Homogeneous selection and stochasticity overrule heterogeneous selection across biotic taxa and ecosystems

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Research article

Species–environment sorting explains latitudinal patterns in spatiotemporal β-diversity for freshwater macroinvertebrates

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Understanding how and why β-diversity varies along latitude is a long-standing challenge in community ecology and rarely addressed in both space and time. We aimed to explore the spatiotemporal variations in macroinvertebrate β-diversity and their underlying drivers in eight biogeographic regions covering a substantial latitudinal gradient of more than 40 degrees. By combining β-diversity partitioning and distance decay of community similarity analyses, we found that subtropical β-diversity varies more in space relative to variation in time compared with temperate β-diversity, as we predicted. This is probably because subtropical β-diversity is shaped by species–environment sorting (SS), caused by habitat heterogeneity and species specialization, more strongly in space relative to time than temperate β-diversity. Our study highlights the importance of SS in shaping latitudinal gradients of β-diversity in space and time.

Keywords: β-diversity, habitat heterogeneity, niche specialization, space, time

Introduction

A fundamental question of community ecology is to understand the ecological processes driving the variation of biological communities across space and though time (β-diversity) (Averill et al. 2019, Jabot et al. 2020). Broadly speaking, spatiotemporal variations in β-diversity are mediated by two sets of ecological processes, particularly at relatively short timescales (e.g. scale of few years) where macroevolutionary processes are usually less relevant (Soininen 2010). (1) niche-based processes, such as species–environment sorting (SS), relying on differences in species' niches in responses to local environments. SS would make communities more dissimilar when environmental conditions differ more among sites and occasions, because of distance decay of community similarity along environment in space and time (Soininen et al. 2007, Korhonen et al. 2010, Averill et al. 2019, Graco-Roza et al. 2022). (2) β-diversity

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stems from dispersal-related processes, such as dispersal limitation or mass effect (i.e. dispersal surplus) (Jabot et al. 2020, Thompson et al. 2020). Among these, SS is highly important in structuring natural communities across space (Cottenie 2005, Soininen 2014, Mruzek et al. 2022) and though time (Cañedo-Argüelles et al. 2020, Jabot et al. 2020). Furthermore, SS shows wide variation in magnitude among different ecological and geographical settings such as across different scales and along latitude (Soininen 2014, Viana and Chase 2019, Nishizawa et al. 2022). Thus, more studies would be necessary to better understand how SS varies in space and time. Such studies may provide important insights into how environmental factors and dispersal limitation affect biodiversity in the context of global climate change (Soininen 2014).

The degree of SS on β-diversity in space and time would vary along latitude, because typically, spatial and temporal environmental heterogeneity and habitat stability vary along latitude (MacArthur 1972, Zuloaga and Kerr 2017, Xing and He 2019, Cao et al. 2021). For instance, the degree of SS on β-diversity in space would decrease from the tropics to the temperate zone because of decrease in spatial environmental complexity, especially at smaller spatial scales (Soininen et al. 2007, Xing and He 2019). Under this SS hypothesis, spatial β-diversity would be stronger at lower latitudes (Soininen et al. 2018), resulting in a faster spatial distance decay of similarity at lower latitudes (Graco-Roza et al. 2022). Alternatively, more stable environmental conditions may lead to greater relative influence of dispersal limitation across space in the tropics (Múrria et al. 2015), hence a faster spatial distance decay of similarity (Salinas-Ivanenko and Múrria 2021). Conversely, as temporal environmental heterogeneity (e.g. temperature variability) is supposed to be lower in the tropics due to their stability (MacArthur 1972, Zuloaga and Kerr 2017, Salinas-Ivanenko and Múrria 2021), the strength of SS and thus β-diversity in time may be weaker at lower latitudes (Hu et al. 2019), resulting in a slower temporal distance decay of similarity at lower latitudes (Korhonen et al. 2010).

