Ecosphere

Stochasticity overrides deterministic processes in structuring macroinvertebrate communities in a plateau aquatic system

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Abstract. Deterministic and stochastic processes are two major factors shaping community dynamics, but their relative importance remains unknown for many aquatic systems, including those in the high-elevation Qinghai–Tibet Plateau. Here, we explored the causes of multidimensional beta diversity patterns (i.e., taxonomic, functional, and phylogenetic) of a macroinvertebrate metacommunity in this large aquatic system by using multiple approaches (i.e., null models, phylogenetic signal testing, and ordination-based approaches). To obtain insights into community assembly mechanisms, we also analyzed beta diversity in two deconstructed sub-metacommunities (e.g., different tributaries and the main lake body). We found that most functional traits showed significant phylogenetic signals, indicating that the functional traits were profoundly influenced by evolutionary history. The null models showed randomness of functional and phylogenetic beta diversities for the whole basin and its tributaries, confirming the importance of stochasticity over deterministic processes in controlling community structure. However, both phylogenetic and functional community structures were clustered in the Qinghai Lake, probably reflecting the importance of environmental filtering. Ordination-based approaches also revealed that both environmental factors and spatial processes accounted for variation in taxonomic, functional, and phylogenetic beta diversity. More specifically, environmental filtering was more important than spatial processes for the functional dimension, but the opposite was true for the taxonomic and phylogenetic dimensions. The paleogeographic history of the Qinghai Lake basin may have contributed substantially to the prevalence of stochastic processes. Overall, this study provides a better understanding of ecological patterns and assembly mechanisms of macroinvertebrate communities across this poorly known high-elevation aquatic system that is highly sensitive to climate warming.

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Introduction

Integrating the multiple dimensions (i.e., taxonomic, functional, and phylogenetic) of biodiversity to examine the degree to which stochastic and deterministic processes structure ecological communities is a modern framework in community ecology (Garcia-Giron et al. 2019).

Empirical evidence suggests that either deterministic processes, such as environmental filtering and biotic interactions (Chase and Myers 2011, Isabwe et al. 2018, Garcia-Giron et al. 2020), or stochastic processes, such as dispersal, extinction, or speciation (Hubbell 2001, Grönroos et al. 2013, Tonkin et al. 2017), drive community assembly at different spatial and temporal scales. Indeed, modern theoretical frameworks emphasize the importance of integrating these two processes when exploring the assembly mechanisms of ecological communities (Leibold and McPeek 2006, Adler et al. 2007).

Most previous studies on community assembly have focused on a purely taxonomic viewpoint (Condit et al. 2002, Ackerly et al. 2003), where species are assumed to be evolutionarily independent and ecologically equivalent. One of the most important sources of criticism to this traditional taxonomic approach is that it does not consider the evolutionary history and ecological functions of the species in ecological communities (Faith and Baker 2006, Devictor et al. 2010). Functional diversity, reflecting the diversity of morphological, ecological, and physiological traits of species (Petchey and Gaston 2006), was initially proposed as an alternative to the traditional taxonomic measures. Since biological traits are sensitive to environmental changes (Aiba et al. 2013, Obertegger and Flaim 2018), trait-based functional diversity can provide better insights into ecosystem functioning than taxonomic diversity (Alahuhta et al. 2019). The existing sets of functional traits in a community is the result of the selection differences of abiotic and biotic factors among species, which provides crucial clues for understanding the relative importance of different processes in community assembly (Kraft et al. 2008, Lebrija-Trejos et al. 2010). However, it is unlikely to be able to a priori identify or quantify all relevant traits for diverse local communities at the metacommunity level (Heino and Tolonen 2017b, Gianuca et al. 2018). Limited numbers of functional traits cannot fully represent the actual ecological niche of each species in the community, so that relevant ecological processes can usually be deduced only partially (Swenson et al. 2013).

Combining phylogeny and functional traits of species is often used to reveal the underlying mechanisms of community assembly. In this regard, phylogenetic diversity provides insights into how evolutionary and ecological processes may interact to shape patterns of species and trait composition, abundance and distribution (Webb et al. 2002). Phylogenetic diversity, typically considered as the mean length of evolutionary pathways that connects a given set of taxa along the phylogenetic tree, was proposed as a tool to explain the role of species interactions, historical imprints, and evolutionary legacy in community assembly (Webb et al. 2002). According to the niche conservatism hypothesis (Webb et al. 2002), phylogenetically closely related species are likely to have similar traits (Darwin et al. 1859), and in the absence of multi-trait information for the species, phylogenetic measures might therefore constitute relevant and integrative surrogates to the functional diversity communities (Webb et al. 2002). However, if the traits considered are labile, functional and phylogenetic patterns can be decoupled and provide complementary insights into community assembly (Heino and Tolonen 2017a, b, Rocha et al. 2018, Garcia-Giron et al. 2019). The overlap between phylogenetic and functional community structure depends on the strength of phylogenetic signals in functional traits, which in turn depends on the underlying processes of species diversification and niche evolution (Burns and Strauss 2011). Therefore, analyzing multiple dimensions of beta diversity may provide a clearer picture of how ecological communities are assembled over different timescales (Webb et al. 2002).

Generally, previous studies on community assembly mainly focused on the taxonomic dimension, while investigations on other dimensions of beta diversity emerged only recently. Moreover, existing studies have mainly been carried out in lowland rivers, streams, lakes, or ponds (Rocha et al. 2018, Garcia-Giron et al. 2019, Hill et al. 2019, Lindholm et al. 2020, Wang et al. 2020). However, studies conducted in high-elevation plateau aquatic ecosystems are still largely lacking and centered on examining taxonomic diversity (Li et al. 2019a, b).

