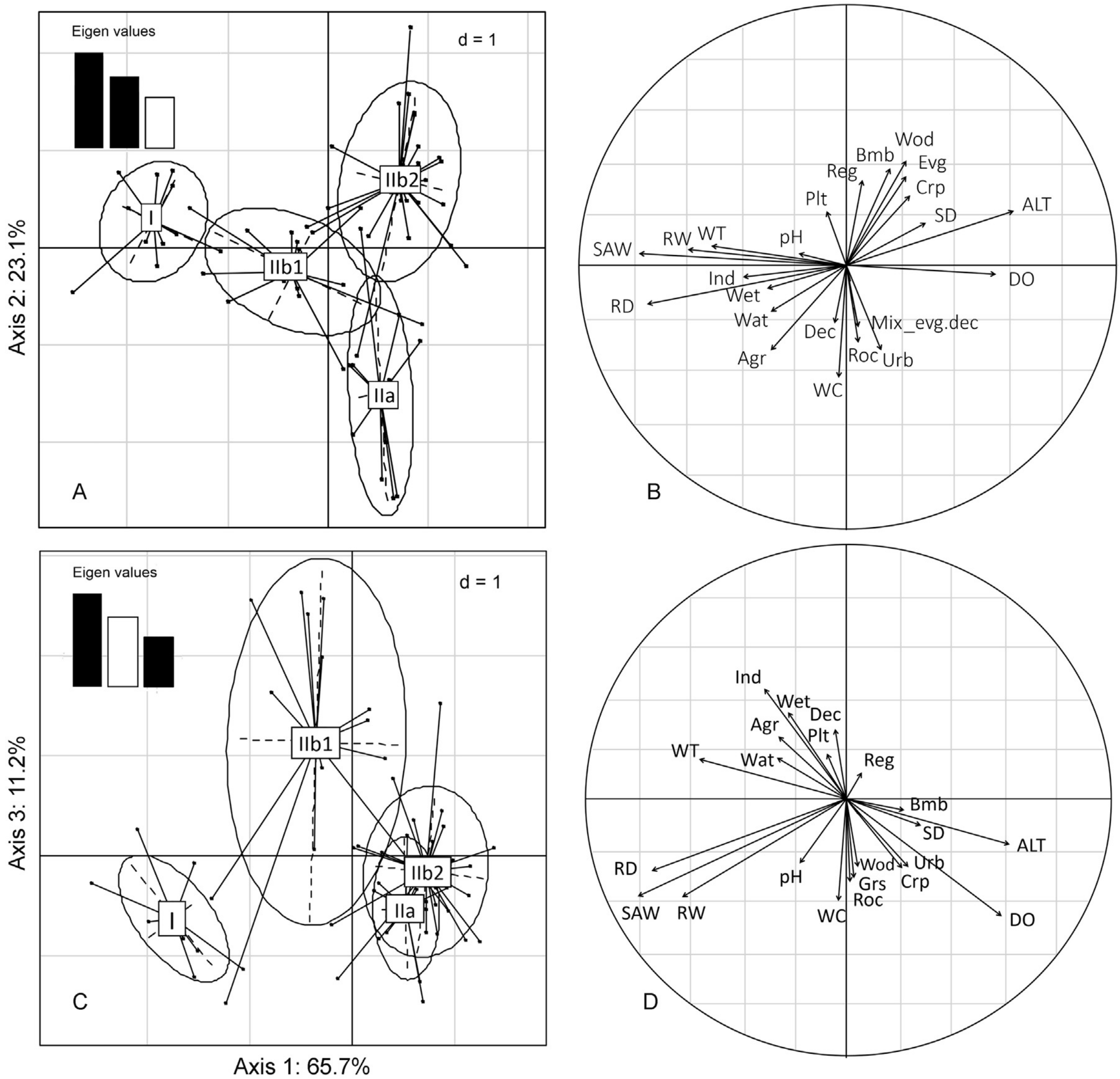

Fig. 4. Results from the LDA discriminating the four clusters (I, II, IIb1, IIb2), representing four macroinvertebrate assemblages, using Axes 1, 2 and 3 that explained the indicated percentage of the total variance in the data (A, C), and correlations of the environmental factors to the corresponding axes (B, D). ALT: altitude, RW: river width, RD: river depth, SD: Secchi depth, WT: water temperature, DO: dissolved oxygen, WC: water conductivity, SAW: the surface area of watersheds, Agr: agricultural land, Bmb: bamboos, Crp: crops, Dec: deciduous forests, Evg: evergreen forests, Grs: grassland, Ind: inundated, Mix_evg. dec: mixed evergreen and deciduous forests, Plt: plantations, Reg: regrowth, Roc: rocks, Urb: urban areas, Wat: water, Wet: wetland, Wod: wood- & shrub-land.

richness, abundance, diversity and the represented indicator taxa of the different taxonomic groups for each assemblage. Although assemblage IIa, IIb1 and IIb2 were characterized by a low and similar macroinvertebrate richness, abundance and diversity, each taxonomic group (i.e. annelids, crustaceans, molluscs and insects) contributed differently to the overall macroinvertebrate community composition for the particular assemblages. On the other hand, assemblage I had a high richness, abundance, diversity and a high number of indicator taxa. Therefore, these findings clearly suggested that the community composition of the four assemblages, particularly assemblage I, is distinctly organized and structured along the environmental gradients of the LMB.

