Science of the Total Environment 574 (2017) 288–299

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Different responses of functional traits and diversity of stream macroinvertebrates to environmental and spatial factors in the Xishuangbanna watershed of the upper Mekong River Basin, China

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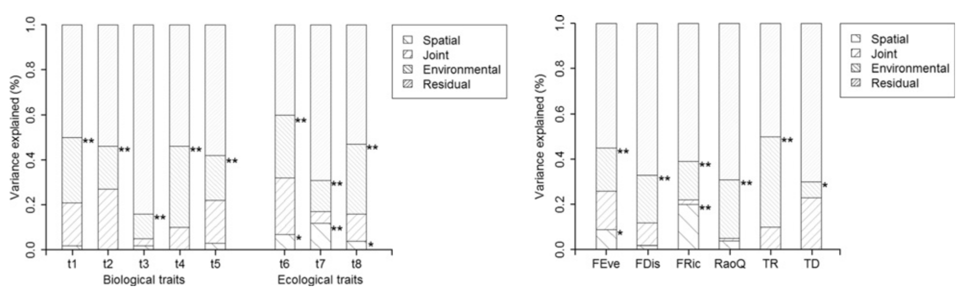
HIGHLIGHTS

- Functional diversity responses of aquatic organisms to stressors have rarely been tested.
- Both functional traits and diversity indices responded greatly to environmental variables.
- Ecological traits were more influenced by spatial vectors than biological traits.
- The spatial vector largely contributed to the variance of functional richness and evenness.
- Four traits and three indices were potential indicators of stream conditions in XSBN.

GRAPHICAL ABSTRACT



Variance partitioning analysis results of eight functional traits (Refuge (t1), Exoskeleton or external protection (t2), Respiration (t3), Body size (t4), Body shape (t5), Rheophily (t6), Habit (t7), Functional feeding groups (t8)) and six functional and trait diversity (FRic, FDis, RaoQ, TR, FEve, and TD) explained by spatial and environmental variables. The level of significance is given next to the bars. (* significance at $\alpha = 0.05$, ** significance at $\alpha = 0.01$).

ARTICLE INFO

Article history:
Received 21 May 2016
Received in revised form 6 September 2016
Accepted 8 September 2016
Available online xxxx

Editor: D. Barcelo

Keywords:
Benthic macroinvertebrates
Bioassessment
Biological traits
Functional diversity
Land use

ABSTRACT

Functional traits and diversity indices have provided new insights into community responses to stressors. Most traits of aquatic organisms have frequently been tested for predictability and geographical stability in response to environmental variables, but such tests of functional diversity indices are rare. We sampled macroinvertebrates at 18 reference sites (RS) and 35 disturbed sites (DS) from headwater streams in the upper Mekong River Basin, Xishuangbanna (XSBN), China. We selected 29 qualitative categories of eight traits and then calculated five functional diversity indices, namely functional richness (FRic), functional evenness (FEve), functional dispersion (FDis), functional divergence (FDiv) and Rao's Quadratic Entropy (RaoQ), and two trait diversity indices, namely trait richness (TR) and trait diversity (TD). We used combination of RLQ and fourth-corner to examine the response of traits and functional diversity to the disturbance and environmental variables. We used variance partitioning to explore the relative role of environmental variables and spatial factors in constraining trait composition and functional diversity. We found that the relative frequency of ten trait categories, and the values of TD, TR, FRic and FDis in RS were significantly different ($p < 0.05$) from DS. In addition, the seven traits (except for "habit") demonstrated a predictable response of trait patterns along the integrative environmental

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http://dx.doi.org/10.1016/j.scitotenv.2016.09.053

gradients. Environmental variables significantly contributed to most of the traits, functional diversity and trait diversity. However, spatial variables were mainly significant in shaping ecological traits, FRic and FEve. Our results confirm the dominant role of environmental variables in the determination of community trait composition and functional diversity, and substantiate the contribution of spatial vectors in explaining the variance of functional traits and diversity. We conclude that the traits "Refuge", "External protection", "Respiration" and "Body shape", and diversity indices FDis, TD, and TR are promising indicators of stream conditions at XSBN.

1. Introduction

In the past two decades, species functional traits, defined in terms of their functional significance relative to both qualitative and quantitative habitat conditions in stream ecology (Poff, 1997), have been proven to serve as a promising proxy of community or ecosystem function in response to various types of disturbance (Tilman et al., 1997; Petchey et al., 2004; Verberk et al., 2013), such as changes in land use (Vandewalle et al., 2010; Dolédec et al., 2011; Forrest et al., 2015), increased amounts of fine sediments (Wagenhoff et al., 2012), and the introduction of pesticides (Magbanua et al., 2013). Functional-trait diversity, which include measures of the functional processes of an entire community across traits relating to ecosystem function such as decomposition, predation, and resilience (Gallardo et al., 2009; Colzani et al., 2013; Heino, 2005), is useful for understanding and predicting the interaction between community function and environmental gradients (Mason and de Bello, 2013; Gagic et al., 2015).