The Tibetan Plateau is the highest (average altitude above 4500 m a.s.l.) and the largest plateau on the Earth (Lin et al. 2017). Over 1000 lakes (area >1 km^2) are distributed across this plateau, most of which are land-locked saltwater

lakes (Ma et al. 2011). Under the current background of global warming, the Tibetan Plateau is warming about three times faster than the global average (Lin et al. 2017). Plateau lakes and streams, with unique and diverse faunas, are among the world's most vulnerable aquatic ecosystems and are severely threatened by climate warming (Jiang et al. 2013, Tonkin et al. 2018). Due to their high levels of endemicity and diversity, high-elevation plateau lakes and streams are considered ideal arenas to examine the mechanisms of community assembly, including those affecting macroinvertebrate communities (Vilmi et al. 2020). Macroinvertebrates are important components of aquatic ecosystems and have become a model group for studying community assembly, biodiversity maintenance, and environmental assessment due to their high taxonomic, phylogenetic, and functional variability (Heino and Tolonen 2017a, b, Hill et al. 2019, Li et al. 2019a, b).

In this study, we combined multiple methods (i.e., null models, phylogenetic signal testing, and ordination-based approaches) to assess whether the role of deterministic and stochastic processes was consistent for the multiple beta diversity dimensions in a macroinvertebrate metacommunity located on the Tibetan Plateau. Here, we tested the following hypotheses: (1) The environmental pressures caused by harsh environmental conditions of the Qinghai–Tibet Plateau (i.e., severe coldness, lack of oxygen, scarce precipitation events, and strong ultraviolet radiation) should lead to environmental filtering on specific lineages and traits, which may also result in convergent evolution of traits and the absence of phylogenetic signals (Zhang et al. 2017); (2) environmental pressures may induce ecological constraints on macroinvertebrate community and lead to non-random beta diversity patterns (Siefert et al. 2013); (3) trait-based and phylogeny-based approaches should provide different insights into community assembly compared with the traditional taxonomic approach that treats all species as equally differentiated from each other (Gianuca et al. 2018); and (4) taxonomic and phylogenetic beta diversity should be controlled jointly by environmental filtering and dispersal limitation (Garcia-Giron et al. 2019), but functional beta diversity should be more strongly influenced by environmental

filtering (Rocha et al. 2018). This assumption was based on the findings of previous studies suggesting that species identity and evolutionary relatedness are significantly associated with dispersal limitation and evolutionary divergence (Mouquet et al. 2012, Cai et al. 2019, Garcia-Giron et al. 2019), while functional traits are more directly related to species sorting due to species trait–environment associations (Hoeinghaus et al. 2007, Heino et al. 2013, Rocha et al. 2018). Our study will help elucidate which factors limit the macroinvertebrate communities in plateau aquatic ecosystems and how biodiversity patterns are maintained in these fragile high-elevation environments in the Anthropocene.

MATERIALS AND METHODS

Study area

This study was conducted in the Qinghai Lake, its tributaries and smaller nearby lakes (latitude 36°23′–37°34′ N, longitude 98°36′–100°59′ E, and altitude 3154–3582 m a.s.l.). Qinghai Lake is located in the northeast of the Qinghai–Tibet Plateau. Qinghai Lake is the largest enclosed lake and saltwater lake in China, and it is also a typical representative of landlocked plateau lentic ecosystems in the world. Qinghai Lake is an important breeding ground and the main node for East Asian migratory waterbirds and is thus listed as International Important Wetland Protectorate (Cui et al. 2011). Qinghai Lake is also considered important for maintaining the biodiversity resource of the Qinghai–Tibet Plateau. This lake has a catchment area of 30,000 km², contributed by the drainage of about 40 rivers. Among these 40 rivers, there are seven major ones, including the rivers Buha, Heima, Caiji, Shaliu, Ganzi, Quanji, and Daotang, which account for 95% discharge of the lake (Wang and Dou 1998). The Qinghai Lake watershed belongs to semiarid continental plateau climate. Under the background of climate warming, the climatic conditions of the Qinghai–Tibet Plateau are gradually moving toward warming and humidification. The water level of Qinghai Lake is rising, and the water area has increased in recent years owing to the increasing precipitation and accelerated melting of glaciers. Since 2005, water levels have increased over three meters (Lin et al. 2017).

Currently, Qinghai Lake encompasses an area of 4549 km^2 and an average depth of 21 m (Fig. 1).

Macroinvertebrate sampling

Benthic macroinvertebrate sampling was carried out in early August in 2019. We set up a total of 57 sampling sites across the studied region, including 30 sites in the main body of Qinghai Lake, three in smaller nearby lakes (Gahai, Erhai, and Jinshawan), and 24 sites in its six major inflowing rivers (the rivers Buha, Shaliu, Quanji, Hema, Caiji, and Daotang; Fig. 1). In each site of the Qinghai Lake and smaller lakes, three quantitative samples were taken with modified Petersen grab (0.0625 m^2 in area). In the six major rivers sites, we took three random quantitative samples by Surber sampler (30 × 30 cm, with 500 μm in mesh size) for benthic macroinvertebrates, and subsequently sieved them using a

500-μm sieve in the field. Specimens were hand-picked within five hours of collection from the sediment on a white porcelain plate, and they were later stored and preserved in 95% ethanol. In the laboratory, macroinvertebrates were identified to lowest possible taxonomic level (i.e., genus or species) according to the relevant references (Brinkhurst 1986, Morse et al. 1994, Dudgeon 1999, Epler 2001, Zhou et al. 2003), and the number of individuals was counted for each taxon.