In addition to habitat heterogeneity, niche specialization also varies along latitude (Brown 2014, Cao et al. 2021, Mruzek et al. 2022), which may have implications for SS and β-diversity dynamics across latitudes. For instance, tropical communities typically contain more environmentally specialized species (e.g. specialists with narrow thermal niches) than communities at higher latitudes (Brown 2014, Múrria et al. 2020, Cao et al. 2021). Increases in habitat specialization at lower latitudes would result in stronger influence of SS on community compositions because habitat specialists are typically more influenced by SS than habitat generalists (Pandit et al. 2009, Wu et al. 2018). Under this latitude–niche breadth hypothesis, β-diversity would be stronger at lower latitudes (Brown 2014, Xing and He 2019, Cao et al. 2021, Mruzek et al. 2022). However, studies comparing niche breadth across latitudes usually address only one dimension (i.e. space) without considering the other (i.e. time). We thus lack a full understanding of how niche breadth variation may contribute to latitudinal gradient of SS and β-diversity in both space and time. Moreover, there are many other hypotheses such as productivity-related and historical (scale of decades and beyond) hypotheses that may not mutually exclusively be invoked to explain the latitudinal gradient of β-diversity, and evaluation of all of them is difficult and not yet possible (Brown 2014, Xing and He 2019, Mruzek et al. 2022). Instead, we focus on variation in habitat heterogeneity and species specialization as two key mechanisms invoking latitudinal gradients of β-diversity.

Logistically, however, it is very challenging to test such latitude-related predictions in single case studies due to difficulties in sampling large study areas multiple times (Averill et al. 2019, Khattar et al. 2021). One way to address this challenge is to use a comparative approach to study the relative importance of SS in space versus in time (that is, spatial SS/temporal SS ratio), as well as the relative variation of β-diversity in space versus in time (that is, spatial β/temporal β ratio), using different spatiotemporal datasets from large biogeographic regions covering broad latitudinal gradients. The advantage of the comparison based on ratio of spatial and temporal SS and β-diversity over their absolute values is that it allows us to avoid confounding effects of variation in the amount of noise and sizes of species pool (Wu et al. 2018, He et al. 2024a) and thus offers a useful metric for among-latitude comparisons. However, comparing absolute values of spatial and temporal SS and β-diversity between different latitudes is problematic, if for instance the size of species pool is not similar between latitudes (Kraft et al. 2011, Myers et al. 2013). Traditionally, it is difficult to estimate the relative rate of spatial and temporal β-diversity due to the lack of analytical tools to analyse spatiotemporal changes (Zhang et al. 2018, Jabot et al. 2020). Recently, a novel framework of β-diversity partitioning in space and time (Khattar et al. 2021) represents a potentially powerful method to overcome such a problem. Moreover, this framework, together with other methods (e.g. distance decay of similarity analyses), has been successfully used to disentangle the relative importance of spatial and temporal SS and dispersal limitation (He et al. 2024a).

Streams are suitable for studying spatiotemporal β-diversity because their environmental conditions and community compositions such as macroinvertebrate β-diversity are highly dynamic in space and time (Sarremejane et al. 2017, Cañedo-Argüelles et al. 2020). Here, our main objectives were to determine whether the spatial SS/temporal SS ratio, the spatial β/temporal β ratio and the rate of distance decay of similarity in space and time vary between distant biogeographical regions covering a substantial latitudinal gradient. Using spatiotemporal datasets of stream macroinvertebrates assembled from different biogeographic regions (subtropical versus temperate zones) as a model system and a combination of β-diversity partitioning and distance decay of similarity analyses, we tested the following predictions (Table 1). **P_1**: the spatial SS/temporal SS ratio would be smaller in the temperate zone than in the subtropics. This will be possible if 1) at low latitudes, environmental gradient (Khattar et al. 2021) and species niche specialization are respectively steeper

Table 1. Summary of the latitudinal predictions, relevant mechanisms, methods used and main results. SS = species–environment sorting, β-DP = β-diversity partitioning, GDM = generalized dissimilarity model, GLM = generalized linear model, EDD = generalized linear model, $d_{0.5}$ = the environmental distance that halves the similarity from its value at one standardized Euclidean distance. Distance decay of similarity analyses included both GDM and GLM.

