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Metacommunity ecology meets bioassessment: assessing spatio-temporal variation in multiple facets of macroinvertebrate diversity in human-influenced large lakes

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Abstract

Metacommunity theory emphasizes that local communities are jointly affected by environmental filtering and spatial processes. However, the roles of spatial processes are often given insufficient attention in bioassessment practices, which may bias the assessments of ecological status based on biotic metrics. Here, we quantified the relative importance and the seasonal stability of spatial processes, natural conditions and human-induced factors in structuring variation in different bioassessment metrics based on macroinvertebrate communities. Our study systems were two extensively sampled large and shallow lakes with strong nutrient gradients related to human disturbance. The roles of different drivers were examined for three kinds of indicators: general diversity, trait-based and taxonomic distinctness metrics, and their performance in characterizing human disturbance was evaluated. Overall, human-induced and spatial factors were all important in explaining variation in the three types of bioassessment metrics. Contrary to our expectations, however, we found that the importance of spatial processes on bioassessment metrics can be comparable to the effects of local environmental conditions at the within-lake scale. Furthermore, the results showed substantial seasonal variability in the relative roles of different drivers, which might be linked to life-cycle seasonality of macroinvertebrates. As expected, trait-based metrics generally were best associated with human-induced variables in both lakes, whereas general diversity and taxonomic distinctness metrics performed poorly. The low effectiveness of taxonomic distinctness metrics might be due to low species richness associated with high nutrient levels. To conclude, our results suggest that bioassessment cannot exclusively rely on the idea of environmental filtering even if we focus on fine spatial scales. We hence strongly urge that spatial processes, natural drivers and temporal variability should be better considered in combination in the development and application of bioassessment approaches. In addition, taxonomic distinctness measures should be used with caution, especially for the ecosystems and organism groups typically characterized by low species richness.

Keywords: environmental filtering, dispersal processes, species diversity, traits, taxonomic distinctness, shallow lakes

1. Introduction

In recent decades, freshwater biodiversity has become increasingly threatened by multiple anthropogenic stressors, including eutrophication, acidification, hydromorphological alterations, land use changes and water overexploitation (Dudgeon et al. 2006, Ormerod et al. 2010). Thus, the development of effective bioassessment approaches is crucial to ecological status assessment and biodiversity conservation planning (Birk et al. 2012, Poikane et al. 2016), but current approaches may fall short in providing accurate enough information about multiple factors affecting biological communities. For example, although some approaches consider regional stratifications to account for regional variation, most bioassessment programs are still generally based on the assumption that variations in community structure and species diversity are mostly determined by local environmental conditions (Heino 2013). Metacommunity theory, however, emphasizes that local community structure is jointly regulated by local environmental conditions (i.e., both natural and anthropogenic factors) and spatial processes (i.e., dispersal and colonization-extinction dynamics) (Leibold et al. 2004, Brown et al. 2017).

The importance of dispersal processes in structuring metacommunities has been examined extensively across spatial scales and taxonomic groups (Heino et al. 2015). Generally, the role of dispersal limitation (i.e., limited dispersal rates) is assumed to increase with increasing spatial scale, which may bias the performance of bioassessment at large scales (Heino 2013). Thus, bioassessment should consider ecoregions or specific typologies as starting points (Hering et al. 2010; Anas et al., 2017). Furthermore, a few recent studies have also found that potentially high dispersal rates can considerably affect community composition and species diversity at small spatial scales (Árva et al. 2014, Vilmi et al. 2016a, Tolonen et al. 2017). Hence, both limited and high dispersal rates may cause spatial patterns in metacommunities, which should be considered in bioassessment through accounting for spatial autocorrelation in biological data (Heino 2013). To our knowledge, however, most previous studies were mainly concerned with community composition, whereas our understanding of how various biotic metrics are potentially affected by dispersal-related spatial processes remains limited (Alahuhta and Aroviita 2016, Vilmi et al. 2016a).

Local biological communities are affected both by natural factors (e.g., geology, climate, hydromorphology) and anthropogenic stressors (e.g. nutrient enrichment, habitat degradation), as was shown by a review of 368 case studies (Stendera et al. 2012). Ideally, bioassessment based on local biological communities should portray only variation among locations due to anthropogenic stressors, whereas other variations related to natural factors should be excluded (Birk et al. 2012, Heino 2013). Indeed, several approaches have been proposed to account for the effects of key natural factors. For example, the effects of natural factors are minimized using *a priori* regionalization (e.g., ecoregions, zoogeographic regions, hydrological regions) or typology-based classifications

(mainly according to their physical and morphological attributes, such as catchment size, altitude or depth) (Moog et al. 2004, Moss 2007). It should be noted that the above regional delineations and typologies are coarse classes of naturally continuous gradients across a wide range of ecosystem characteristics (Hering et al. 2010). Thus, in the case of continuous variation, it is not surprising that weak correlations have commonly been detected between regional delineations or typologies and biogeographic patterns of local freshwater communities (Hawkins and Norris 2000, Davy-Bowker et al. 2006).

The effects of natural factors on biological communities can be studied at different spatial scales. Stendera et al. (2012) found that the majority of studies on natural drivers of biological communities were concentrated on large spatial scales. In reality, however, many natural parameters influence community composition even if we only focus on relatively small spatial extents (Vilmi et al. 2016c, Cai et al. 2017). In this context, modelling the variation of biotic metrics based on natural factors is also increasingly applied to the development of multimetric indices (Cao et al. 2007, Pereira et al. 2016, Tang et al. 2016), but rarely at fine spatial scales (Carvalho et al. 2009). In this context, the responses of biotic metrics to natural factors should be examined for various biological groups and at different spatial scales.