Environmental variables

Altitude, latitude, and longitude were recorded using a portable GPS (UniStrong MG721W). Surface water samples of one liter were collected at each sampling site and stored in plastic bottles. The water samples were kept at low temperature and in shade. A portable
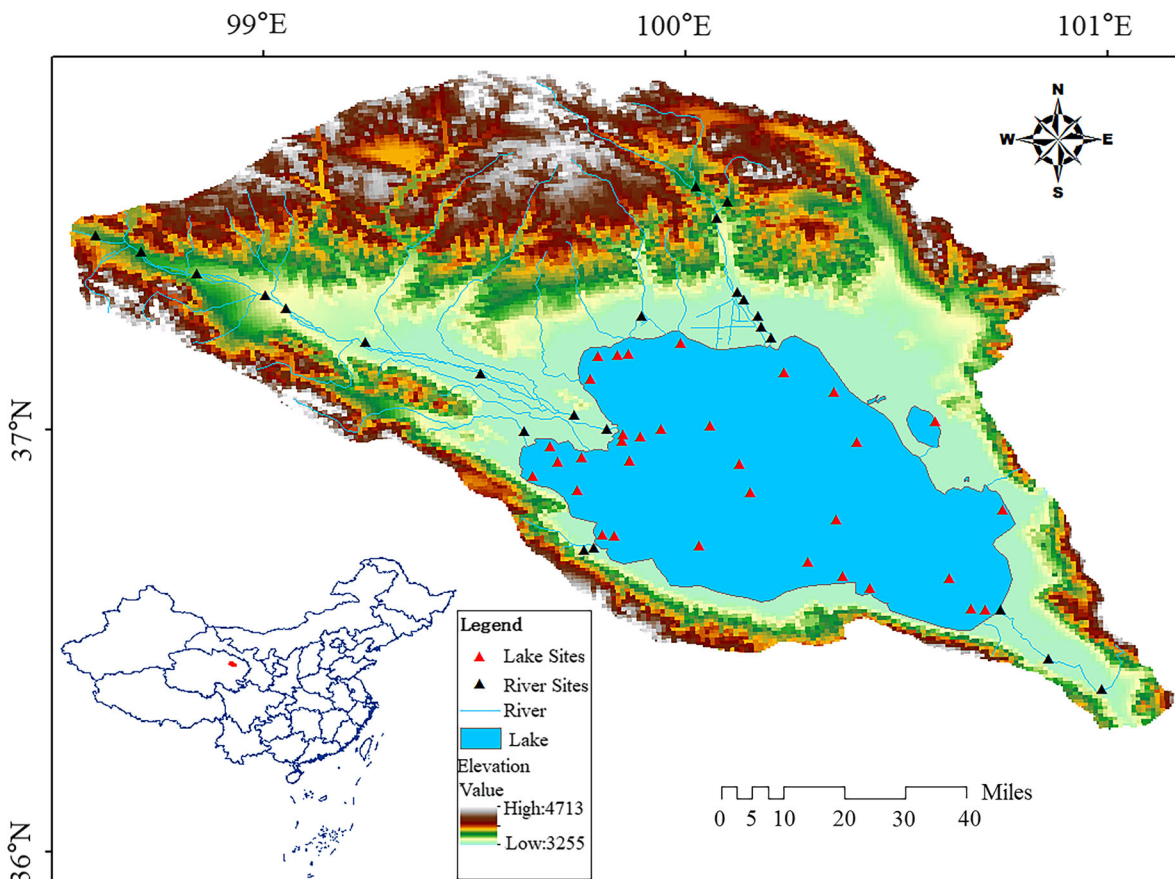

Fig. 1. Location of the Qinghai Lake basin in China and the distribution of the 57 sampling sites in the Qinghai Lake, its tributaries, and smaller lakes across the study area.

multiparameter water quality analyzer (Hach HQ40D) was used to record water temperature (T), water transparency (Trans), pH, dissolved oxygen concentration (DO), dissolved oxygen saturation (DOS), electrical conductivity (COND), total dissolved solids (TDS), and other water physical and chemical parameters. Water samples were taken to the laboratory for analysis; ten chemical variables including total nitrogen (TN), total phosphorus (TP), ammonia nitrogen (NH_4^+–N), nitrate nitrogen (NO_3–N), nitrite nitrogen (NO_2–N), silicate (SiO_3–Si), soluble phosphorus (SRP), permanganate index (COD_{Mn}), alkalinity, and salinity were analyzed according to the standards provided by Wei et al. (1989) and Huang et al. (1999). Detailed information regarding the laboratory testing methods is listed in Appendix S1.

Spatial variables

Moran Eigenvectors maps (MEM), formerly called principal coordinates of neighbor matrices (Borcard and Legendre 2002), were used to identify and model spatial structures from relatively broad (e.g., the entire sampling area) to small (e.g., relations among nearby sampling sites) scales (Borcard et al. 2018). Moran Eigenvectors maps can model any type of spatial structure and are known to provide appropriate spatial structures of different geographical areas (Borcard et al. 2018). Of all the MEMs produced, we retained those associated with significant Moran's I and positive eigenvalues in the subsequent analyses, because they represent positive spatial autocorrelation (Gilbert and Bennett 2010). The spatial analysis was conducted with the pcnm function from vegan package in R v3.6.1 (R Core Team 2018).

Constructing the phylogenetic tree

We constructed a phylogeny that contained 75 of the total number of macroinvertebrate (only insects) taxa in the Qinghai Lake watershed (Fig. 2). A DNA supermatrix was established by sequencing two mitochondrial (cytochrome c oxidase subunit I [COI] and small subunit ribosomal 16S rRNA [16S]) and two nuclear (ribosome rRNA 18S gene [18S] sequence and ribosome rRNA 28S gene [28S]) from the macroinvertebrate samples. The DNA supermatrix was then analyzed using RAXML v.8.2.0

(Stamatakis 2014) to infer a maximum-likelihood phylogeny. Finally, r8s software (Sanderson 2003) was used to process the taxon-level maximum-likelihood tree by the penalized likelihood approach. Detailed information regarding the phylogenetic tree reconstruction is listed in Appendix S2.

