Original Articles

Uniqueness of sampling site contributions to the total variance of macroinvertebrate communities in the Lower Mekong Basin

Ratha Sor[a,b,*], Pierre Legendre[c], Sovan Lek[a]

[a] *Laboratoire Evolution & Diversité Biologique, UMR 5174, CNRS - Université Paul Sabatier -Toulouse 3, 118 route de Narbonne, 31062 Toulouse cédex 4, France*
[b] *Department of Biology, Faculty of Science, Royal University of Phnom Penh, Russian Boulevard, 12000, Phnom Penh, Cambodia*
[c] *Département de Sciences Biologiques, Université de Montréal, C.P. 6128, Succursale Centre-ville, Montréal, Québec, H3C 3J7, Canada*

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ABSTRACT

Species co-occurrence and site-specific characteristics have a great influence on biotic community composition at local scales and thus contribute to large variations at broad spatial scales. In this paper, we studied invertebrate communities in 63 river sites of the Lower Mekong Basin (LMB) sampled over 609 thousand km^2. We identified important macroinvertebrate taxa of the component communities (i.e. annelids, crustaceans, mollusks and insects), and key geo-environmental factors that explained the total variance (BD_{Total}) of the communities at large spatial scale. We used the *"Species Contributions to Beta Diversity"* (SCBD) and *"Local Contributions to Beta Diversity"* (LCBD) approaches to partition total beta diversity (BD_{Total}), identified the important macroinvertebrate taxa (those with high SCBD indices), and estimated the uniqueness of sites in community composition (LCBD indices). SCBD indices showed which taxa were the most important in structuring the four component communities: there were 29 insect taxa, which mainly characterized the upstream sites, and 18 mollusk, 7 annelid and 6 crustacean taxa, which all represented the downstream sites. We used linear regression models to investigate the influence of geo-environmental factors and of component communities on LCBD indices. Our results showed great variation in composition within the LMB (BD_{Total} = 0.80 on a 0-to-1 scale). Five sites of the main channel exhibited significant uniqueness (LCBD indices) in community composition. One of them was a hotspot location occupied by a community with exceptional taxonomic composition, which should be protected. Four other sites were degraded by human activity and in need of restoration. Multiple regressions indicated that the global LCBD indices are better explained by the environmental factors, i.e. water conductivity, river depth and Secchi depth (adjusted R^2 = 0.26), than by the geographical factors. Among the component communities, mollusks' and insects' LCBDs were the determinants responsible for the variation in the global LCBD indices (adjusted R^2 = 0.84). The uniqueness in community composition of the sites (i.e. LCBDs) that we estimated provides useful ecological information, which could be used to support restoration and conservation planning for the LMB.

1. Introduction

The variation in community composition among sites, or beta (β) diversity (Legendre and De Cáceres, 2013; Whittaker, 1960), is of primary interest to community ecology. Beta diversity is an important component of biodiversity as it links local (α) to regional (γ) diversity, and it varies as a function of the spatial scales and gradients of the study areas (Anderson et al., 2011; Legendre and Legendre, 2012; Whittaker, 1972, 1960). Therefore, understanding the variation in species composition among sites, i.e. β diversity, enables community ecologists to disclose evolutionary and ecological processes at work in a community

of interest (Valdujo et al., 2013), by analyzing and testing such processes in a way that indicates how they affect and maintain biodiversity in the ecosystems (Legendre and De Cáceres, 2013).

Co-occurrence of species within their own taxonomic group or between different taxonomic groups is one of the factors that can lead to different patterns of β diversity (Hillebrand and Blenckner, 2002; Tonkin et al., 2015), and thus affect ecosystem functioning. Environmental gradients, habitat heterogeneity (López-González et al., 2015), and natural and human-derived disturbances (Lamy et al., 2015; Legendre and Salvat, 2015) have been shown to also influence β diversity. For aquatic macroinvertebrates, β diversity is mainly related to

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drainage basins and within-stream environmental factors, while it has been reported not to be significantly related to habitat degradation, eutrophication, longitude and altitude (Friberg et al., 2010; Md Rawi et al., 2013). However, longitude and altitude have been found to be substitute variables (proxies) for major drivers patterning β diversity of macroinvertebrates at broad geographical scales (J. Wang et al., 2012). The environmental variables related to the geographical proxies may play important roles in structuring the broad-scale pattern of β diversity in a given region.

Several papers have reported patterns of β diversity in tropical ecosystems for plants and vertebrate animals (e.g. Legendre et al., 2009; López-González et al., 2015; Mena and Vázquez-Domínguez, 2005; Wearn et al., 2016). β diversity of macroinvertebrates has also recently been analyzed by several authors (e.g. Costa and Melo, 2008; Leigh and Sheldon, 2009; Ligeiro et al., 2010), but only a few studies have taken place in South-East Asia (e.g. Al-Shami et al., 2013; Salmah et al., 2014). As the ecosystems in that region are highly endangered and heavily impacted by human disturbances (Salmah et al., 2014; Sodhi et al., 2004; Strayer and Dudgeon, 2010), assessing the patterns of macroinvertebrate β diversity and their relationships to geo-environmental factors and to related biotic communities is urgently needed.

