



Original Articles

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



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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 km². 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 R² = 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 R² = 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 km² (77% of the whole basin) (Zalinger 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; Zalinger 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 macroinvertebrates, 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. Analyses 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 $\beta = \gamma/\alpha$, where γ is the total number of species in a given region and α 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 macroinvertebrates 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 macroinvertebrate and geo-environmental variables to represent each site in our analyses, 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 analyses (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 analyses (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

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