4.2. Relationship between assemblages and key environmental variables

Site-specific characteristics, as mentioned above, are known to influence local community and composition of macroinvertebrates. At an assemblage level, connection in habitats and mesohabitats and variation in river morphology strongly affect community structure and composition from the upstream to the downstream parts of rivers (Mazão and Bispo, 2016; Thorp and Delong, 1994; Zilli and Marchese, 2011). Our study demonstrated that among the measured environmental variables, physical conditions and land cover types are the key factors determining macroinvertebrate assemblages along the LMB. These results support the previous finding that macroinvertebrate community structures in the Chishui river basin and in the river-connected lakes of the Yangtze river are strongly influenced and well predicted by physical habitat variables, e.g. water depth and altitude (Jiang et al., 2010; Pan et al., 2014). In other tropical/sub-tropical (Pearl and Qiangtang rivers, southern China) and temperate river basins (e.g. the Olo, Corgo, Pinhao and Tua rivers in northern Portugal), characteristics of land cover have been reported to better explain and predict benthic macroinvertebrate communities (Allan, 2004; Cortes et al., 2011, 2013).

In the LMB, the surface area of watershed, river depth and altitude are the most important variables discriminating the upstream assemblages (IIa and IIb2) from the downstream assemblage (I). This discrimination is clearly explained by the axis 1 of the LDA accounting for 65.7% of the total variance of the data and by a high predictive reliability for each particular assemblage. Because of the observed physical conditions, together with other related variables (e.g. water temperature, dissolved oxygen and land cover types), the assemblages were characterized by a very different community structure, composition and diversity.

The intermediate assemblage (IIb1) in-between was positively linked to three types of land cover: agricultural land, inundated and wetland. Along axis 3 of the LDA model, these land cover types are the key factors best explaining the macroinvertebrate composition of assemblage IIb1 (Fig. 4C and D). However, the proportion of inundated and wetland constituted a small percentage of the land cover, and together with agricultural land, they only explained a limited amount of the variance of the data for axis 3 of the LDA model (11.2%). As a result, the predictive performance for this assemblage (Kappa = 0.80) was not as high as the performance for the other assemblages. A broad range of values of physical-chemical variables (e.g. dissolved oxygen, river width and depth, the surface area of watershed and altitude) found at sites belonging to this assemblage could also explain the performance yielded. On the other hand, assemblage IIa was associated with two important factors (water conductivity and urban areas) according to the LDA axis 2, which explained a higher variance of the data (23.1%). Therefore, these two factors, together with other measured environmental variables, could correctly predict this assemblage with a higher reliability (Kappa = 0.85). The possible explanation for the association found is that many sites that belong to this assemblage are located along the tributaries (e.g. the Mun and Chi river basins in Thailand) and the main channel where cities were built. The tributaries are surrounded by intensified agriculture and the cities are exposed to a high level of anthropogenic disturbance (Dao et al., 2010; Kudthalang and Thanee, 2010). Therefore, the runoff from the surrounding agricultural areas and the discharge of urban wastewaters may cause the increase in water conductivity (Wetzel, 2001).

4.3. Recommendations for management of the LMB

Macroinvertebrate diversity is of great importance for ecosystem structure and functioning as it interacts with both biotic and abiotic factors. Crustaceans and insects are generally responsible for regulating decomposition, shredding detritus and bioturbation. Molluscs also contribute to bioturbation, sediment formation and filtering of water, while most annelids regulate decomposition and autotrophs although some of them also promote bioturbation and sediment formation (Palmer et al., 1997). The different processes enhanced by these taxa promote ecosystem functioning in the LMB, particularly in its lower reaches. Assemblage I, occupying the downstream part of the LMB, was characterized by a high macroinvertebrate diversity and was represented by a number of indicator taxa from each group of macroinvertebrates, which could be expected to increase ecosystem stability. These taxa are key components of the ecosystem and of the food web supporting a rich biodiversity of fish, which are a main source of proteins for local people. Thus, a change in the composition of one of these taxa may result in disproportionate or unexpected responses of other taxa in the LMB (Naeem, 1998), and consequently alter ecological processes (Covich et al., 1999) such as organic matter processing (Palmer et al., 1997).

For management purposes, indicator taxa identified in this study representing the ecological importance of each site and each community are of great significance. By using the results of this study such as the indicator taxa and the correlated environmental factors for each assemblage, habitat quality and suitability for the most vulnerable native taxa could be more conveniently monitored, which could provide an advantage for decision-making concerning conservation and management of these keystone taxa. Moreover, this study can serve as a baseline for future research in a biodiversity hotspot region that has not been investigated intensively.

5. Conclusion

The macroinvertebrate assemblages in the Lower Mekong Basin (LMB) were characterized by an increasing richness, abundance and diversity from the upstream to the downstream sites. Sites located in the upper tributaries (cluster IIb2) and upper main channel (cluster IIa) were characterized by a high altitude, high levels of dissolved oxygen, a high water conductivity, large fractions of wood-/shrub-land and evergreen forests. Macroinvertebrate assemblages in these two clusters were dominated by insects. In the Mekong delta (cluster I), the macroinvertebrate assemblage largely consisted of a great number of molluscs and an average number of annelids, crustaceans and dipteran insects. This assemblage could be discriminated based on a large surface area of watershed, the river depth and width and a high water temperature. The assemblage (cluster IIb1) found in-between the tributaries and the upper main channel and the delta region was associated with sites characterized by inundated, wetland and agricultural land and was represented most by molluscs. Overall, our study found that the number of macroinvertebrate taxa and the diversity remain relatively high across the basin, especially in the delta region which can be considered a hotspot zone for biodiversity. Therefore, the LMB deserves a particular attention for conservation.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.limno.2017.04.001.

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