The Mekong River Basin is divided into Upper and Lower Mekong Basins (LMB). The LMB, covering an area of about 609,000 km^2 (77% of the whole basin) (Zalinge et al., 2003), includes portions of four densely populated countries: Thailand, Laos, Cambodia and Vietnam. This basin harbors diversified communities of fish and invertebrates, forming biologically important food webs that support high biodiversity (Sodhi et al., 2004). Many aquatic taxonomic groups such as fishes, mollusks, crustaceans and insects are highly dependent on this basin as a breeding ground (Davidson et al., 2006; Zalinge and Thuok, 1998). In spite of high suspected biodiversity in the LMB, the β diversity and community patterns of its aquatic taxonomic groups, particularly the macro-invertebrates, have seldom been studied. The biomonitoring surveys conducted by the Mekong River Commission (MRC) represent the only major work conducted on aquatic macroinvertebrates in the LMB. In this study, we used this biomonitoring data to explore the β diversity pattern of aquatic macroinvertebrates. Analyzes of this dataset, collected from sites sampled over 5 successive years (2004–2008), should significantly contribute to increase our scientific knowledge of the LMB.

Beta diversity can be computed in different ways (Koleff et al., 2003; Whittaker, 1960). A classical approach is to compute β diversity as $\beta = \gamma / \overline{\alpha}$, where γ is the total number of species in a given region and $\overline{\alpha}$ is the average number of taxa for a sample set within the region (Whittaker, 1960). This classical measurement is still preferred by many authors (Higgins, 2010; Jost, 2007; Sor et al., 2015) although new approaches have been developed (Anderson et al., 2011; Legendre et al., 2005; Legendre and De Cáceres, 2013).

In this study, we used the total variance of the macroinvertebrate communities among the study sites of the LMB as a measure of beta diversity (BD$_{Total}$) and partitioned it into "*Local Contributions to Beta Diversity*" (LCBD) and "*Species Contributions to Beta Diversity*" (SCBD) (Legendre and De Cáceres, 2013). We identified the important taxa contributing most to total β diversity, i.e. those with high among-site variance, as well as the geo-environmental factors that were associated with the macroinvertebrate communities throughout the sites. In addition, we investigated the influence of the LCBD indices of the component communities (i.e. annelids, crustaceans, mollusks and insects) on the LCBD indices of the global macroinvertebrate community composition (including all component communities). Our questions of interest are the following: 1) Is there a moderate or a large amount of variation in macroinvertebrate community composition among the sites in the LMB? 2) What are the taxa that contribute most to the total β diversity? We expect the important taxa of annelids, crustaceans and mollusks, measured as richness and abundance, to be associated with sites located downstream, whereas the important taxa of insects should be associated with sites located farther upstream, as has been shown by

Arscott et al. (2005) and Królak and Korycińska (2008). 3) Are there sites that have exceptionally unique taxonomic compositions? We hypothesize that some sampling locations exhibit significant uniqueness in taxonomic composition. 4) What are the geo-environmental conditions that characterize the sites with significant LCBD indices? We expect the LCBD indices to increase with river width and pH, following the β diversity patterns found in tropical streams in Malaysia (Al-Shami et al., 2013), and decrease with latitude and altitude, following the β diversity patterns observed in major geographical diversity gradients (J. Wang et al., 2012). 5) What are the component communities that mainly influence the LCBD indices of the global macroinvertebrate communities?

2. Materials and methods

2.1. Macroinvertebrate and geo-environmental variables collection

From 2004 to 2008, the Mekong River Commission (MRC) conducted biomonitoring surveys and sampled macroinvertebrates at 60 sites along the LMB once a year in March during the dry season (Fig. 1). To harmonize the data being collected, the sampling locations were selected from different habitats such as those in or close to villages or towns, at rivers with substantial shipping, next to crop fields and meadows with livestock, upstream or downstream of dams or weirs, and at more pristine areas surrounded by forest with only few houses. At each sampling site, benthic macroinvertebrates and geo-environmental variables were collected at the same time. For the detailed information on the collection process, we refer to Sor et al. (2017).

In 2008, 3 sampling sites were sampled farther away from their original sampling coordinates, and thus they were regarded as new sampling sites (see Appendix S1 in Supplementary material). Therefore, we considered a total of 63 sampling sites in the present study.

2.2. Data processing and statistical methods

For the 63 sampling sites, 108 samples of biological and geo-environmental variables were available. Due to unequal sampling efforts, a small number of sites were sampled only once, twice or thrice during the 5-year sampling period. Since this is the first survey of macro-invertebrates ever conducted in the LMB and the sampling protocol insured that the collected samples were comparable among sites, these data are important to obtain a first assessment of beta diversity. Therefore, we used median values from data collected on macro-invertebrate and geo-environmental variables to represent each site in our analyzes, as suggested for small sample size by McCluskey and Lalkhen (2007). The community composition data was partitioned into a global macroinvertebrate community data table (including all component communities), and component community data tables (for annelid, crustacean, mollusk and insect communities).