Multimetric indices and predictive models are the two most commonly used bioassessment approaches (Hering et al. 2010). In the multimetric approach, a number of metrics are calculated based on biological communities, typically including information on species richness, abundance and composition in terms of diversity, feeding guilds, habitat preference and sensitivity to stressors (Birk et al. 2012). Many traditional diversity metrics are based on species richness and abundance, which vary greatly among locations, especially at large spatial scales (Koperski 2011). In contrast, trait-based community metrics have been increasingly advocated as one of the most useful tools for freshwater biomonitoring (Menezes et al. 2010, Van den Brink et al. 2011, Berger et al., 2018). The theoretical basis is that environmental filtering selects a suite of species in a local community typically via species traits (Poff 1997), which makes trait-based community descriptors well matched with local environmental conditions. Several studies have also shown that, unlike taxonomic composition, the trait composition of freshwater organisms is more stable across broad geographical extents (Statzner and Bêche 2010, Van den Brink et al. 2011). A weakness of species-based and trait-based community metrics is that phylogenetic relationships, an important aspect of biodiversity, among species are not considered (Clarke and Warwick 1998). Taxonomic distinctness (TD) indices measure biodiversity by incorporating the taxonomic or phylogenetic relatedness among species in a community (Clarke and Warwick 2001). A major advantage of these indices is their insensitiveness to sampling effort and species richness, supporting their efficiency in bioassessment (Clarke and Warwick 1998). Nowadays, integration of species traits and identity into the development of bioassessment approaches is becoming a promising tool in

providing a comprehensive understanding of human impacts on aquatic ecosystems (Menezes et al. 2010, Saito et al. 2014). To our knowledge, however, how these different types of biotic metrics are regulated by spatial processes, anthropogenic impacts and natural drivers has been rarely evaluated simultaneously using the same dataset and analytical approach (Vilmi et al. 2016a, Wu et al. 2016, Tolonen et al. 2017). Also, little is known about seasonal variations in the efficiency of biotic metrics in freshwater bioassessment.

To quantify and disentangle the response of multiple biotic metrics to different drivers, lake benthic macroinvertebrates were used as the model organismal group. Benthic macroinvertebrates are commonly used in the ecological status assessment of freshwaters due to the fact that they are sensitive to human disturbance (Poikane et al. 2016). Our study systems are two subtropical shallow lakes, Lake Taihu and Lake Chaohu (Fig. 1), which belong to the list of the five large freshwater lakes in China (Cai et al. 2016). The two lakes present strong nutrient gradients and considerable habitat heterogeneity related to human disturbance and natural background environmental conditions (Fig. S1), providing an excellent opportunity to explore roles of different drivers in structuring variation in biotic metrics used in bioassessment. We compared the spatio-temporal patterns in three kinds of biodiversity measures: general diversity metrics, trait-based metrics and taxonomic distinctness metrics. We distinguished anthropogenically and naturally induced variation in local environmental conditions, in addition to spatial dispersal processes, to quantify the relative importance of these sources of variation for the bioassessment metrics. We hypothesized that variations in multiple aspects of biotic metrics are related to both local environmental (human-induced and natural) and spatial variables following recent findings from lake littoral diatoms and macroinvertebrates (Vilmi et al. 2016a, Tolonen et al. 2017). Specifically, we expected that human-induced variables should contribute most to the metrics' variation due to strong environmental gradients associated with human activities, whereas spatial processes are less important since we focus on a relatively fine spatial scale and highly-connected systems. Here, we expected that high dispersal rates (i.e., mass effects) could be the main spatial process (rather than dispersal limitation) at the within-lake scale (Heino 2013). We also hypothesized that trait-based and taxonomic distinctness metrics would better portray human disturbance compared with general diversity metrics (Clarke and Warwick 1998, Van den Brink et al. 2011). We also examined the temporal stability of the metrics-environment relationships by using data from four sampling periods in each lake.

2. Methods

2.1 Study area

The two lakes in this study are located in the lower reaches of the Yangtze system (Fig. 1), and their outflow rivers to the Yangtze River are regulated by sluice gates. Lakes Taihu and Chaohu, have water surface areas of 2338

km² and 770 km², and mean water depths of 1.9 m and 3.0 m, respectively (Cai et al. 2016). In the past three decades, the two lakes have been experiencing dramatic ecosystem degradations due to eutrophication and other human activities. Cyanobacterial blooms is one of the most serious environmental problem affecting these lakes, occurring annually and being increasing in spatial extent, duration and intensity over the past decades (Qin et al. 2015, Zhang et al. 2015). On the other hand, each lake presents a great spatial heterogeneity in trophic state and habitat conditions. For example, in Lake Taihu, nutrient and chlorophyll-*a* levels generally increase across the lake from the southeast to northwest where some of the large polluted tributaries enter the lake. Wind-wave induced disturbance of sediment is very intensive, especially in the open area, due to its long wind fetch and high dynamic ratio. Aquatic macrophytes mainly occur in the eastern sheltered bay areas (Fig. S1a). As for Lake Chaohu, the freshwater input is dominated by the south-eastern watersheds, which discharge via the Yuxi River, whereas nutrient inputs are mainly from the western inflowing rivers. The hydrology of the lake and nutrient inputs result in a strong trophic gradient from west to east (Fig. S1b).



Fig. 1 Locations of Lake Taihu and Lake Chaohu along the lower reach of the Yangtze River in China.

2.2 Macroinvertebrate sampling

Thirty-two and thirty-five sites were set up for Lake Taihu and Lake Chaohu, respectively, taking into account lake morphometry and habitat heterogeneity, as well as inflowing and outflowing rivers (Fig. S1). Benthic samples were collected quarterly in February, May, August and November 2013 in Lake Taihu, and in January, April, July and October 2013 in Lake Chaohu. Samples were collected using a 0.05 m² a modified Peterson grab, with three grabs comprising a pooled sample, and were sieved *in situ* through a 250 µm aperture mesh size sieve. The materials retained on the sieve at one site were stored in a cooler box and transported to the laboratory for further processing during the same day. In the laboratory, the samples were sorted on a white tray, and all specimens were

picked out and preserved in 7% buffered formalin solution. Specimens were identified to the lowest feasible taxonomic level, usually species or genus (Table S1, S2).