Prediction	Latitude	Potential mechanisms	Method	Result
P_1: Spatial SS/temporal SS	Subtropic > temperate	In subtropics, environmental gradient and species niche specialization are respectively steeper and higher in space than in time; while these patterns are the opposite in temperate zones	β-DP and GDM	Supported
P_{2a}: Spatial β/temporal β	Subtropic > temperate	If **P_1** is true	β-DP	Supported
P_{2b}: Spatial $d_{0.5}$/temporal $d_{0.5}$	Subtropic < temperate	If **P_1** is true	β-DP and GLM	Supported

(Fig. 1A) and higher (Fig. 1C, E) in space than in time, so that species can track along environmental gradients more effectively in space than in time; and 2) at middle latitudes, environmental gradient and species niche specialization are respectively steeper (Fig. 1B) and higher (Fig. 1D, F) in time than in space, so that species can track along environmental gradients more effectively in time than in space. **P_2**: If **P_1** is true, (**P_{2a}**) it would lead to a higher spatial β/temporal β ratio in the subtropics compared with the temperate zone; and (**P_{2b}**) the subtropical community similarity would decrease with environmental distance faster in space relative to time than temperate community similarity.

Material and methods

Data sources

We first assembled spatiotemporal datasets on stream macroinvertebrates from two biogeographic regions that

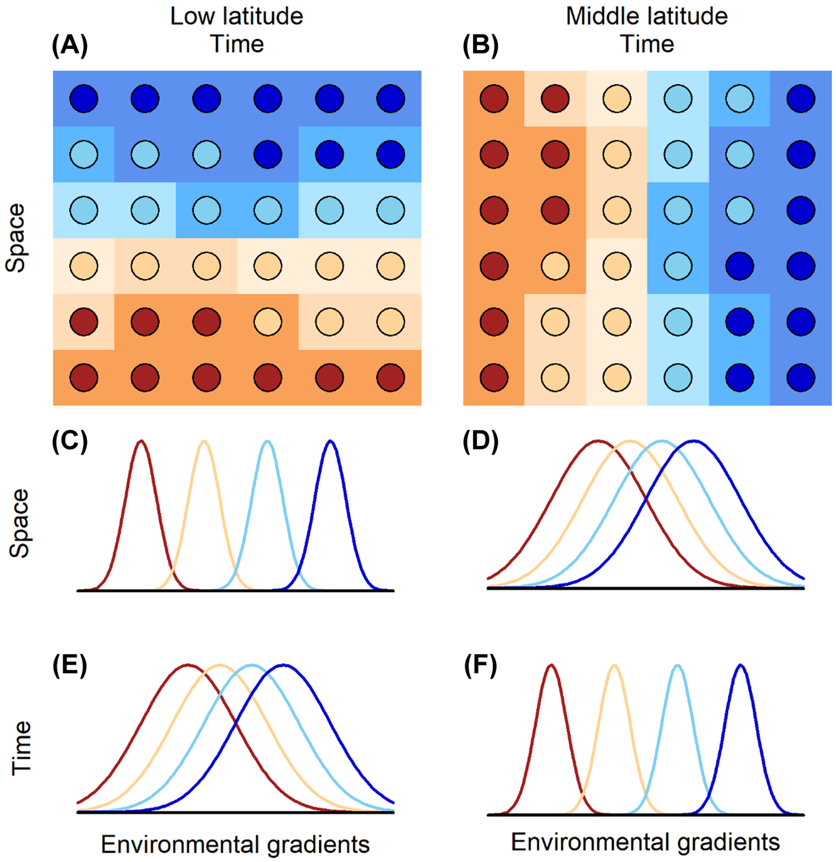

Figure 1. A conceptual illustration of the latitudinal patterns of the species distributions in space and time. Spatial and temporal patterns of species distribution along environmental gradients illustrated with the colour of underlying boxes in low and middle latitudes (A and B). Points represent the spatial and temporal arrangement of individuals of each species. Species are distributed along environmental gradients in space (C and D) and time (E and F) depending on each species' characteristics as illustrated with the colour of curves.