The community composition data were Hellinger-transformed at the beginning of the analyzes (Legendre and Gallagher, 2001; Legendre and Legendre, 2012). For Hellinger-transformed data, the total variance, or total β diversity (BD$_{Total}$), of a community composition data table is an index between 0 and 1, and it can be partitioned into local contribution (LCBD) and species contribution (SCBD) indices. An LCBD value is an index showing the degree of uniqueness in taxonomic composition in each site, computed as the relative contribution of a site to BD$_{Total}$, so that the LCBD indices sum to 1, whereas an SCBD index shows the relative degree of variation of a taxon across all sites. The BD$_{Total}$, LCBD and SCBD indices were computed using the function "beta.div" available in the *adespatial* package in R (Dray et al., 2016). The Hellinger transformation was used because the corresponding Hellinger distance is one of the dissimilarity functions admissible for beta diversity analyzes (Legendre and De Cáceres, 2013; Legendre and Gallagher, 2001); it does not give high weights to the rare species. To identify significant uniqueness in taxonomic composition of the sampling sites, the LCBD indices were tested for significance against a significance level
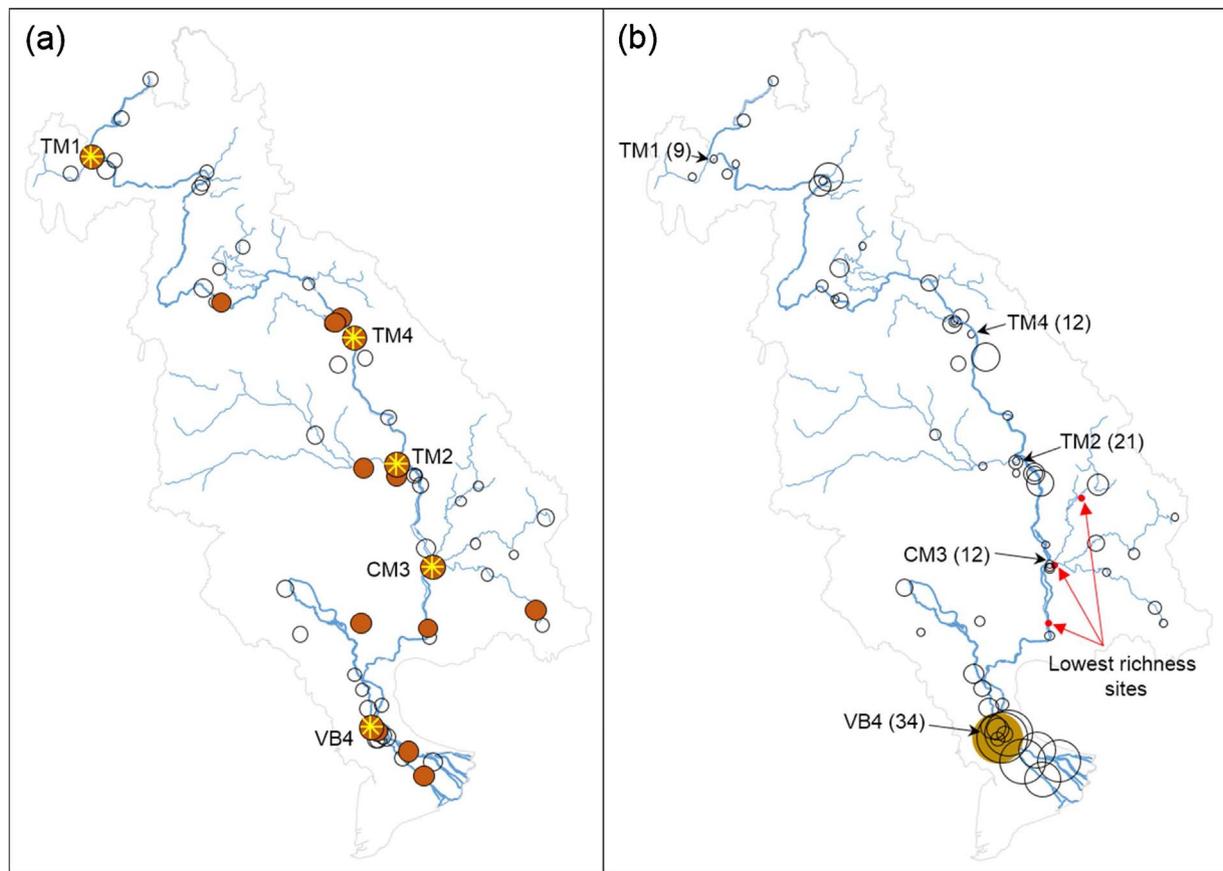
Fig. 1. Map of the sampling sites in the Lower Mekong Basin (LMB). (a) LCBD indices with significant p-values uncorrected (shaded circles) and corrected for multiple testing by applying Holm correction (shaded circles with star); open circles: non-significant LCBD indices. (b) Richness (number of taxa) of the sampling sites. Three red dots indicated with red arrows: lowest richness, 6; large shaded circle: highest richness, 74. The richness for the five sites having significant LCBD indices is shown in the parentheses. The sizes of the circles are proportional to LCBD (a) or richness (b) values. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

$\alpha = 0.05$. The p-values were corrected for multiple testing using the Holm correction to reduce the experimentwise type I error rate of multiple tests. In addition to LCBD, Hellinger-transformed data also allow researchers to compute SCBD indices; this is not allowed by most other admissible dissimilarity functions (Legendre and De Cáceres, 2013; Legendre and Gallagher, 2001). In the following paragraphs, BD_{Total}, LCBD and SCBD designate the indices of the global macro-invertebrate communities, whereas BD_{ATotal}, BD_{CTotal}, BD_{MTotal}, BD_{ITotal}, and $LCBD_A$, $LCBD_C$, $LCBD_M$ and $LCBD_I$ designate the BD_{Total} and LCBD indices for annelid, crustacean, mollusk and insect communities, respectively.