2.3 Bioassessment metrics

We examined 12 macroinvertebrate metrics for possible inclusion in final regression analyses (Table 1). The metrics were categorized into three groups: general diversity, trait-based and taxonomic distinctness metrics. Prior to statistical analyses, we evaluated these metrics for redundancy using Spearman correlation tests and eliminated some metrics ($r \geq 0.7$, Table S3). The metric “Filterers” was removed due to the absence or extremely low abundance in many samples. Finally, two metrics of each group were retained for further analyses. Detailed information and calculation of each index are presented in Appendix A in supplementary materials.

Table 1 Candidate bioassessment metrics for describing different aspects of macroinvertebrate diversity in Lake Taihu and Lake Chaohu.

Metric	Abbreviation	References
General diversity measures		
Species richness	Richness*	(Hill 1973)
Shannon diversity	Shannon	(Hill 1973)
Pielou evenness	Evenness*	(Hill 1973)
Trait-based measures		
Abundance of maximum size < 2 cm	Small size	(Usseglio-Polatera et al. 2000)
Abundance of life cycle ≤ 1 year	Short-lived*	(Usseglio-Polatera et al. 2000)
Abundance of deposit feeders	Deposit feeders *	(Rawer-Jost et al. 2000)
Abundance of filterers	Filterers	(Rawer-Jost et al. 2000)
Taxonomic distinctness measures		
Taxonomic diversity	D	(Warwick and Clarke 1995)
Taxonomic distinctness	TD	(Warwick and Clarke 1995)
Average taxonomic distinctness	AvTD*	(Clarke and Warwick 1998)
Total taxonomic distinctness	ToTD	(Clarke and Warwick 2001)
Variation in taxonomic distinctness	VarTD*	(Clarke and Warwick 2001)

* indicates that these metrics were retained after preliminary screening.

2.4 Explanatory variables

Three sets of explanatory variables were employed in our study: (1) human-induced variables, (2) natural environmental variables and (2) spatial variables.

Human-induced variables

Secchi depth (SD) was measured in the field using Secchi disk. Dissolved oxygen (DO), pH and conductivity (Cond) were measured using a YSI 6600 V2-4 Multi-Parameter Water Quality Sonde. In addition, at each site, a vertically-integrated water sample was taken at the same time with invertebrate sampling, and was kept cool and

shaded before determination. In the laboratory, total nitrogen (TN), ammonium (NH₄-N), nitrate (NO₃-N), total phosphorus (TP), orthophosphate (PO₄-P), total suspended solids (TSS) and chlorophyll a (Chl-a), permanganate index (COD_{Mn}) in the water column were measured. An additional Peterson grab sediment sample was taken at each site in April 2013 in Lake Chaohu and in May 2013 in Lake Taihu for measurement of chemical parameters in surface sediments (ca. the upper 5 cm). These included total nitrogen from the sediment (TNs) and total phosphorus from the sediment (TPs). Finally, percentage cover of aquatic macrophytes (Cover) was estimated visually on six classes (0, 1–5, 5–25, 25–50, 50–75, and 75–100% at sampling site). For detailed analytical methods, see Appendix B and Table S4 in the supplementary materials.

To avoid collinearity between predictor variables, Spearman correlations were tested separately for each lake to remove some strongly correlated variables ($r \geq 0.8$). This procedure resulted in the set of 14 (Lake Taihu) and 15 (Lake Chaohu) predictor variables that were used in final statistical analyses (Table S5, S6).

Natural variables

Wind-wave action and water depth (WD), which play crucial roles in structuring benthic communities of large shallow lakes, were considered here as natural predictor variables. Water depth was measured by a Speedtech SM-5 Portable Depth Sounder. Mean effective fetch (F_m) was calculated to illustrate wind-wave action. For details of the calculation of F_m , see Appendix B in supplementary materials.

Spatial variables

Spatial variables were obtained by using distance-based Moran's eigenvector maps (MEM) (Dray et al. 2012). Significant spatial variation shown by MEMs may be caused by environmental autocorrelation, dispersal processes, historical effects, or other processes. MEMs can help illustrate complex spatial patterns of biological communities and univariate metrics values (in our case), with the first MEM variables representing broad-scale spatial variation among sites, while the last ones with small eigenvalues indicate finer-scale variation. In the present study, geographic coordinates of sampling sites were employed to calculate MEMs, and only positive eigenvectors based on minimum truncation distances were used in regression analyses. Finally, 11 and 13 spatial variables were generated for Lakes Taihu and Chaohu, respectively. MEMs were calculated using the function *eigenmap* with default values in the package *codep* in R base version 3.3.2 (R Core Team 2016). We strongly believe that the unique roles of spatial variables should reveal dispersal-related processes occurring at multiple spatial scales because a wide variety of abiotic variables were also considered in the same statistical analyses.

2.5 Data analysis

To identify explanatory factors significantly explaining variation in each metric, multiple linear regression

models were built following a conservative method of forward selection (Blanchet et al. 2008). We first tested if the global test of the regression model was significant. If the global model was significant, forward selection was conducted with two stopping rules: (1) either exceeding the critical p value ($p = 0.05$) or (2) the adjusted R^2 value of the reduced model exceeded that of the global model (Blanchet et al. 2008). This procedure was run using the function *ordiR2step* in the R package *vegan* (Oksanen et al. 2016), and was done separately for each set of explanatory variables (i.e., human-induced, natural and spatial). Prior to analyses, two abundance metrics (i.e., short-lived and deposit feeders) were square-root transformed to better conform to normal distributions.