were located in different drainage systems in China: the Huangshui River (HR) in Qinghai Province and the Tiaoxi River (TR) in Zhejiang Province. The study regions differ in climatic conditions with HR located in a temperate climate while TR is in a subtropical monsoon climate (Supporting information). The HR database had 48 sites sampled on eight occasions between 2015 and 2018. The TR database had 28 sites that were sampled on eight occasions between 2007 and 2009. By concentrating on spatiotemporal community patterns, our analysis did not require spatial or temporal consistency between datasets, only that both spatial and temporal macroinvertebrate samples were collected. This is because we mainly made cross-data comparison based the ratio of spatial and temporal SS and β-diversity rather than their absolute values. However, in our comparative analyses, cross-data comparison based on these absolute values is problematic, because the sizes of species pool are different between datasets, as suggested by Kraft et al. (2011) and Myers et al. (2013). Macroinvertebrates were collected from a 100 m-long reach at each sampling site, and counted and identified in the laboratory. We collected macroinvertebrates using a Surber-net (300 × 300 mm, 250 μm mesh size) from three riffles and two pools with a total sampling area of 0.45 m^2 once the samples were pooled into a single composite sample (Wang et al. 2012). In the laboratory, macroinvertebrate individuals were sorted, counted and identified to the lowest practical taxonomic level, in most case to genus (> 94 % of taxa). In the HR, a total of 16 environmental variables including 11 chemical variables (e.g. total nitrogen) and five physical variables (e.g. current velocity) were measured (Supporting information). In the TR, a total of 13 environmental variables including nine chemical variables and four physical variables were measured (Supporting information). All the environmental variables were measured following Wang et al. (2012).

To further evaluate how spatiotemporal patterns of β-diversity vary with latitude, we also searched for spatiotemporal datasets that have survey data of stream macroinvertebrates sampled using similar methodology from at least 10 sites and on three occasions (i.e. season and/or month). In total, we obtained six datasets from published literature (Chen et al. 2014, Nguyen et al. 2014, Cook et al. 2018, Edegbene et al. 2019, Castillo-Escrivà et al. 2020, Siebers et al. 2022). Commonly, taxa in the datasets were identified at the genus and family level (Table 2). Datasets provided raw data of taxa abundances, spatial coordinates of study sites and date of sampling times if available, and originated from six continental regions (China, Nigeria, Spain, Switzerland, USA and Vietnam) with a latitudinal range from 5°57′36″N to 46°24′36″N (Table 2). For China data (the Li River data, Chen et al. 2014), we also included seven environmental variables (Supporting information) in a later analysis.

Habitat niche breadth

We estimated habitat specialization using three different analyses. First, we used Levins' approach (Levins 1968, Pandit et al. 2009) to measure the habitat niche breadth index (B) for macroinvertebrates by computing as:

$$B_j = 1 / \sum_{i=1}^{n} P_{ij}^2$$

where B_j is the niche breadth of taxa j in a metacommunity, P_{ij} is the proportion of the individuals of taxa j in community i, and n is the total number of communities in a metacommunity. Since we only used community data without considering environmental conditions and spatial locations, the calculated B-values may reflect both habitat specialization and dispersal ability. However, the B-values showed a strong relationship with environmental distance but no or weak relationship with geographical distance in the LR, TR and HR regions (Supporting information), suggesting that low B-values indicate narrow habitat niche breadth (i.e. the taxon occurs narrowly and unevenly along a range of habitats) rather than weak dispersal abilities. We measured the average B-values from all taxa in a single metacommunity as an indicator of habitat niche breadth at the metacommunity level (Bmeta) (Wu et al. 2018). In each region, we defined macroinvertebrate assemblages across all sites on a single occasion as a spatial metacommunity and across all occasions in a single site as a temporal metacommunity. We excluded region h (Val Roseg, Switzerland, Table 2) in the niche breadth analyses due to the lack of individual species data.