SCBD indices that were higher than the mean of SCBD values identified the taxa that were the most important contributors to BD_{Total}. Before associating these important taxa with the geo-environmental factors, we normalized these variables using the indications provided by function "boxcoxfit" in the *geoR* package in R (Ribeiro Jr and Diggle, 2015). The Box-Cox transformation was performed on the geo-environmental variables because this transformation attempts to normalize the variables, thus meeting the assumptions of linear models and residuals' normal distributions (Ahola et al., 2011). Then, we conducted a Redundancy Analysis (RDA, Legendre and Legendre 2012) on the Hellinger-transformed abundance data. To identify which component community was more related to which part (downstream or upstream) of the LMB, we computed Pearson correlations between the richness (number of taxa) and abundance (number of individuals) of the important taxa pertaining to each component community, on the one hand, and the geographical factors on the other hand.

We independently ran simple and multiple regression analyzes to determine which, among the geographical and environmental variables,

mainly accounted for the variation of the LCBD indices. To identify the strength of the regression models, we computed stepwise selection with the Akaike Information Criterion (AIC). The models having the lowest AIC and highest adjusted R^2 were considered to have the strongest influence on the LCBD indices. To investigate the influence of component communities on the LCBD indices, we computed $LCBD_A$, $LCBD_C$, $LCBD_M$ and $LCBD_I$, and regressed the LCBD indices (for the global communities) on the LCBD indices of the four component communities. We computed four types of linear regression models: 1) Simple regression models, e.g. LCBD ~ $LCBD_A$; 2) 2-component multiple regression, e.g. LCBD ~ $LCBD_A$ + $LCBD_C$; 3) 3-component multiple regression, LCBD ~ $LCBD_A$ + $LCBD_C$ + $LCBD_M$ and 4) all-component multiple regression, LCBD ~ $LCBD_A$ + $LCBD_C$ + $LCBD_M$ + $LCBD_I$. Model selection, based on the AIC, was conducted to obtain a descriptive assessment of the components that contribute most to the variation of the global LCBD indices. All statistical analyses were performed in R (R Core Team, 2013).

3. Results

3.1. General macroinvertebrate composition and environmental variables

In total, 21,810 individuals representing 299 taxa and 90 families were identified in the dataset (see Appendix S2 in Supplementary material). Taxonomic richness was highest at the Mekong delta sites (Fig. 1). Among the taxa, 32 belonged to annelids (2,672 individuals), 38 to crustaceans (2,054), 98 to mollusks (10,603) and 131 to insects (6,481). The most common families of annelids were Naididae (47% of occurrence) and Nereididae (16%); of crustaceans were Palaemonidae (26%) and Corophiidae (16%) and of mollusks were Unionidae (18%),

Table 1

Observed environmental factors, richness (number of taxa) and abundance (number of individuals) of macroinvertebrates across the 63 sampling sites.

Variables	Unit	Min	Max	Mean	Standard deviation
Altitude	m	3	546	127	132
Water temperature	°C	17	31	27	3
Dissolved oxygen	mg/L	2.7	9.3	7.4	2.6
Water conductivity	mS/m	3.9	66.6	17.9	11.9
River width	m	11	1629	467	466
River depth	m	0.4	15	4.8	3.9
Secchi depth	m	0.2	3	0.9	0.6
pH	–	6.8	8.4	7.6	0.6
Richness	taxa/sample	6	74	23	16
Abundance	individuals/ sample	13	1997	315	396

Corbiculidae (14%), Viviparidae (12%) and Stenothyridae (9%). Insect communities were characterized by Diptera (28%), Ephemeroptera (24%), Odonata (17%) and Trichoptera (15%).

Three taxa were most widely distributed; two belonged to insects: *Ablabesmyia* sp. (73% occurrence) and *Polypedilum* sp. (70%) and one was a mollusk, *Corbicula tenuis* (67%). In addition to being widely distributed, these 3 taxa were among the top 10 most abundant. Of the total individuals, *Ablabesmyia* sp. accounted for 2.9%, *Polypedilum* sp. for 3.8%, whereas the 3 most abundant species, *Corbicula leviuscula*, *Limnoperna siamensis* and *Corbicula tenuis*, accounted for 8.4%, 6.1% and 5.8%, respectively. The data on taxonomic richness and abundance, and the environmental variables are summarized in Table 1.

3.2. Beta diversity and important taxa − habitat relationship

The total β diversity of macroinvertebrates in the LMB was $BD_{Total} = 0.80$, and there was a total of 60 taxa contributing most to the BD_{Total}. The value of BD_{Total} is very high, considering that the maximum that can be obtained for Hellinger-transformed data is 1, when all sites have entirely different species compositions. This great variation was also observed for each component community: annelids ($BD_{ATotal} = 0.72$), mollusks ($BD_{MTotal} = 0.78$) and insects ($BD_{ITotal} = 0.74$), excepted for crustaceans ($BD_{CTotal} = 0.38$). Over all 299 taxa, 60 important taxa had SCBD indices larger than the mean SCBD (0.003), 29 of which belong to insects, 18 to mollusks, 7 to annelids and 6 to crustaceans (see Appendix S3 in Supplementary material). The SCBD values are small because the SCBD indices are relative to the total sum of squares in the community composition table and sum to 1. SCBD indices indicate taxa that have the highest variance across sites. The 3 highest SCBD indices belonged to insect taxa: *Polypedilum* sp. (0.054), *Ablabesmyia* sp. (0.039), *Cryptochironomus* sp. (0.037), followed by *Corbicula tenuis* (mollusk, 0.037), *Goeldichironomus* sp. (insect, 0.035) and *Corbicula leviuscula* (mollusk, 0.034).