Data analysis

Measurement of phylogenetic, taxonomic, and functional beta diversity.—Firstly, we estimated abundance-weighted phylogenetic beta diversity based on the phylogenetic distance matrix using mean pairwise phylogenetic dissimilarity (Swenson 2014) using the function COMDIST from the R package picante (Kembel et al. 2010). Specifically, we used only insects to estimate phylogenetic, taxonomic, and functional beta diversity because non-insect taxa (i.e., *Gammarus lacustris* and *Nais elinguis*) are phylogenetically very distant from insects. This could bias our analysis by overestimating the phylogenetic diversity of sites that harbored these non-insect taxa and by decreasing the phylogenetic importance of single-insect taxa (see also Swenson 2014). Secondly, pairwise taxonomic beta diversity was calculated based on abundance data using Bray-Curtis dissimilarities with the function beta.pair.abund in the R library betapart (Baselga et al. 2013). Thirdly, functional diversity represents the diversity of morphological, ecological, and physiological traits in the multidimensional niche space (Petchey and Gaston 2002). We selected eight biological traits of macroinvertebrates, which were further subdivided into 24 different categories (Table 1). The eight traits included descriptions of life history, mobility, and basic biological characteristics, which are commonly linked to ecosystem functions in inland aquatic ecosystems (Usseglio-Polatera et al. 2000). We obtained the trait information of macroinvertebrates mainly from published accounts (Morse et al. 1994, Beche et al. 2006, Poff et al. 2006), but we also referred to some relevant Chinese literatures for further verification (Zhou et al. 2003, Li et al. 2019*a, b*). Abundance-weighted functional beta diversity was also calculated using the function COMDIST, based on Gower's multi-trait distance matrix (Gianuca et al. 2018).
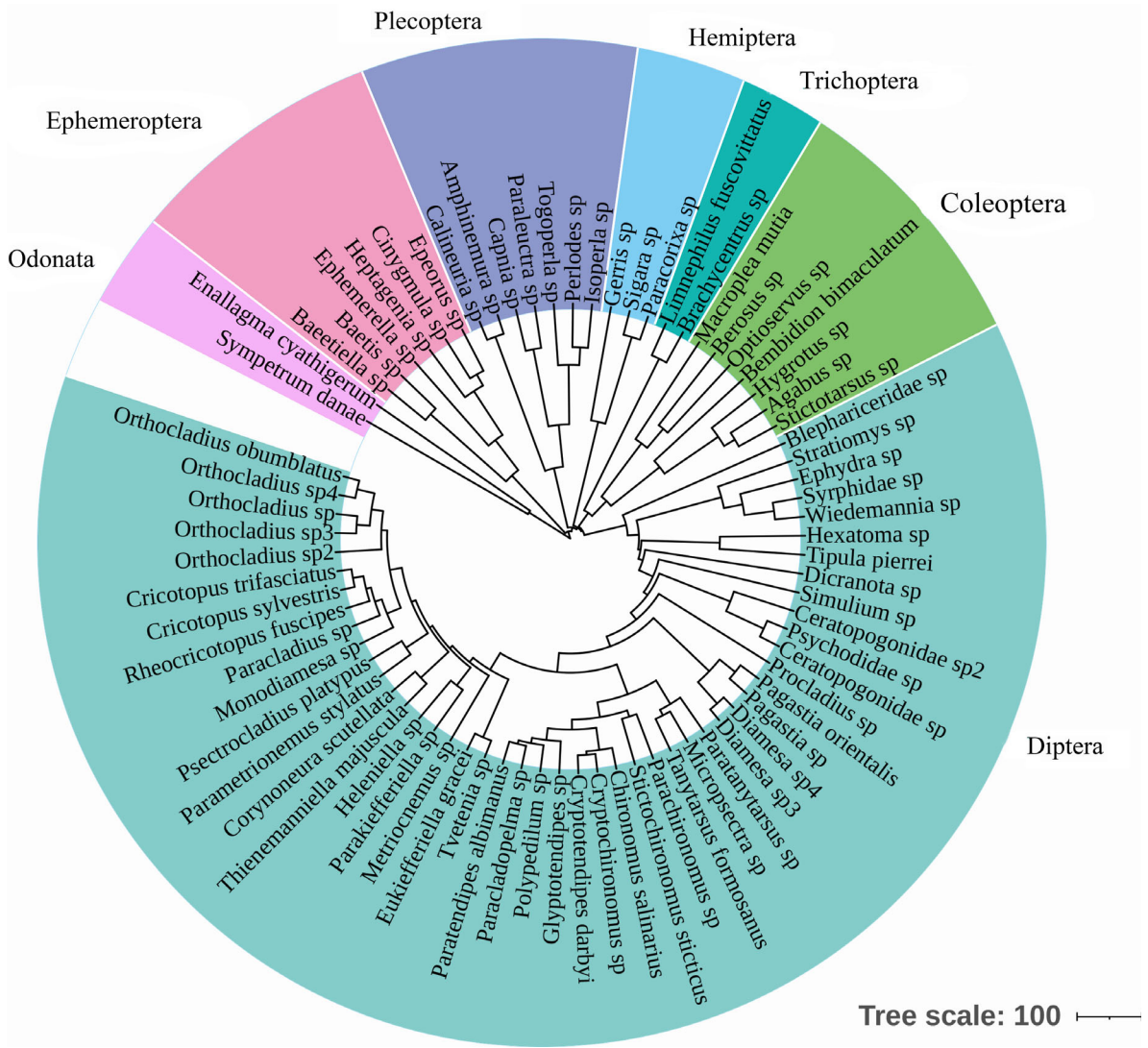
Fig. 2. Phylogenetic tree constructed using COI, 16S, 18S, and 28S genes of the 75 study macroinvertebrate taxa in Qinghai Lake basin.

Phylogenetic signal tests.—The phylogenetic signal in functional traits was deduced by the distribution of functional traits in the phylogenetic tree produced, and the degree of phylogenetic niche conservatism for different traits was estimated by strength of phylogenetic signal (Revell et al. 2008). For binary or categorical trait variables, we estimated phylogenetic signal of each trait categories, using Purvis' D statistic (Fritz and Purvis 2010). A D value of 1 indicates that traits are randomly distributed across the tips of the phylogeny (i.e., no evidence for phylogenetic

signal in the functional traits studied); a value of D less than 1 suggests the traits diverge along the phylogeny; a value of 0 indicates that traits follow a Brownian threshold model; and if the D is less than 0, traits are less labile than the Brownian motion expectation and therefore have strong phylogenetic signals (Fritz and Purvis 2010).

To assess the statistical significance of phylogenetic signals for each binary trait, we randomly displaced the binary traits at the end of the phylogenetic trees for 999 times to obtain the null distribution. By comparing the observed values

Table 1. Trait classifications and results of phylogenetic signal test by Purvis' *D* statistic for benthic macroinvertebrates in the Qinghai Lake basin.