Variation partitioning based on partial linear regression was utilized to reveal the unique and shared effects of the three explanatory variable groups on each bioassessment metric. This method produced seven fractions plus unexplained variation using the three sets of explanatory variables. Variation partitioning analyses were conducted with the function *varpart* in the R package *vegan* (Oksanen et al. 2016). The results presented are based on adjusted R^2 values, which are unbiased estimates of explained variation, being corrected for the number of explanatory variables (Peres-Neto et al. 2006). Differences in the amount of variation in bioassessment metrics explained by different explanatory variable groups and the differences in the amount of variation in the three types of metrics explained by human-induced variables were examined using Kruskal-Wallis tests, followed by Mann-Whitney tests for pairwise comparisons with sequential Bonferroni correction.

3. Results

3.1 Environmental features and structure of the lake macroinvertebrate metacommunities

Overall, most human-induced variables, in particular nutrients and Chl-a, varied greatly among sites, indicating strong environmental gradients within each lake (Table S5, Fig. S2, Fig. S3). For instance, TN varied from 0.48 to 7.86 mg/L in Lake Taihu, and from 0.63 to 29.93 mg/L in Lake Chaohu, with the highest values observed in sites close to inflowing rivers. Similarly, TP varied considerably, with the range of 0.017-0.601 mg/L and 0.011-2.714 mg/L in Lake Taihu and Lake Chaohu, respectively. Chl-a varied from 1.67 to 75.89 $\mu\text{g/L}$ in Lake Taihu and from 1.92 to 135.41 $\mu\text{g/L}$ in Lake Chaohu (Table S5). According to annual mean concentration of Chl-a and the fixed boundary classification system for lake trophic status accepted by OECD (1982), the trophic status of the sampling sites varied from mesotrophic to hypertrophic in Lake Taihu, and from eutrophic to hypertrophic in Lake Chaohu. Spatially, trophic status generally increased across the lake from southeast to northwest in Lake Taihu (Fig. S2), and increased from east to west in Lake Chaohu (Fig. S3). Natural variables also showed considerable variations among sites, with mean effective fetch ranging from 0.5 to 24.0 km in Lake Taihu and from 2.4 to 13.2 km in Lake Chaohu, indicating strong spatial heterogeneity of wind-wave action.

In total, 36 and 27 taxa were recorded from Lake Taihu and Lake Chaohu, respectively (Table S1, S2). Generally, abundances of benthic communities in both lakes were mainly dominated by pollution-tolerant species belonging to Oligochaeta and Chironomidae. In Lake Taihu, the oligochaete *Limnodrilus hoffmeisteri*, the chironomid *Tanypus chinensis* and the bivalve *Corbicula fluminea* were the most abundant taxa accounting for 60.9%, 6.9% and 10.6% of the total abundance (Table S1). Additionally, strong spatial differences in taxonomic composition and abundance were evident across Lake Taihu, with total abundance ranging from 125 to 23210 ind./m² (Fig. S4a). High abundance was recorded at sites in Meiliang Bay, Zhushan Bay and site TH10, mainly dominated by Oligochaeta, Chironomidae and Malacostraca. Gastropods were mainly distributed in the eastern sheltered bays, while Bivalvia and Polychaeta mainly occurred in the open water zone. In Lake Chaohu, the benthic community showed relatively weak spatial heterogeneity (Fig. S4b) and was exclusively dominated by a few species of chironomids (i.e., *Prosilocerus akamusi*, *Tanypus chinensis*, *Clinotanypus* sp.1, *Microchironomus tabarui*) and oligochaetes (*L. hoffmeisteri* and *Branchiura sowerbyi*) with these species together constituting 88.4% of the total abundance (Table S2). The six metrics also varied greatly among sites, especially for the two trait-based metrics (Table 2). Furthermore, five of the six metrics in Lake Chaohu showed significant differences among seasons with the exception of VarTD (Fig. S6). In contrast, only one metric (i.e., abundance of short-lived) in Lake Taihu presented significant seasonal differences in the context of great within-lake variation (Fig. S5).

Table 2 Descriptive statistics of bioassessment metrics in Lake Taihu and Lake Chaohu

Lake	Metric	Min	Max	Median	Mean	SD	CV (%)
Taihu	Richness	2	13	5	5.0	1.7	35.1
	Evenness	0.11	1.00	0.80	0.74	0.20	27.7
	Short-lived	0	4180	51	276	663	240.3
	Deposit feeders	0	33280	160	1195	4487	375.5
	AvTD	49.2	100.0	88.4	84.9	10.4	12.3
	VarTD	0	1632.4	366.2	515.3	444.0	86.2
Chaohu	Richness	2	12	5	5.2	2.0	38.0
	Evenness	0.11	1.00	0.79	0.74	0.20	26.7
	Short-lived	0	2720	93	249	418	168.3
	Deposit feeders	0	3520	180	378	539	142.6
	AvTD	25.3	100.0	75.1	69.6	15.3	22.0
	VarTD	0	1580.7	1238.6	1050.4	378.4	36.0

SD: standard deviation; CV: coefficient of variation

3.2 Relative importance of environmental factors and spatial variables

Variation partitioning showed that human-induced and spatial variables were all important in explaining variations in the bioassessment metrics (Fig. 2), yet their relative roles varied among seasons and different types of response variables (Fig. 3, Fig. 4). Furthermore, the amount of unexplained variation was relatively high in most cases (41.6%–96.2%), and one-fourth of the 48 cases could not be explained by any of the three explanatory variable data sets.