Based on the correlation analyzes, the richness and abundance of the important taxa of annelids, crustaceans and mollusks were significantly and negatively correlated with latitude and altitude; the richness and abundance of the important taxa of insects were significantly and positively correlated with latitude and altitude (Table 2). As the Mekong River generally runs from north to south, decreasing latitude and decreasing altitude are both associated with going downstream.

The first two axes of the RDA model (Fig. 2a, b) accounted for 15.7% of the total variance of the community of important taxa. Axis 1 (9.4%) of the plot showed the river gradients opposing river depth and river width (left of the plot), which were strongly associated with communities in the Mekong delta, to altitude and latitude, which were associated with communities in the upstream sites. Along axis 2 (6.3%), the communities from some tributaries and main channel sites located upstream in the LMB (Thailand and Laos) were found in the positive part of the axis and associated with high values of dissolved oxygen, while many other tributary sites were found in the lower part of the axis and related to high values of Secchi depth.

3.3. Uniqueness in taxonomic composition and its association with geo-environmental factors

Five sampling sites exhibited significant global LCBD indices at the $p = 0.05$ level after Holm correction for multiple testing. These sites were CM3 (LCBD = 0.023, $p = 0.006$), TM2 and TM4 (LCBD = 0.021, $p = 0.006$), and TM1 and VB4 (LCBD = 0.020, $p = 0.012$) (Fig. 1). CM3 also exhibited significant LCBD indices for all component communities (LCBD$_A$ = 0.026, $p = 0.032$; LCBD$_C$ = 0.038, $p = 0.006$; LCBD$_M$ = 0.023, $p = 0.006$; LCBD$_I$ = 0.027, $p = 0.006$). LCBD indices of the global communities and of component communities, which indicate the uniqueness in taxonomic composition at the sites, are provided in Appendix S4 in Supplementary material. LCBD values are scaled to add up to 1 over the whole study; the mean LCBD value in this study was thus $1/63 = 0.016$.

Results of the simple and multiple regressions between the global LCBD indices and geo-environmental variables are shown in Table 3. Only water conductivity, river depth and Secchi depth were significantly associated with the global LCBD indices, and these variables remained significant after the stepwise selection of the model (Table 3). Water conductivity and river depth were positively associated and accounted for 14% and 12%, and Secchi depth was negatively associated and accounted for 6% of the variation of LCBD indices (Table 3).

3.4. Influence of component communities on global LCBD indices

Among the simple regression models, LCBD$_I$ indices were the strongest determinant of the variation of the global LCBD indices, whereas LCBD$_C$ indices were the weakest determinant. In multiple regressions (2-, 3-, and 4-components), the combination of LCBD$_I$ and LCBD$_M$ indices best explained the variation of the global LCBD indices (Table 4). The detailed results of the regression models are shown in Table 4.

Table 2

Pearson correlation coefficients between the normalized geographical factors and richness and abundance of each component community among the important taxa. R: richness (number of taxa), A: abundance (number of individuals), LONG: longitude (m), LAT: latitude (m), ALT: altitude (m). Significant relationships are marked with stars.

	Annelids		Crustaceans		Mollusks		Insects	
	R	A	R	A	R	A	R	A
LONG	0.15	0.06	0.03	0	−0.01	−0.04	−0.03	−0.05
LAT	−0.58**	−0.36**	−0.70***	−0.25*	−0.65***	−0.35**	0.47***	0.33**
ALT	−0.65***	−0.42***	−0.65***	−0.26*	−0.69***	−0.35**	0.41***	0.25*

* p < 0.05, ** p < 0.01, *** p < 0.001.

Fig. 2. RDA ordination plots showing the association of taxa having SCBD higher than the mean value (i.e. important taxa) with the geo-environmental factors. (a) Plot showing the sites and geo-environmental factors. VB4, CM3, TM1, TM2 and TM4 in bold are the sites with significant LCBD indices. LAT: latitude, ALT: altitude, WT: water temperature, DO: dissolved oxygen, WC: water conductivity, RW: river width, RD: river depth, SD: Secchi depth. (b) Plot showing taxa with high SCBD indices and geo-environmental factors for the same analyzes. The first letter of each taxon name represents the component of macroinvertebrate communities (A: annelid, C: crustacean, B and G: mollusk, and I: insect). Geo-environmental variables and taxa that have small loading score were removed to improve legibility.

Table 3
Contribution of geo-environmental factors to the variation of LCBD indices of global macroinvertebrate communities. The model showing the strongest contribution is in bold.