Table 2. Brief description of the assembled datasets. Values in parentheses are percent of taxa identified to genus. No. S = the number of study sites, No. T = the number of sampling times, MGD = maximum of geographical distance (in kilometres), SP = spring, SU = summer, FA = fall, WI = winter.

Code	Region	Location	No. S	No. T	MGD	Study duration	Resolution
a	Niger Delta, Nigeria	05°57′36″N, 06°06′00″E	11	12	136	2008–2010; monthly	Genus (98)
b	Cau river basin, Vietnam	21°42′36″N, 105°06′00″E	15	4	27	2009–2010; June and October	Family
c	Li River basin, China	25°25′12″N, 110°23′24″E	67	4	139	2008–2010; SP, FA	Genus (93)
d	Tiaoxi River basin, China	30°31′48″N, 119°33′00″E	28	8	45	2007–2009; SP, SU, FA, WI	Genus (98)
e	Oklahoma and Arkansas, USA	36°03′36″N, 94°34′12″W	35	12	94	2014–2016; every other month	Genus (98)
f	Huangshui River basin, China	36°46′12″N, 101°28′48″E	50	8	123	2015–2018; every other season	Genus (94)
g	Iberian Peninsula, Spain	39°22′12″N, 00°33′00″W	10	11	35	1993–1995; seasonally or monthly	Species or genus (96)
h	Val Roseg, Switzerland	46°24′36″N, 09°52′12″E	30	3	5	2017, FA; 2018, SP, SU	Family

Second, we calculated the niche breadths as taxa distributions along environmental gradients with outlying mean index (OMI) analysis (Dolédec et al. 2000). We measured this index using principal components analysis of the environmental variables and retained the first three principal component axes (> 57% of explained variation). OMI analysis measures, for instance, taxon tolerance to environmental conditions (Supporting information). High tolerance values indicate that the taxon occurs across a broad range of environmental conditions in the sampling area and duration, while low tolerance values indicate that the taxon occurs across limited environmental ranges in the sampling area and duration.

Third, we used two functional diversity metrics (functional dispersion, FDis; functional β-diversity, Fβ; Mouchet et al. 2010, Villéger et al. 2013) to infer niche breadth, because functionally diverse assemblages usually comprise trait variability associated with habitat heterogeneity (Múrria et al. 2020). We selected a total of eight traits (refuge, exoskeleton or external protection, respiration, body size, body shape, rheophily, habit and functional feeding groups) for macroinvertebrates from published literature (Morse et al. 1994, Usseglio-Polatera et al. 2000, Schmidt-Kloiber and Hering 2015, Múrria et al. 2020). We assigned macroinvertebrate functional traits at genera level as these provide good coverage of functional variability across regions (Sarremejane et al. 2020). Genera for which trait data are not available were excluded from the analysis.

β-diversity partitioning

Spatial, temporal and spatiotemporal dimensions

We used a novel analytical framework proposed by Khattar et al. (2021) to partition the total variance of a taxa-by-sites-by-time matrix (i.e. total β-diversity, β_{total}) into its purely spatial (i.e. variation in space independent of time, β_{space}), purely temporal (i.e. variation in time independent of space, β_{time}) and spatiotemporal (i.e. variation across different sites across different moments in time, β_{SpxT}) components (**P**$_1$) as follows:

$$\beta_{total} = \beta_{space} + \beta_{time} + \beta_{SpxT}$$

where

$$\beta_{total} = \sum_{j=1}^{n-1} \sum_{i=j+1}^{n} D_{ji} \,/\, [n(n-1)]$$

$$\beta_{space} = \sum D_{space} \,/\, [n(n-1)]$$

$$\beta_{time} = \sum D_{time} \,/\, [n(n-1)]$$

$$\beta_{SpxT} = \sum D_{SpxT} \,/\, [n(n-1)]$$

where n is the number of samples (local communities) and D_{ji} is the compositional dissimilarity (i.e. Sørensen dissimilarity) between the *i*th and *j*th communities. D_{space}, D_{time} and D_{SpxT} represent the compositional dissimilarity between any pair of local communities in space alone, time alone and in space and time simultaneously, respectively. For example, consider a focal community *i* located at site S1 in time T1 (represented as S1T1). The dissimilarity between community *i* and another community *j* estimates D_{space} if *j* located at site S2 and in time T1 (S2T1); D_{time} if *j* located at site S1 and in time T2 (S1T2); finally, it estimates D_{SpxT} if *j* located at site S2 and in time T2 (S2T2). See Khattar et al. (2021) for more detailed calculations.