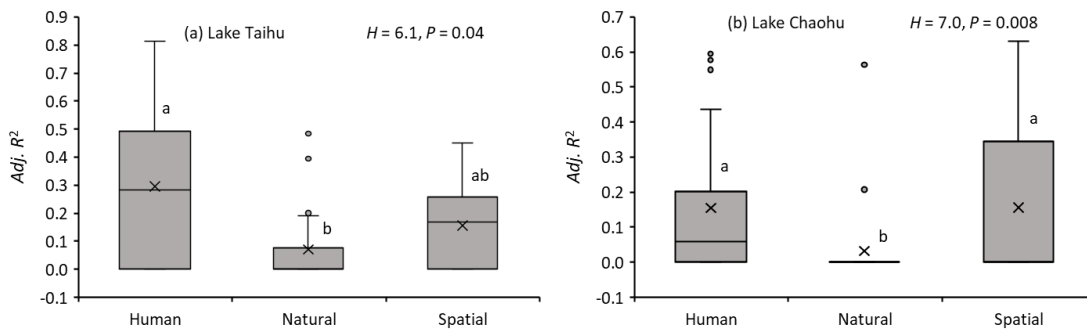


Fig. 2 Boxplots illustrating the amount of variation in bioassessment metrics explained by human-induced, natural and spatial variables in (a) Lake Taihu and (b) Lake Chaohu. Kruskal-Wallis tests were employed for comparing the relative importance of different explanatory variable groups. Mann-Whitney tests were used for pairwise comparisons with sequential Bonferroni correction. Different letters indicate significant differences ($P < 0.05$).

Overall, in Lake Taihu, bioassessment metrics were best explained by human-induced variables, followed by spatial variables and the least by natural variables (Kruskal-Wallis test, $H = 6.1$, $P = 0.040$, Fig. 2). The averages of total variation explained were 31.4% (0–81.4%, 0 indicates no predictor variables were selected) of the human-induced variables, 14.9% (0–44.9%) of the spatial variables, and 6.7% (0–48.5%) of the natural variables. In over two-thirds of the cases (17 out of 24), the forward selection did not find any significant natural variables in the regression models of certain metrics (Fig. 3).

For Lake Chaohu, human-induced and spatial variables were roughly important in explaining the variation in bioassessment metrics, which accounted for 15.5% (0–59.5%) and 15.6% (0–63.1%) of the total variation, respectively. Natural variables were only important in two cases (Kruskal-Wallis test, $H = 7.0$, $P = 0.008$, Fig. 2). Moreover, there were one third (8 out of 24) models with no explanatory variables selected (Fig. 4).

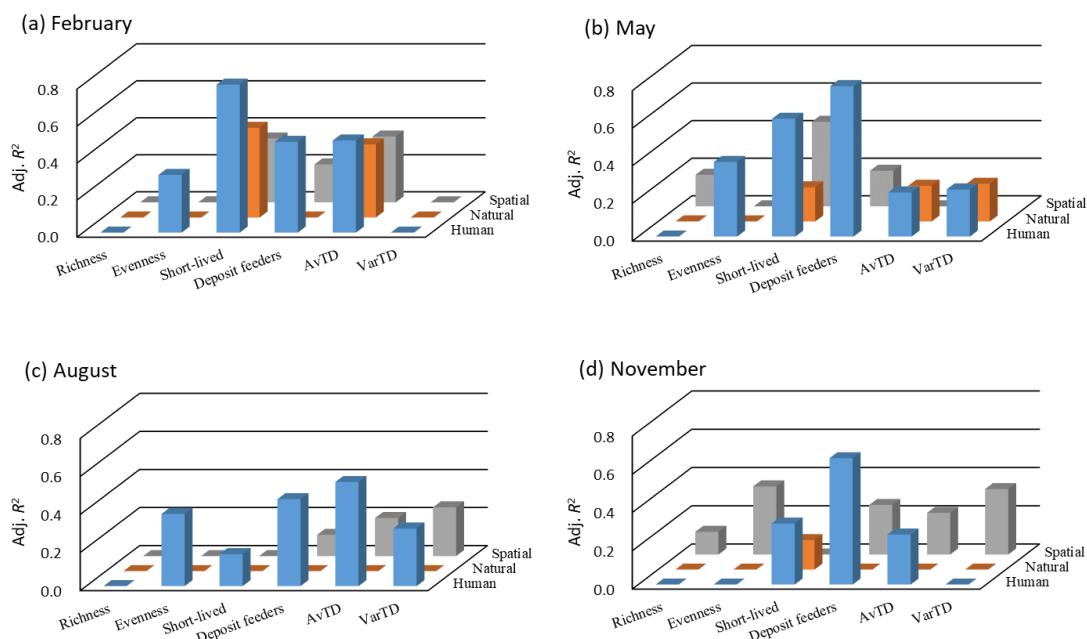


Fig. 3 The amount of variation in bioassessment metrics explained by human-induced, natural and spatial (MEMs)

variables in Lake Taihu in four different months: (a) February, (b) May, (c) August, and (d) November. 0 indicates no variables were selected in forward selection.