Model	Adjusted R^2	AIC	Stepwise selection	F-stat	p of the model
Environmental factors					
LCBD ~ WT	–	−551.2	–	0.01	0.956
LCBD ~ DO	–	−551.5	–	0.3	0.609
LCBD ~ WC	0.135	−561.4	–	10.7	0.002
LCBD ~ RW	0.010	−552.9	–	1.6	0.206
LCBD ~ RD	0.120	−560.2	–	9.5	0.003
LCBD ~ SD	0.061	−556.2	–	5.1	0.029
LCBD ~ pH	–	−551.5	–	0.3	0.590
LCBD ~ all factors	0.235	−563.6	WC + RD + SD	3.7	0.002
LCBD ~ WC + RD + SD	**0.260**	**−569.4**	**WC + RD + SD**	**8.3**	**< 0.001**
Geographical factors					
LCBD ~ LONG	–	−551.8	–	0.6	0.449
LCBD ~ LAT	0.001	−552.3	–	1.0	0.314
LCBD ~ ALT	0.010	−552.9	–	1.6	0.207
LCBD ~ all factors	–	−549.7	–	0.8	0.511

WT: water temperature, DO: dissolved oxygen, WC: water conductivity, RW: river width, RD: river depth, SD: Secchi depth, LONG: longitude (m), LAT: latitude (m), ALT: altitude (m).

Table 4
Contribution of the composition of component communities to the LCBD indices of the global macroinvertebrate communities. The model showing the strongest contribution is in bold.

Model	Adjusted R^2	AIC
LCBD ~ $LCBD_A$	0.331	−577.6
LCBD ~ $LCBD_C$	0.053	−555.7
LCBD ~ $LCBD_M$	0.241	−569.7
LCBD ~ $LCBD_I$	0.776	−646.5
LCBD ~ $LCBD_A + LCBD_C$	0.358	−579.3
LCBD ~ $LCBD_A + LCBD_M$	0.429	−586.6
LCBD ~ $LCBD_A + LCBD_I$	0.778	−646.3
LCBD ~ $LCBD_C + LCBD_M$	0.264	−570.7
LCBD ~ $LCBD_C + LCBD_I$	0.772	−644.5
LCBD ~ $LCBD_M + LCBD_I$	**0.843**	**−668.0**
LCBD ~ $LCBD_A + LCBD_C + LCBD_M$	0.444	−587.4
LCBD ~ $LCBD_A + LCBD_C + LCBD_I$	0.841	−666.2
LCBD ~ $LCBD_C + LCBD_M + LCBD_I$	0.841	−666.1
LCBD ~ $LCBD_A + LCBD_C + LCBD_M + LCBD_I$	0.834	−664.3

$LCBD_A$, $LCBD_C$, $LCBD_M$, $LCBD_I$ are the LCBD indices of each component community (annelids, crustaceans, mollusks and insects, respectively).

4. Discussion

4.1. Macroinvertebrate communities of the LMB

Macroinvertebrate communities in the LMB has been scarcely studied, in particular at a broad large spatial scale. To our knowledge, most of the existing studies were conducted at local sub-watershed scales of the LMB (e.g. Clavier et al., 2015; Cuong et al., 2016; Getwongsa et al., 2010; Quang et al., 2013), except for a macroinvertebrate pilot study by Pathoumthong and Vongsombath (2007), which was conducted over 13 sampling sites of the LMB and reported 218 macroinvertebrate taxa. The number of macroinvertebrate species (299) identified in the present study is the largest ever reported from the basin. Each component (i.e. annelids, crustaceans, mollusks and

insects) comprised a higher number of taxa than previous reports of field studies (see Appendix S2, Table A1 in Supplementary material). Moreover, we found that 36 macroinvertebrate families were represented by only one species (see Appendix S2, Table A2 in Supplementary material). This indicates that the LMB could support numerous rare or endemic taxa as found for mollusks that at least 111 species are endemic to the LMB (Köhler et al., 2012).

4.2. Variation of important taxa and their relationship to habitat characteristics

As stated in our second research question, the annelids, crustaceans and mollusks that have high SCBD indices are more abundant in the downstream part of the LMB, as reflected by the strong negative correlation with latitude and altitude (Table 2). Unsurprisingly, this result also supports previous studies (Arscott et al., 2005; Collier and Lill, 2008; B. Wang et al., 2012). The important taxa included *Corbicula*

leviuscula (code B34 in Fig. 2b), *C. lamarckiana* (B32), *Limnoperna siamensis* (B03) and *Branchiura sowerbyi* (A16), which mostly and abundantly occurred in the downstream part. However, an insect (i.e. *Cricotopus* sp., I023) was also an important taxon found in the delta. This could be due to the fact that many species in this genus are capable of withstanding low oxygen concentrations, are resistant to heavy metals, able to withstand high salt concentrations or pollution and can feed on rice (Boesel, 1983; Sinclair and Gresens, 2008), which are all characteristics observed in the delta.