Traits	Category	Code	Estimated D	$P(D < 1)$	$P(D > 0)$
Adult life span	<1 week	Life1	−0.574	0	0.931
	<1 month	Life2	−0.322	0.001	0.712
	>1 month	Life3	−1.18	0	0.966
Leave habitat ability	Absent	Lea1	−0.799	0	0.975
	Present	Lea2	−0.989	0	0.995
Crawling speed	Very weak	Cra1	−0.76	0	0.969
	Weak	Cra2	−0.638	0	0.847
	Strong	Cra3	−0.999	0	0.977
Swimming ability	None	Swim1	−1.149	0	0.995
	Weak	Swim2	−1.681	0	1
	Strong	Swim3	−1.299	0	0.983
Armoring	None (soft-bodied)	Arm1	−0.71	0	0.96
	Poor (heavily sclerotized)	Arm2	−0.598	0	0.82
	Good (e.g., some cased caddisflies)	Arm3	−1.413	0	0.988
Shape	Streamlined (flat, fusiform)	Shap1	−0.732	0	0.945
	Not streamlined (cylindriform, round or bluff)	Shap2	−0.775	0	0.98
Respiration	Tegument	Res1	−0.107	0.001	0.572
	Gills	Res2	−0.72	0	0.964
	Air (spiracles, tracheae, plastron)	Res3	-1.516	0	0.976
Life form	Burrow	Form1	0.534	0.158	0.21
	Climb	Form2	0.032	0.066	0.516
	Sprawl	Form3	−0.108	0	0.648
	Cling	Form4	−0.4	0	0.827
	Swim	Form5	−1.256	0	0.988

Note: $P(D < 1)$ is the significance level in the test of random distribution of traits along the phylogeny, and $P(D > 0)$ is the result of testing whether or not *D* is significantly different from zero.

and the null distribution, we determined whether the p-values were significant. The D test of phylogenetic signals was conducted with package Caper (Orme et al. 2012) in R v3.6.1 (R Core Team 2018).

Variation partition of taxonomic, phylogenetic, and functional beta diversity.—The derived distances obtained from pairwise taxonomic, phylogenetic, and functional beta diversity matrices were synthesized into principal coordinate analysis (PCoA) with the Lingoes correction (Borcard et al. 2018) using the function pcoa from the R package ape (Paradis et al. 2004). The PCoA eigenvectors for taxonomic, phylogenetic, and functional beta diversity were used as response variables for subsequent variance partitioning analyses (Cai et al. 2019). The non-normally distributed local environmental variables (except pH) were transformed (log10 for continuous data) to improve their normality. Redundancy analysis (RDA; Borcard et al. 2018) employed the ordiR2step ($P < 0.05$ after 999 random permutations)

function in the vegan R package to run forward selection for environmental variables and spatial (MEMs) variables, respectively (Oksanen et al. 2016). To examine the relative contribution of local environmental variables and spatial variables (MEM eigenvectors) on the patterns of taxonomic, phylogenetic, and functional beta diversity for the main body of Qinghai Lake, surrounding rivers and entire Qinghai basin, the variance partitioning analysis was conducted using the varpart function in the R package vegan (Oksanen et al. 2016). RDA was carried out including all significant environmental and spatial variables identified after forward selection. In addition, we tried to set a group of dummy variables to distinguish between lentic and lotic sites. However, we could not get significant dummy variables in each beta diversity dimension after we ran forward selection. The total percentage of variation in each beta diversity dimension explained was divided into unique and shared contributions of environmental and spatial predictors using variance

partitioning. We reported adjusted R^2 of pure and shared contributions of the spatial and environmental variables from the constrained RDA ordinations. Statistical significance of the unique and shared contribution in each set of predictors was undertaken with the function anova vegan in the R package vegan (Oksanen et al. 2016).

Null model analysis.—We used null models to assess whether the observed functional and phylogenetic beta diversity patterns were consistent with their expected values under the null hypothesis that assumed that the detected pattern results from a random draw (Swenson 2014). For functional and phylogenetic beta diversity, the null model was created by reshuffling species names on the phylogenetic tips with 999 random runs for randomizing the phylogenetic relatedness of species. We first calculated the phylogenetic and functional beta diversities with the function COMDIST for each random metacommunity (based on a total of 999 randomizations), and then, these values were used to approximate the null distribution. We calculated deviations of the observed metrics from their null expectation as standardized effect sizes (SES):

$$SES = \frac{x - \mu}{\sigma}$$

where x represents the observed beta diversity, and μ and σ represent the mean and standard deviation values from the null model. Values of SES lower or higher than 0 indicate clustering or overdispersion, respectively (Swenson 2014). Two-sided Wilcoxon signed rank test was used to test whether the mean overall value of each beta diversity dimension was different from the expected value of zero for random data. Null model analyses were conducted using the R packages picante (Kembel et al. 2010) and vegan (Oksanen et al. 2016).

RESULTS

A total of 89 taxa were identified, belonging to three phyla, six classes, and 38 families (Appendix S3: Table S1). Of them, 36 and 74 taxa occurred in the main body of Qinghai Lake and in its surrounding tributaries, respectively. Only 21 taxa were shared between Qinghai Lake and the tributary streams studied. In these streams, aquatic insects contributed 49% of the total

taxonomic richness, with Chironomidae (19.6% relative abundance, 38 taxa overall), non-chironomid Diptera (2.1%, 12 taxa), Plecoptera (1.3%, eight taxa), Ephemeroptera (4%, six taxa), and Coleoptera (0.8%, seven taxa) being the taxonomically richest groups. However, the amphipod *Gammarus pengi* (45.9% relative abundance) was undoubtedly the numerically dominating species in the study streams. The mayflies *Baetis* sp. (11.7%) and *Baetiella* sp. (5.2%) were the other dominant taxa in the tributaries of Qinghai Lake. In the main body of the Qinghai Lake, aquatic insects contributed 89.2% of the total richness, with Chironomidae (61.6% relative abundance, 19 taxa overall), non-chironomid Diptera (4.9%, seven taxa), and Coleoptera (22.7%, five taxa), being the taxonomically richest groups. The dominant macroinvertebrate taxa in the Qinghai Lake were the non-biting midge *Chironomus salinarius* (27.7%), the water boatman *Sigara* sp. (21.9%), the non-biting midges *Cricotopus sylvestris* (12.2%) and *Tanytarsus formosanus* (10.3%), and the amphipod *Gammarus lacustris* (8.5%).

The D statistic denoting phylogenetic signal indicated that, with the exception of two trait categories (i.e., burrow and climb), the functional features examined showed stronger phylogenetic signal than expected by a Brownian motion model of trait evolution, with estimated D values ranging from −1.68 to −0.11. The estimated D values for burrow and climb trait categories were greater than 0 and less than 1, respectively, thereby showing relatively weak phylogenetic signals (Table 1).