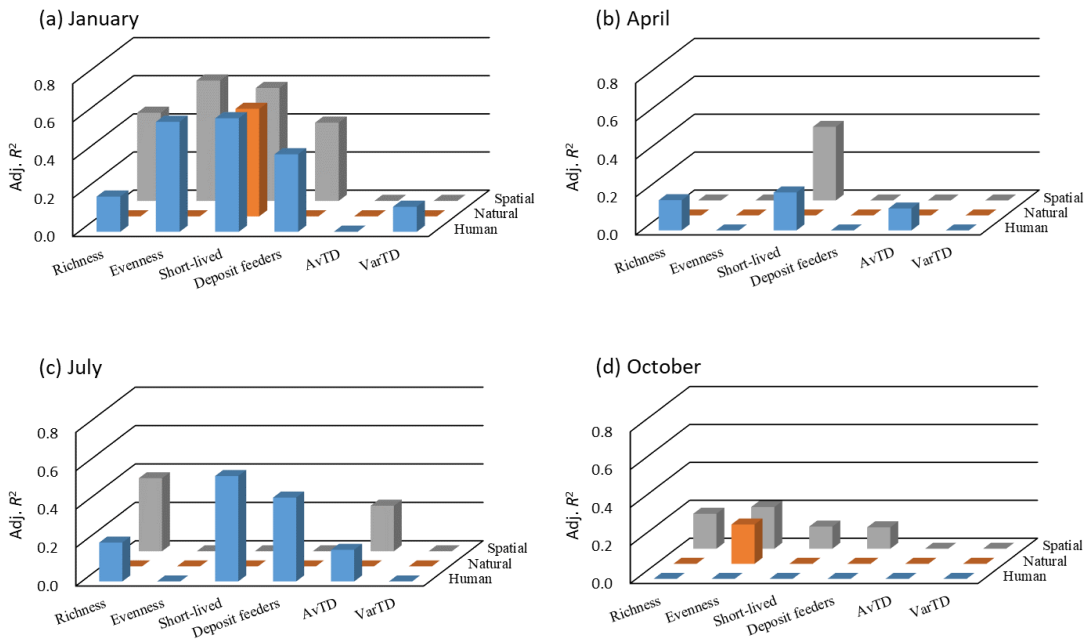


Fig. 4 The amount of variation in bioassessment metrics explained by human-induced, natural and spatial (MEMs) variables in Lake Chaohu in four different months: (a) January, (b) April, (c) July, and (d) October. 0 indicates no variables were selected.

As expected, trait-based metrics were best correlated with human-induced variables in both lakes, whereas general diversity metrics (i.e., richness and evenness) performed poorly, with 10 out of the 16 cases that could not be explained by any human-induced variables. Specifically, the total variation in trait-based metrics was well explained by human-induced variables in Lake Taihu (on average, 54.3%, 16.8%-81.4%) and Lake Chaohu (on average, 27.3%, 0%-81.4%). In contrast, the low averages of the total variation in general diversity metrics explained were observed in Lake Taihu (13.6%) and Lake Chaohu (14.0%). Taxonomic distinctness metrics were also commonly associated with human-induced variables in Lake Taihu, accounting for 26.2% (0–54.7%) of the total variation. However, their relationships were quite weak, with no human-induced variables being selected in five out of the eight multiple regression models (Fig. 5).

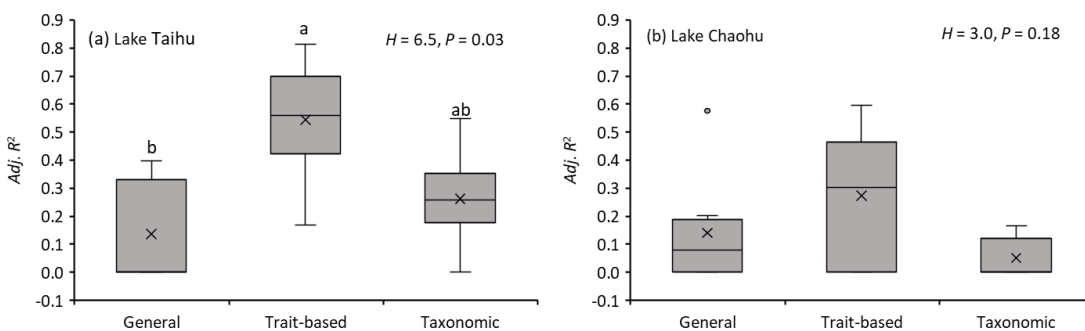


Fig. 5 Boxplots illustrating the amount of variation in different bioassessment metrics explained by human-induced variables in (a) Lake Taihu and (b) Lake Chaohu. Kruskal-Wallis tests were employed for comparing the performance of

different groups of metrics in reflecting human disturbance. Mann-Whitney tests were used for pairwise comparisons with sequential Bonferroni correction. Different letters indicate significant differences ($P < 0.05$).

4. Discussion

4.1 Roles of human-induced factors, natural conditions and spatial processes on bioassessment metrics

The roles of environmental filtering versus spatial processes on diversity indices and bioassessment metrics have not been well enough examined (Alahuhta and Aroviita 2016, Vilmi et al. 2016a, Tolonen et al. 2017). Overall, our results indicated that, at the within-lake scale, the importance of spatial processes on bioassessment metrics can be comparable to the effects of local environmental filtering processes. Even if we focus on the unique effects of spatial variables, the fractions varied from 0 to 40% of variation with an average of 13.6%. These results are in contrast with our hypothesis which assumed that human-induced factors would contribute most to the metrics' variation in the context of strong environmental gradients. These findings also suggest that many bioassessment metrics are probably strongly regulated by dispersal-related processes at within-lake scales, through the effects of these processes on species distributions. A few studies have also found similar patterns when evaluating the roles of dispersal versus environmental control on species diversity and bioassessment metrics in similar highly-connected freshwater lakes. For example, Tolonen et al. (2017) and Vilmi et al. (2016a) found that the effects of spatial variables can override the influences of local environmental conditions in controlling the variation in 10 littoral macroinvertebrate diversity indices and 14 commonly-used diatom bioassessment metrics in a large boreal lake system. In addition, even in an across-lakes study, unique effects of spatial variables also significantly structured all six biological metrics (phytoplankton, macrophytes, diatoms, littoral and profundal macroinvertebrates, and fish) (Alahuhta and Aroviita 2016). As for the roles of dispersal processes, metacommunity theory suggests that both limited (i.e., dispersal limitation) and high dispersal rates (i.e., mass effects) could generate spatially-structured patterns in community structure (Brown et al. 2017). However, in contrast to across-lakes studies at large spatial extents (Heino 2013), high dispersal rates facilitated by high connectivity among sites is a more likely explanation for the patterns observed in our within-lake study systems (Heino et al. 2015). A previous study has found significant spatial autocorrelation between neighbouring sites of four common species in Lake Taihu, suggesting the potential importance of mass effects (Cai et al. 2017). Thus, we propose that mass effects rather than dispersal limitation are the most relevant mechanisms influencing variation in bioassessment metrics at within-lake scale. This is because our study was conducted at a relatively small spatial scale in two highly-connected lake systems. In addition, one should keep in mind that many sites of the two lakes were highly eutrophic and, consequently, mainly dominated by short-lived and small-sized chironomids and oligochaetes, particularly in Lake Chaohu (Fig. S4).