Most of the important taxa characterizing the upstream sites belong to insects. In tropical as well as temperate regions, clear water and high values of dissolved oxygen are mostly found in tributaries and upstream sites, which are mainly preferred by insect taxa (Collier and Lill, 2008; Dobson et al., 2002; Królak and Korycińska, 2008). Of the 3 taxa found with the highest SCBD indices (*Polypedilum* sp.; *Ablabesmyia* sp. and *Cryptochironomus* sp.), *Polypedilum* sp. (code I033 in Fig. 2b) and *Ablabesmyia* sp. (I017) were highly associated with sites having high values of SD (Fig. 2b), which were mostly observed in tributaries. *Cryptochironomus* sp. (I024) and other taxa such as *Bezzia* sp. (I013) and *Anagenesia* sp. (I051) were more associated with high values of dissolved oxygen, which occurred at three of the sites with significantly unique taxonomic composition (TM1, TM2, TM4). Surprisingly, *Corbicula* sp. (B36) and Oligochaeta sp. (A11) were also more associated with these sites. These two taxa may have important taxonomic and ecological value because they were restricted to the main channel shared by Thailand and Laos and its nearby sites.

4.3. Beta diversity and uniqueness in community composition

The β diversity of macroinvertebrates in tropical river systems, particularly in South-East Asia, has not been extensively studied (Boyero et al., 2009; Dudgeon, 2008). Furthermore, the published papers (Al-Shami et al., 2013; Salmah et al., 2014) did not estimate the β diversity of macroinvertebrates as the total variance (BD_{Total}) of the communities found at the sampling sites and computed the contributions of individual sampling sites (LCBD indices) to total β diversity. This measure (i.e. BD_{Total}) quantified "the variation in macroinvertebrate composition among studied sites in the LMB", to which is referred as β diversity by ecologists (Anderson et al., 2011; Legendre et al., 2005; Legendre and De Cáceres, 2013; Whittaker, 1972; , 1960). The BD_{Total} computed here is an independent derived quantity that can certainly measure community differentiation of studied taxa, and thus more suitable to analyse beta diversity of macroinvertebrates in the LMB, when compared to the classical approach (i.e. the additive or multiplicative) which is dependent on alpha and gamma diversity. The great variation of macroinvertebrate composition ($BD_{Total} = 0.80$) found may reveal complex evolutionary and ecological processes operating at a site-to-global spatial scale of the LMB.

The contributions of sampling sites (LCBDs) to BD_{Total} can indicate the ecological uniqueness of each sampling site in terms of community composition and provide valuable information on the level of habitat degradation of sampling sites. These ecological indications can be used to support ecological assessments, restoration and conservation planning of the LMB. For example, we found that sites with large LCBD indices, which are the most different from the centroid of the distribution of the sites in a PCA ordination and hence the most interesting to examine in detail, mostly occurred along the main channel of the LMB. In particular, the 5 sites that had significant uniqueness in species composition (after Holm correction) occurred along the main channel and not in tributaries (Fig. 1a). The discussion on what triggered these sites to have higher degrees of uniqueness in species composition than others is provided in the following paragraphs.

4.4. Environmental factors responsible for uniqueness in community composition

Three environmental factors were found to be positively (water conductivity and river depth) or negatively (Secchi depth) associated with the degree of site uniqueness in taxonomic composition (Table 3). These 3 factors collectively explained 26% (adjusted $R^2 = 0.26$) of the variance in degrees of site uniqueness in taxonomic composition (global LCBD indices). However, our results did not find the types of relationships between β diversity and geo-environmental factors found in previous studies conducted over smaller areas (Al-Shami et al., 2013; J. Wang et al., 2012). This could be due to the dominant effect of anthropic pressure, which is spread along the LMB (Dao et al., 2010; Kudthalang and Thanee, 2010).

Previous papers have shown that conductivity had a positive influence on macroinvertebrate diversity (Lods-Crozet et al., 2001; Rizo-Patrón et al., 2013). However, we found that most of the sites with significant uniqueness in taxonomic composition had low taxonomic richness. High values of conductivity were mostly measured in the main channel sites (e.g. sites TM2, TM4 and the nearby sites) where they receive runoffs and discharge of urban wastewaters from intensified agriculture and from surrounding river basins and cities (Dao et al., 2010; Kudthalang and Thanee, 2010; Sor et al., 2017), and consequently lead to high conductivity (Wetzel, 2001). When sources of pollution (i.e. high concentration of inorganic dissolved solids) enter the rivers, only pollution- or disturbance-tolerant taxa (e.g. Oligochaeta, Chironomidae (Diptera) and Gastropoda) can resist (Feld and Hering, 2007; B. Wang et al., 2012). Pollution is the connection between high conductivity and low taxonomic richness.

Deep rivers (i.e. with high values of river depth) that have low Secchi depth can be considered proxies for anthropic activities (Baird and Flaherty, 2005; Dao et al., 2010), which is why they appear to influence LCBD indices. For example, we found small values of LCBD indices at most of the tributary sites where clear water and low pollution are observed, whereas large values of LCBD indices (e.g. > mean LCBD value) were found at sites with high river depth (e.g. most sites in the delta) and at other sites along the main channel of the upper part of the basin (Fig. 2a, see Appendix S4 in Supplementary material) where high levels of anthropic disturbance were observed. A clear evidence of the association between anthropic activities and high LCBD indices is found at the sites with significant LCBD indices (e.g. CM3, TM1, TM2 and TM4), all of which receive a moderate to high pressure of human impacts. Site CM3 is surrounded by houses, animal wastes and rubbish disposal. Site TM1 seems to be in a very high pressure area since it is opened to many anthropic activities such as animal and human waste disposal, artificial bank creation, local markets, dense population (~10,000 inhabitants), constructions, fishing and boat traffic. Sites TM2 and TM4 are also exposed to waste disposal and fishing, floating houses, tourism (TM2) and agriculture (TM4) (Dao et al., 2010; Kudthalang and Thanee, 2010; Sor et al., 2017). As a result, these sites supported low numbers of taxa (TM1, 9 taxa; TM2, 12; TM4, 21; CM3, 12), which indicate that ecological restoration is needed for these sites and their surroundings.