The null model approach used also revealed that macroinvertebrate communities showed no significantly lower or higher functional and phylogenetic beta diversities than the null expectation when considering data from the tributary streams and the entire basin. This suggests that functional-based community assembly and lineage-related compositional patterns were most likely to be random. Interestingly, however, most of the SES values in the Qinghai Lake showed significant underdispersion, suggesting that community assembly based on particular traits and lineage compositions was dominated by deterministic processes (Fig. 3).

When we considered the entire basin, RDA and associated variation partitioning showed that the sets of environmental and spatial
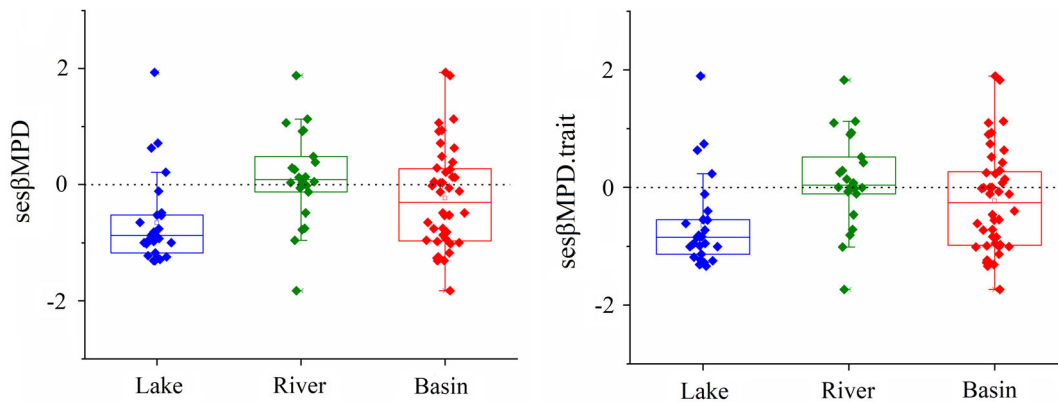
Fig. 3. Boxplot of the standardized effect size for phylogenetic (MPD) and functional beta diversity indices (MPD.trait) for the main body of Qinghai Lake (Lake), its tributaries (River), and the entire basin (Basin). Negative/positive SES values represent underdispersion and overdispersion of trait distribution compared with the random expectation, respectively.

variables selected as significant predictors of the three beta diversity dimensions were similar (Appendix S3: Table S2). The most commonly selected key environmental factors for taxonomic, functional, and phylogenetic beta diversity dimensions included salinity and depth (Appendix S3: Table S2). The most commonly selected spatial variables for taxonomic, functional, and phylogenetic beta diversity dimensions included two broad-scale (MEM5 and MEM4) and one medium-scale (MEM15) variables (Appendix S3: Table S3). Combining the significant spatial and environmental drivers of beta diversity revealed that the total explained variation (Fig. 4) was highest for the phylogenetic dimension (Adj. $R^2 = 0.48$), followed by the functional dimension (Adj. $R^2 = 0.34$) and the taxonomic approaches (Adj. $R^2 = 0.28$).

Variation partitioning further revealed some differences in the relative contribution of environmental and spatial variables to variation in taxonomic, functional, and phylogenetic community compositions. Pure spatial effects better explained the taxonomic dimension compared with the pure environmental effect. By contrast, environmental filtering, mainly through variations in salinity and water depth, was the most influential mechanism controlling both functional and phylogenetic community compositions (Fig. 4). Importantly, however, the shared effects between environmental and spatial variables accounted for the largest amount of

variation (Adj. $R^2 = 0.12$ to 0.27) in all beta diversity dimensions. For the tributaries of Qinghai Lake, the pure effect of spatial variables better explained all beta diversity dimensions. Regarding the main body of Qinghai Lake, only significant environmental filtering effect was detected (Appendix S3: Table S2 and Fig. 4).

DISCUSSION

In this study, we combined three methods (i.e., null models, phylogenetic signal evaluations, and ordination-based modeling) and used a multidimensional approach encompassing taxonomic, functional, and phylogenetic perspectives to examine the macroinvertebrate metacommunity organization in a high-altitude aquatic system. Most previous studies have relied on taxonomic distances as proxy for true phylogenetic relatedness due to the lack of molecular data for most macroinvertebrate taxa (Heino and Tolonen 2017a, b, Rocha et al. 2018, Hill et al. 2019). Our study is therefore unique since it does not only provide one of the first DNA-based phylogenetic perspectives for a relatively wide set of aquatic macroinvertebrate species (Múrria et al. 2012, 2018) but also bridges together different dimensions of beta diversity to infer mechanisms of community assembly in freshwater macroinvertebrates (Heino and Tolonen 2017a, b, Rocha et al. 2018). Our study suggests that the functional and phylogenetic compositions across
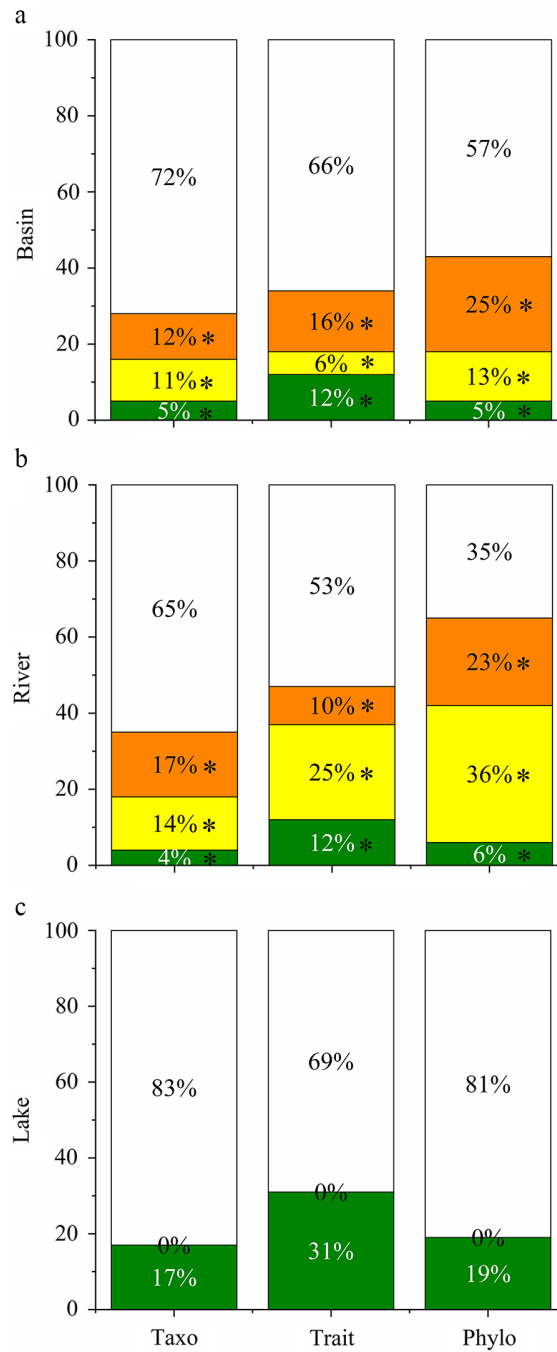
Fig. 4. Results of variation partitioning depicting the relative contribution (% based on Adj. R^2) of local environmental features (green), spatial effects represented by MEM eigenvectors (yellow), shared environmental and spatial effects (orange), and unexplained (white) to variation in different dimensions of beta diversity, that is, taxonomic structure (Taxo), functional structure (Trait), and phylogenetic structure (Phylo). (a, b, and c) represent basin, river, and lake scales. Asterisks indicate significant results.