Therefore, differences in bioassessment metrics among sites are reduced, weakening their potential effectiveness in informing about anthropogenic environmental variation.

The human-induced variables explained a considerable amount of variation in bioassessment metrics, which is in accordance with our first specific hypothesis. It was not surprising since the two lakes presented strong environmental gradients associated with intensive human activities (e.g., nutrients inputs) (Qin et al. 2015, Zhang et al. 2015). The results of variation partitioning also showed that the variables related to nutrient enrichment and organic pollution (e.g., nitrogen and phosphorus in the water column and surface sediments, Chl-a, COD_{Mn}) were most commonly selected in the multiple regression models (Fig. S7, S8). The effects of eutrophication on macroinvertebrate diversity of the two lakes has been well documented in previous studies (Cai et al. 2012a, 2012b). Additionally, the amount of variation in bioassessment metrics explained by human-induced factors in Lake Taihu (31.4% on average) was higher than that in the case of of Lake Chaohu (15.5%), which probably due to the relative strong environmental gradients in Lake Taihu. In some cases, spatial variation in bioassessment metrics was also affected by natural variables (mainly F_m) to some extent (Fig. S7, S8). These results are reasonable since wind-wave action is a crucial natural process shaping biological community structure in large lakes (Hofmann et al. 2008, Cai et al. 2017). Thus, the results indicated that the role of natural gradients should better be taken into account in bioassessment even if we focus on a single lake. In addition, we found that natural variables were less important in Lake Chaohu, with only two significant models having been detected. A possible explanation is that wind-wave action is less intensive in Lake Chaohu with a relatively low dynamic ratio ($\sqrt{\text{surface area}/\text{mean depth}} = \sqrt{770}/3.0 = 9.2$) (Håkanson 1982), contrasting with an extreme high value of Lake Taihu ($\sqrt{2338}/1.9 = 25.4$) owing to its large surface area and shallow waters. Therefore, the effects of wind-wave action on bioassessment metrics are dependent on lake morphology, which may have important implications for the development of multi-metric indices and other bioassessment approaches.

The shared fraction of the three explanatory variable datasets also accounted for a considerable proportion of the variation in bioassessment metrics, indicating the spatially-structured environmental effects. The results are reasonable since environmental variables are often strongly spatially structured (i.e., spatial autocorrelation) in highly-connected systems (Kühn and Dormann 2012). For example, the intensity of wind-wave action at a site strongly depends on its spatial location (Håkanson 1982). Thus, the shared fractions of environmental and spatial variables on bioassessment metrics may be rather explained by environmental filtering than by dispersal processes.

It should be noted that the relatively high amount of unexplained variation was observed (41.6% –96.2%) in our study, and even non-significant models were detected in some cases. Such results are common in the very conservative statistical analyses based on adjusted R^2 (Peres-Neto et al. 2006, Vilmi et al. 2016c), and the high

unexplained variation may also be associated with some unmeasured important environmental factors and/or inadequate modelling of spatial processes. We, however, are confident that this explanation does not fit well in our study since a large number of spatial variables across different scales and various different environmental factors were considered. Rather, it is possible that stochastic processes (e.g., colonization, extinction and ecological drift) may result in complex spatial patterns given the high connectivity among sites (Vellend et al. 2014). Furthermore, we cannot preclude the importance of biotic interactions, such as competition, predation and mutualism, in affecting variation in the metrics' values.

Our results showed considerable seasonal variability in the contribution of environmental and spatial factors to the patterns of bioassessment metrics (Fig. S7, S8). The seasonal variations may be linked to the phenology and life-cycle patterns of different species, such as emergence, recruitment and overwintering (Clarke and Hering 2006). Several studies have demonstrated that seasonal succession of community composition is a major confounding factor affecting metacommunity organization and bioassessments (Clarke and Hering 2006, Erös et al. 2012). Regarding our two eutrophic lakes, the benthic communities were generally exclusively dominated by short-lived and small-sized chironomids and oligochaetes, which generally exhibited great differences in abundance among seasons (Table S1, S2). For example, the abundance of pollution-tolerant *Limnodrilus hoffmeisteri*, accounting for 60.9% of the total macroinvertebrate abundance in Lake Taihu, was lower in August than in the other three months (Table S1). In Lake Chaohu, the abundance of chironomids constituted 77.5% of the total macroinvertebrate abundance, with those dominant taxa varying considerably among seasons. Specifically, the first dominant chironomid, *Prosilocerus akamusi* (32.5% of the total macroinvertebrate abundance), showed extremely low abundance in April (1.2 ind/m²) and July (6.3 ind/m²) owing to emergence and aestivation into deep sediments (Zou et al. 2018), contrasting with very high abundance in January (142.7 ind/m²) and October (314.9 ind/m², Table S2). Evident seasonal patterns were also observed for other two dominant chironomids *Tanytus chinensis* and *Microchironomus tabarui* (Table S2). In contrast, the abundance of large-sized and long-lived molluscs generally exhibited weak or no seasonality, which might be due to considerable overlap of cohorts (Cai et al. 2010). Thus, life-cycle seasonality of chironomids and oligochaetes was probably responsible for the observed differences in metrics' values among seasons. Additionally, the seasonality of the environmental factors could also be important in regulating the contribution of different types of ecological drivers to the seasonal patterns of macroinvertebrate community assembly (Wojciechowski et al. 2017). Hence, the high temporal variability in the strength of different processes supports the idea that results from single snapshot surveys may be biased (Erös et al. 2012, Wojciechowski et al. 2017).