On the other hand, site VB4 has a significant LCBD value with a moderate number of taxa (34 taxa); the site with highest richness in our study was VB1 (74 taxa), located close to VB4. VB4 is located at the border between Cambodia and Vietnam and comprises a set of natural land cover (e.g. wood-, shrub-, grass-, inundated and wetland) on the west side of the river. Although the other side of the river has some anthropic activities including houses, fishing and small-scale business, VB4 still had a unique and rich taxonomic composition (Fig. 1a, b). Thus, VB4 and the surrounding sites/areas, particularly on the west side with natural land covers, may have high conservation value. Sites with high LCBD values may have high or low species richness, as shown in Legendre and De Cáceres (2013) and found in the research reported here.

4.5. Influence of component communities on global LCBD indices

The multiple regressions indicated the most striking relationship (adjusted $R^2 = 0.84$) between the uniqueness in taxonomic composition of the macroinvertebrate communities (global LCBD indices) and the combination of uniqueness in taxonomic compositions of the mollusk and insect communities ($LCBD_M + LCBD_I$ indices). Note that the global LCBD indices are not simply the sum of the component community LCBD indices; LCBD indices are computed separately for the global study and each component group as the squared distances of the sites to the multivariate ordination centroid. However, the degree of uniqueness in taxonomic composition of macroinvertebrate communities (global LCBD indices) is expected to be contributed by the component communities. In the LMB, LCBDs of mollusk and insect communities, which had a higher total variation ($BD_{MTotal} = 0.78$ and $BD_{ITotal} = 0.74$, respectively), explained most of the global LCBD variation because these two groups had higher abundances and wider distributions than the annelid and crustacean communities, which had lower total variation ($BD_{ATotal} = 0.72$ and $BD_{CTotal} = 0.38$, respectively). De'ath (2002) and Davidson et al. (2010) mentioned that taxa with low richness and low occurrence explained less variance of the community composition, and this is similar to our findings for the annelid and crustacean communities.

Co-occurrence among different component communities can directly or indirectly constrain the spatial distributions and the taxonomic abundance of the component communities (Miller, 1994; Wootton, 1994). Predators (e.g. Odonate taxa and some of the Diptera) may prey upon the taxa of other taxonomic communities, and thus affect the taxonomic occurrence and abundance of the global macroinvertebrate communities. Golfieri et al. (2016) reported that the abundance of the Odonates is closely linked to the abundance of their prey in the ecosystems. However, the Odonates preferring high water quality in the upstream sites may not directly influence the annelids or crustaceans, most of them being associated with habitats with lower water quality (annelids) or brackish water (crustaceans) in the downstream sites. For the communities that had a wide distribution in the LMB (e.g. insects and mollusks), their co-occurrence may be the result of niche expansion or competition, and thus they may have indirect interactions by competing for or facilitating resource availability. For example, an increasing topographical complexity of the streambeds, which can alter the near-bed flow, might enhance feeding success of mussel and suspension-feeding caddisfly communities (Cardinale et al., 2002; Vaughn et al., 2008). Moreover, the wide distribution of insects and mollusks with high abundance are functionally important in governing the uniqueness in overall community composition, and thus influencing beta diversity and composition of macroinvertebrate communities in the LMB.

5. Conclusion and remarks

The present study revealed the highest number of macroinvertebrate species ever reported from the LMB. The large diversity of different components (annelids, crustaceans, insects and mollusks) led to a great amount of variation, or beta diversity, in overall community composition among studied sites. The important taxa of annelids, crustaceans and mollusks were mostly found in the downstream sites, particularly in the delta, whereas the important taxa of insects were more related to the upstream sites. Most of sites located along the main channels had a high degree of uniqueness in macroinvertebrate taxonomic composition (i.e. high LCBD indices), of which the sites with significant LCBD indices had an exceptionally low richness, which is most likely due to anthropic impacts. An exception was found for one site located in the delta that had a significant LCBD value and moderate macroinvertebrate richness. This is perhaps because of the natural land covers observed on the west side of the river. Three environmental variables (water conductivity, river depth and water transparency)

were found to be mainly responsible for the variation in LCBD indices. For the component communities, mollusks and insects had a high variation, and their LCBDs greatly contributed to β diversity of global communities.

Our results provide valuable ecological information for selecting locations for conserving different taxonomic groups of macroinvertebrates at broad and small spatial scales. For example, site CM3 and the three other sites (TM1, TM2 and TM4) with significant LCBD indices and low richness are of particular interest for restoration planning, as these locations are experiencing severe degradation of local environments. Site VB4 and the surrounding sites/areas on the west side of the river deserve attention for protection since VB1 had very high richness and VB4 had a significant LCBD index and high richness. The combination of LCBD indices and species richness of the four component communities can thus be used to support restoration and conservation planning.

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.ecolind.2017.08.038.

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