the entire basin and across the surrounding rivers were merely random draws from the regional pool of traits and taxa. In addition, we detected significant phylogenetic conservatism in all the studied traits based on Purvis' D statistic, and only two trait categories (i.e., burrow and climb) showed weak phylogenetic signals. Our results also revealed that both environmental and spatial factors accounted for significant variation in taxonomic, functional, and phylogenetic beta diversities. However, environmental filtering contributed more than spatial processes to the functional dimension, whereas the opposite was true for the taxonomic and phylogenetic dimensions.

The role of stochastic (historical) processes in community assembly

Contrary to our expectations, we found that functional and phylogenetic beta diversities showed no difference from that expected by chance across the whole basin and across the surrounding rivers, suggesting the prevalence of stochasticity in structuring variation of trait and lineage composition. This finding suggests that processes shaping variation in trait and lineage compositions were mostly shaped by random draws from the regional trait and phylogenetic pool (Garcia-Giron et al. 2019). The patterns we detected may also stem from the combined effects of different habitat preferences and dispersal dynamics of distantly related lineages (Roa-Fuentes et al. 2019). More strikingly, the observed functional and phylogenetic beta diversities were consistently low relative to random expectations in the main body of Qinghai Lake, suggesting that both trait and phylogenetic community compositions were very similar in different sites within the lake.

The paleogeographic history of the Qinghai Lake basin may have contributed substantially to the prevalence of stochastic processes. The species pool hypothesis incorporates the idea that macroevolution and historical and geographic factors determine the size of a regional species pool (Taylor et al. 1990, Zobel et al. 1992). Thus, historical contingencies may have profound effects on the assembly of ecological communities (Macpherson et al. 1962, Ricklefs et al. 2011). In association with the uplift of Tibetan Plateau, the formation and development of Qinghai Lake

basin occurred during the Middle Pleistocene, whereby the Quaternary glacial, retreat and uplift of the surrounding mountains. Geologic data indicate that at approximately 0.15 Ma BP, the Gonghe Movement of the Tibetan Plateau led to the separation of Lake Qinghai from the upper reaches of the Ancient Yellow River system, after which Lake Qinghai became a landlocked lake with no connection to sea (Pan et al. 1994, Li et al. 1996). As the climate turned colder and drier at the dawn of the Holocene (10,500–7500 yr BP), Qinghai Lake gradually shifted from a freshwater lake to a saltwater lake, and only one large fish, the naked carp (*Gymnocypris przewalskii*), survived to this major change (Zhu and Wu 1975, Zhang et al. 2015). The excavated fossils of *Bellomya dispisalis*, a snail that lives in freshwater environments, were widely developed in the strata of the lakeshore in the west of Qinghai Lake, belonging to the Middle Pleistocene series. This suggests that freshwater fauna once flourished in the Qinghai Lake (Hu 1989). These historical processes manifested by the plate collisions, the uplift promoted by tectonic activities, the Quaternary glacial activities, the shift from a freshwater lake to a saltwater lake, and the highland climate (i.e., severe coldness, lack of oxygen, scarce precipitation, and strong ultraviolet radiation) led to an impoverished regional species pool. The frequent disturbance events, as well as the unsaturated species pool, may also lead to a decrease in the number of species potentially occupying the same niche. Therefore, by creating many vacant niches and reducing potential for interspecific competition, historical events contributed to such macroinvertebrate communities in the Qinghai Lake basin that were overwhelmingly dominated by stochastic process. Originating from the collision of the Cenozoic (~80 million yr BP) of the India-Pakistan plate and the Asia-Europe plate, the Qinghai–Tibet Plateau is considered the youngest plateau. The young geological history, frequent disturbance events, and impoverished species pool may be similar to that of the early Earth's environment. This may explain why the surveyed regional communities are consistent with the paleocommunities (i.e., Ediacaran paleocommunities; Mitchell et al. 2019) that are often dominated by stochastic processes.