4.2 Performance of multiple metrics in bioassessment

Our results indicated that the performance of the three groups of metrics varied greatly in characterizing anthropogenic stressors. Overall, the trait-based metrics performed best with the highest variation associated with human-induced variables, which strongly supported our second specific hypothesis. This finding is not surprising because local community composition is rather selected by environmental filters mainly via species traits than their species identity, with appropriate traits passing through the habitat filters to be present in the community (Poff 1997). Several studies have highlighted the promise of the functional trait approach for freshwater bioassessment (Menezes et al. 2010, Van den Brink et al. 2011).

Contrary to our expectation, taxonomic distinctness (TD) metrics were only moderately strongly associated with human-induced variables in Lake Taihu, whereas the relationships were rather weak in Lake Chaohu. TD metrics were originally developed and further examined extensively in marine ecosystems (Clarke and Warwick 2001), yet their applicability for freshwater ecosystems has not been well evaluated (Vilmi et al. 2016b, Stojkoviã et al. 2017). Previous results have been both for (Stenger-Kovács et al. 2016) and against (Abellán et al. 2006, Vilmi et al. 2016a) the efficiency of TD in indicating ecological status of freshwater ecosystems. The challenge with TD metrics is that the taxon richness of a community should be high enough for the calculation of reliable index values (Clarke and Warwick 2001). Although TD indices are assumed to be immune to sampling efforts, they are not independent of low richness typically observed in several organismal groups (Vilmi et al. 2016b). In our data set, species richness was very low in many samples (e.g., species richness in 45% of samples ≤ 4 in Lake Chaohu, the value was 44.5% in Lake Taihu, see the histograms in Fig. S9), which may generate biased AvTD and VarTD values of these samples. In a study examining the response of AvTD and VarTD of three freshwater organism groups along nutrient gradients, Vilmi et al. (2016b) also found that low taxon richness of macrophytes resulted in problematic relationships between TD indices and nutrient levels. Hence, the low effectiveness of TD indices in our lakes, in particular in Lake Chaohu, might be a consequence of low taxon richness associated with high levels of trophic state.

General diversity measures of benthic macroinvertebrates (e.g., richness, Shannon and Pielou indices) are used as a core metric in numerous biological assessment methods (Birk et al. 2012). However, our results showed their questionable usefulness as an element of bioassessment in our lakes. The decrease of their values in freshwater organisms along with increasing anthropogenic disturbance is the underlying assumption of their utility in bioassessment (Koperski 2011). This assumption is based on the theoretical notions that increasing anthropogenic stress excludes taxa because each taxon has a limited range of conditions it can tolerate. Increasing exposure to stress should induce sequential loss of certain taxa, making decreasing diversity a convincing indicator of

ecological status. However, species diversity often has limited efficiency because different taxa are usually divergent in their ecological preferences and not related in a simple way with any single limiting factor or a stressor. Benthic faunas in lakes and streams have different preferences for certain conditions such as oxygen concentrations, water chemistry, bottom substrate and food availability (Sundermann et al. 2015; Berger et al., 2018). Consequently, even if species replace each other, diversity may not change along the gradient of targeted environmental stressors. In this instance, the effects of certain, potentially very important, environmental factors on benthic macroinvertebrate diversity seem to be doubtful, weak and unclear. For instance, no significant, linear or non-linear relationships were detected between any of general diversity measures of littoral invertebrates and TP in a study of 45 lakes (Donohue et al. 2009). Similarly, an intensive study of 66 lowland European streams clearly indicated that the general diversity measures of invertebrates showed the weakest response to nutrient enrichment and, moreover, had lower indicative value than those of benthic diatoms, macrophytes and fish (Johnson and Hering 2009). Hence, the weak relationships found in our research and many previous studies suggested that general diversity measures could provide limited information for monitoring the effects of eutrophication using lake macroinvertebrates in our study systems. Lastly, a weakness of this study is that only few bioassessment metrics were tested, which may question the generality of our results to other metrics. In the future, more metrics and types of aquatic ecosystems should be considered to understand their usefulness in bioassessment.

5. Conclusions

Freshwater ecosystems are severely threatened by multiple anthropogenic pressures, urging the development of efficient bioassessment approaches that can discriminate the signal due to human disturbance from the natural variation inherent to ecosystems. Usually, dispersal-related spatial processes are neglected in bioassessment techniques at fine spatial extents. However, our present findings highlighted that spatial variables are important for the variation in all the three types of biotic metrics even at the within-lake scale. Therefore, we propose that future bioassessment should better take spatial processes into consideration because a failure to do so may give a biased classification of ecological status. Furthermore, considering the substantial seasonal variability, we strongly corroborate the idea that bioassessment should go beyond snapshot sampling, as the mechanisms controlling biotic metrics may be temporally variable and to some degree unpredictable. The poor performance of general species diversity indices and taxonomic distinctness metrics suggests that these measures should be used with caution, especially for biological communities suffering severe anthropogenic stressors and showing typically low species richness. Alternatively, utilizing trait-based metrics that are less sensitive to spatial processes would provide more robust information about the ecological status of aquatic systems. To this end, despite our work was confined to two lakes, the findings may have important general repercussions for other large lakes and similar highly-connected aquatic ecosystems, such as sets of connected small lakes or networks of ponds.

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Appendix A-D. Supplementary data

Supplementary data to this article can be found online.

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