To remove the potential influences from the imbalance in the number of entries in D representing each dimension, we divided the values obtained for β_{space}, β_{time} and β_{SpxT} by the-number of entries in D representing D_{space}, D_{time} and D_{SpxT}, respectively. After this adjustment, these dimension components are comparable, and can be understood as the average contribution of each dimension to β_{total} (Khattar et al. 2021).

Distance decay of similarity

We used the generalized linear model (GLM) following a quasi-binomial family with log-link (Millar et al. 2011) to calculate (i) the relationship between community similarity and environmental distance in space and time from each pair of communities, environmental distance decay of similarity; (ii–i) the relationship between community similarity and distance in space from each pair of sites at each occasion, spatial distance decay of similarity; and (ii–ii) the relationship between community similarity and distance in time from each pair of occasions at each site, i.e. temporal distance decay of similarity. We further used generalized linear mixed-effects model (GLMM, Bolker et al. 2009) to assess environmental distance decay of similarity. We included the spatial and temporal location of samples as a random effect to account for the non-independence of the distance matrices, such as the covariance between distances that originates from the same sampling sites (e.g. the covariance d_{12} and d_{13}; d_{ij} is the distance between site i and j). We also used a novel site-block resampling method (Martínez-Santalla et al. 2022) with three different functions (i.e. negative exponential, power-law and Gompertz) to estimate the nonlinear spatial and temporal distance decay of similarity. We calculated spatial distances using geographical distances (in km) between each pair of sites, which have been a common method used to estimate spatial distance decay (Soininen et al. 2007, Graco-Roza et al. 2022). We conducted the environmental distance decay of similarity analyses in only the HR, TR and LR regions where environmental variables were available and analysed using similar methods. Environmental distance was the pairwise Euclidean distance in the full set of normalized (mean = 0 and SD = 1) environmental variables between sites and occasions. We excluded region c and h (Cau river basin, Vietnam and Val Roseg, Switzerland, Table 2) in the GLM due to the lack of spatial coordinate data and information on sampling date. We then used the initial similarity (e.g. the similarity at one km and day distance) and the halving distance (e.g. the distance that halves the similarity from its value at one km and day distance) as small-scale and large-scale turnover. The advantage of the initial similarity and halving distance is that it offers a very useful and easily comprehensible metric for among-latitude comparisons (Soininen et al. 2007).

Assessing the importance of environmental factors

We applied the generalized dissimilarity model (GDM) to assess the effect of environmental factors on pairwise dissimilarity of macroinvertebrates in the TR and LR regions (i.e. the same as those in the environmental distance decay analyses). In brief, the GDM is an extension of matrix regression, and accommodates 1) the non-linear relationship between community dissimilarity and explanatory factors when β-diversity is high and 2) the variation in the rate of community dissimilarity (non-stationarity) at different positions along explanatory gradients (Ferrier et al. 2007, Khattar et al. 2021). We fitted GDMs for macroinvertebrate dissimilarity matrices with default parameters of three I-splines per predictor. To facilitate the comparisons between different datasets, we retained the first four environmental variables in each dataset. We summed the coefficients of the I-splines (Coeff-I) to quantify the relative importance of environmental variables in driving community dissimilarity.