Phylogenetic signal in functional traits

We found that most traits evaluated in this study were phylogenetically relatively conserved. Therefore, functional traits and phylogenetic relatedness were significantly coupled in the studied freshwater metacommunity. These findings suggest that phylogenetic lineages of aquatic macroinvertebrates can be used as proxies for functional dissimilarity due to strong phylogenetic signal exhibited by species traits (Murria et al. 2012). The strong phylogenetic signal may be due to a reduction in the potential range of character evolution caused by the fixation of ancestral traits (i.e., developmental constraints; Westoby et al. 1995). The impoverished species pool and a relatively short period of evolutionary time might also explain the seemingly conservative evolution of trait patterns (Barrett et al. 1993). Importantly, however, there are two trait categories that showed weak phylogenetic signals, indicating that phylogenetic and trait patterns might also differ in the Qinghai Lake basin. Environmental pressures could lead eventually to alteration in ecological characters over evolutionary time (Webb et al. 2002). Hence, we cannot rule out the possibility that the effects of environmental pressures caused by the highland topography of the Qinghai–Tibet Plateau (i.e., high elevation, high radiation, cold temperatures, saline conditions, and other harsh environmental conditions) and weak genetic constraints may have induced the convergent evolution of life histories (Danks 2007). For example, reproductive and physiological strategies may not necessarily be evolutionarily conserved (Clark et al. 2004, Cartier et al. 2011), thereby leading to the absence of phylogenetic signals in macroinvertebrate faunas. However, the applicability of the phylogenetic niche conservatism hypothesis (Webb et al. 2002, Múrria et al. 2018) for freshwater macroinvertebrates certainly requires further attention and needs to be confirmed by similar analyses in other areas of the world.

Disentangling the role of stochastic (dispersal) and deterministic (environmental filtering) processes in community assembly

Consistent with our expectations, we observed that the explanatory power of the constrained ordination models increased from taxonomic to functional and phylogenetic beta diversities for the whole Qinghai Lake basin. This finding was consistent with previous studies (Gianuca et al. 2018, Garcia-Giron et al. 2019) and further suggests that functional and phylogenetic dimensions may provide complementary information on assembly processes of ecological communities (Rocha et al. 2018, Hill et al. 2019). A likely reason to these findings is that closely related taxa possess similar functional attributes and thus respond in the same way to environmental gradients (Heino et al. 2007, Li et al. 2019a, b).

We also observed high residual variation in community structure based on taxonomic, functional, and phylogenetic dimensions, which may be attributed to site-specific context dependency, priority effects, historical legacies, and stochastic species distributions (Alahuhta and Heino 2013, Heino et al. 2013, Garcia-Giron et al. 2019). The unexplained variability may also refer to the importance of stochastic events for the assembly of freshwater macroinvertebrate metacommunities (Heino et al. 2015a, b, c), and the stochasticity that we detected might thus also be related to chance colonization, drift, establishment, and extinction (Garcia-Giron et al. 2019).

Variation partitioning results revealed a significant role of both environmental filtering and spatial processes on macroinvertebrate community structure. As expected from the fourth hypothesis, environmental filtering affected more than spatial processes the functional dimension, and the pattern detected was opposite for taxonomic and phylogenetic dimensions. This is a reasonable finding because functional beta diversity should be more directly associated with environmental filtering than spatial processes due to species trait–environment relationships (Heino et al. 2013, Rocha et al. 2018, Cai et al. 2019). Taxonomic and phylogenetic beta diversity patterns also suggested the importance of spatial processes at the focal regional scale. More specifically, dispersal limitation might hinder species from tracking suitable habitat patches (i.e., environmental variation), thereby weakening the strength of environmental filtering (Heino et al. 2015a, b, c, Garcia-Giron et al. 2019). Our results therefore corroborated the idea that there should be no clear boundaries between dispersal limitation and species sorting; that is, both metacommunity archetypes are extremes along a

continuum of processes underlying the observed patterns of community assembly.

Our finding that environmental filtering overrode the importance of spatial processes in explaining functional beta diversity suggests that some macroinvertebrate taxa are adapted to a certain limited part of the environmental gradient (Fu et al. 2019). Hence, it can be speculated that there might be some physiological or ecological trade-offs associated with important environmental thresholds (Meynard et al. 2013), which will translate into functionally similar macroinvertebrate taxa occurring in similar habitats along the environmental gradient (Heino and Tolonen 2017*a*, *b*).

Salinity and water depth were the most important single environmental factors for variation in benthic macroinvertebrate communities (Appendix S3: Table S2). As a typical Qinghai–Tibet highland lake–river system, the high concentration of salt in the main body of Qinghai Lake (average salt concentration 12‰) serves as a physiological barrier for macroinvertebrate survival and resulting distributions (Williams et al. 1990, Cartier et al. 2011, Meng et al. 2016). Macroinvertebrates regulate osmotic pressure to adjust the concentration of ions in the body fluids, so that the animal's internal environment is in a state of hyperosmotic or hypo-osmotic stage to adapt to changes in salinity (Cognetti and Maltagliati 2000). Saline-tolerant species able to develop successful reproductive and physiological strategies acclimate to highly saline conditions (Clark et al. 2004, Meng et al. 2016). Also, many studies showed that water depth is key factor affecting the community structure of macroinvertebrates in both lentic and lotic ecosystems. With the change of water depth, other physical and chemical factors (e.g., temperature, water pressure, light intensity, dissolved oxygen, and the subsidence of organic debris) will covary simultaneously, thereby indirectly affecting the distributions of freshwater macroinvertebrates (Meng et al. 2016). The saline conditions and water depth formed a sieve for environmental filtering, only allowing the coexistence of few taxa with suitable traits. In other words, the local environmental conditions may have directly filtered certain taxon-specific traits (Anacker and Harrison 2012, Li et al. 2019*a*, *b*).

Tibetan lakes are experiencing a wide range of changes in salinity and water depth in response to global warming, with warming leading to melting of glaciers and to changes in precipitation–evaporation balances (Lin et al. 2017). For example, since 2005, the water level of Qinghai Lake has risen more than three meters, and the salinity has also decreased to varying degrees. Consequently, increasing water depth and changing salinity might strongly alter the selective pressures on aquatic organisms, such as benthic macroinvertebrates.

The fate of many organisms in a changing environment depends on their ability to track the shifting environmental conditions by migration and/or by local adaptation (Lin et al. 2017). Hence, the ongoing climate warming may result in significant changes in the distribution, abundance, population dynamics, and ecophysiological responses of organisms, including the responses by many freshwater macroinvertebrates (Garcia-Raventos et al. 2017, Heino et al. 2020). As we showed in this study, acknowledging the relative influences of deterministic and stochastic processes on variation in different dimensions of ecological communities is highly important for understanding global change impacts on biodiversity maintenance and ecosystem dynamics in the Anthropocene.

Acknowledgments

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DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.76hdr7swq

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3675/full