The functional-trait diversity is often represented by a number of widely used indices and may improve our understanding of the functional response to environmental constraints among organisms (Mason et al., 2005, 2008; Mouchet et al., 2010). However, the functional traits of an organism are related to its specific functional role at a trophic level and may greatly differ among organisms and also in trait values (e.g., continuous traits and discrete traits) (Poff et al., 2006; Gagic et al., 2015). However, functional-trait diversity, rather than functional traits, has been applied far less frequently to aquatic than to terrestrial organisms (Heino et al., 2013; Gagic et al., 2015). Thus, the performance of functional-trait diversity estimates of aquatic organisms in response to disturbance has not been as thoroughly evaluated as traits have been, particularly for groups on which full trait information at the species level is absent, such as benthic macroinvertebrates. This is of significance because these organisms are used worldwide as indicators of stream health (Jackson and Fuereder, 2006).

Functional traits and functional diversity of macroinvertebrate have a close relationship with environmental variables. The response of functional traits to environmental gradients or variables was predictive and relatively stable, even across biogeographic regions, because environmental constraints or stressors play the dominant role in shaping the trait composition of local communities (Bonada et al., 2006; Statzner and Bêche, 2010). However, in these studies the expected trait responses that reflect the effects of environmental changes on communities were related to the spatiotemporal variance of stressors. The "habitat templet concept" and "landscape filter assumption" (from regional to stream reach scale) are two major theories explaining trait responses to stressors, such as frequency of disturbance (temporal), the availability of refugia (spatial), and trait filters operating across hierarchical scales (Southwood, 1977; Townsend and Hildrew, 1994; Poff, 1997). Several intensive studies have been conducted on the relationship between traits and environmental variables (sensu Statzner and Bêche, 2010; Heino et al., 2013), whereas fewer studies have addressed the relationships between functional diversity and environmental variables. A number of diversity indices have been established for use in aquatic ecosystems (Bêche and Statzner, 2009; Vandewalle et al., 2010) that can be used for this analysis.

Recently, an increasing number of studies have focused on geographical variations in trait composition and functional diversity of stream communities (Heino, 2005; Colzani et al., 2013; Heino et al., 2013; Schmera et al., 2013) that are influenced by the finding that trait composition of stream communities appears less stable geographically than previously suggested (Statzner et al., 2004). Spatial factors (e.g. distance among sites, location within the stream network) can affect traits composition relative to species dispersal (Colzani et al., 2013; Erős et al., 2012) and niche differentiation from upstream to downstream (Vannote et al., 1980). However, the relative role of spatial factors in shaping the trait composition and functional diversity in streams is poorly understood (Colzani et al., 2013). Heino et al. (2013) have suggested that a meta-community perspective (e.g., dispersal limitation) could improve our understanding of the variations among traits across sites. However, studies on the role of geographical location in shaping traits composition and diversity are very rare. Among these studies, Heino (2005) reported a strong contribution of spatial variables to trait richness and functional evenness (FEve) across five ecoregions in Finland. Pease et al. (2012) found that the functional evenness and functional divergence (FDiv) of fish generally increased with latitude. Colzani et al. (2013) discovered that functional dispersion (FDis), but not functional divergence (FDiv), was markedly explained by spatial vectors. In terms of taxon traits, only Erős et al. (2012) found spatial vectors to play an important role in shaping the functional groups of fish in a human-modified landscape. In addition, the effects of spatial vectors on traits patterns and diversity are assumed to be different.

Most past studies of trait-environmental and trait-spatial relationships have focused on streams in temperate (Bêche et al., 2006; Charvet et al., 1998) and boreal climates (Heino, 2005). To our knowledge, only few studies of the topic have focused on tropical streams (Colzani et al., 2013), and no studies have been undertaken in the Asian tropical region. Specific evidence of how trait patterns vary along different environmental gradients in different geographical regions would provide useful insight into general trait response patterns within a macroecological perspective (Heino et al., 2013).

The overall aim of our study was to provide an integrated picture of the response of the functional traits and diversity of stream macroinvertebrates to environmental variables and spatial vectors at the Xishuangbanna (XSBN) watershed of the upper Mekong River Basin in Yunnan Province, China. Our specific aim was to find promising functional traits and diversity indices of macroinvertebrates for detecting the effects of anthropogenic disturbances on streams in the studied area. We hypothesized that (1) functional traits, functional diversity and trait diversity could discriminate between disturbed and undisturbed sites affected by land use changes; and (2) environmental variables rather than spatial vectors play a dominant role in structuring trait composition and determining functional and trait diversity.

2. Methods

2.1. Study area and sampling sites

We conducted our study in Xishuangbanna (XSBN), a tropical rain forest area in southern Yunnan Province, China, (Fig. 1). The tropical monsoon climate of XSBN provides a mean annual precipitation of 1193–2491 mm and has a mean annual temperature of 21 °C (Zhang and Cao 1995; Ren et al., 2001). XSBN is a biodiversity hotspot (Myers