Finally, to test $\mathbf{P_1}$ and $\mathbf{P_2}$ we compared the ratio of spatial/temporal SS (i.e. the summing coefficients of the I-splines in space divided by the summing coefficients of the I-splines in time) and the ratio of average $\beta_{space}/\beta_{time}$ (i.e. the average contribution of β_{space} to β_{total} divided by the average contribution of β_{time} to β_{total}), rather than their absolute values between different biogeographical regions. We conducted all statistical analyses in R ver. 4.0.5 (www.r-project.org), using the 'base' package with the *scale* function for environmental normalization; 'ade4' (Dray and Dufour 2007) with *dudi.pca* and *niche* for niche breadth analyses; 'FD' (Laliberté and Legendre 2010) with *dbFD* and 'BAT' (Cardoso et al. 2020) with *beta* for functional diversity analyses; 'stats' with the function *glm* and 'betapart' with the function *decay. model* for GLM; 'lme4' with the function *glmer* for GLMM, and the R scripts provided by Khattar et al. (2021) for β-diversity partitioning; and 'gdm' (Fitzpatrick et al. 2022) with the function *gdm* for GDM.

Results

Environmental distances

The standardized Euclidean distances (SED) for the environmental variables were more variable (i.e. with higher coefficient of variation) in space than in time (Table 3). However, this difference was not substantial in the temperate HR region, compared with the large differences in the subtropical TR and LR regions (Table 3), indicating that the relative steepness of environmental gradients across space and over time was higher in the subtropical TR and LR regions than in the temperate HR region.

Niche breadth

The bulk metacommunity habitat niche breadths (Bmeta) for macroinvertebrate communities were higher in space than in time in both the subtropical TR region and the temperate HR region. However, this difference was not substantial in the subtropical TR region (mean Bmeta: space, 2.44; time, 1.60), compared with the large differences in the temperate HR region (mean Bmeta: space, 3.10; time, 1.33) (Fig. 2). Moreover, we found that, in space, the Bmeta increased significantly with latitude; however, in time, the Bmeta decreased significantly with latitude (Fig. 2). Outlying mean index (OMI) analyses showed that the habitat niche breadths were higher in time than in space in the subtropical TR (mean tolerance: space, 0.90; time, 1.47, Supporting information) and LR regions (mean tolerance: space, 0.56; time, 0.69, Supporting information). However, in the temperate HR region, the habitat niche breadths were higher in space than in time (mean tolerance: space, 1.38; time, 0.63, Supporting information). We also found that the relative rate of spatial and temporal functional diversity (i.e. $FDis_{space}/FDis_{time}$ and $F\beta_{space}/F\beta_{time}$ ratios) showed a significant negative relationship with latitude (Supporting information), suggesting that

Table 3. Mean, minimum, maximum and coefficient of variation (CV) of the standardized Euclidean distances for the environmental variables, and parameter estimates (s_1, $d_{0.5}$, Z and P) for environmental distance decay models of community similarity in the temporal (time), spatial (space) and spatiotemporal (SpxT) dimensions in the Li River (LR) region, the Tiaoxi River (TR) region and the Huangshui River (HR) region. s_1 = the similarity at one standardized Euclidean distance, $d_{0.5}$ = the environmental distance that halves the similarity from its value at one standardized Euclidean distance. Z and P values are the fixed-effect (environmental distance) parameters in the generalized linear mixed-effects model.

Region	Dimension	Mean	Min–max	CV	S_1	$d_{0.5}$	Z	P
LR	Time	0.92	1.27–8.11	0.45	0.47	15.65	−1.27	0.20
	Space	2.83	0.30–10.97	0.63	0.44	3.51	−13.41	< 0.001
	SpxT	3.49	0.43–10.90	0.48	0.28	4.46	−3.86	< 0.001
TR	Time	3.14	0.12–9.63	0.60	0.57	60.93	−1.33	0.18
	Space	2.83	0.27–12.92	0.83	0.53	9.64	−6.83	< 0.001
	SpxT	3.84	0.17–14.38	0.64	0.46	10.05	−10.33	< 0.001
HR	Time	2.84	0.29–18.54	0.72	0.23	18.04	−2.32	0.02
	Space	3.17	0.13–19.46	0.79	0.3	19.72	−5.31	< 0.001
	SpxT	3.71	0.17–24.30	0.68	0.15	22.39	−4.03	< 0.001

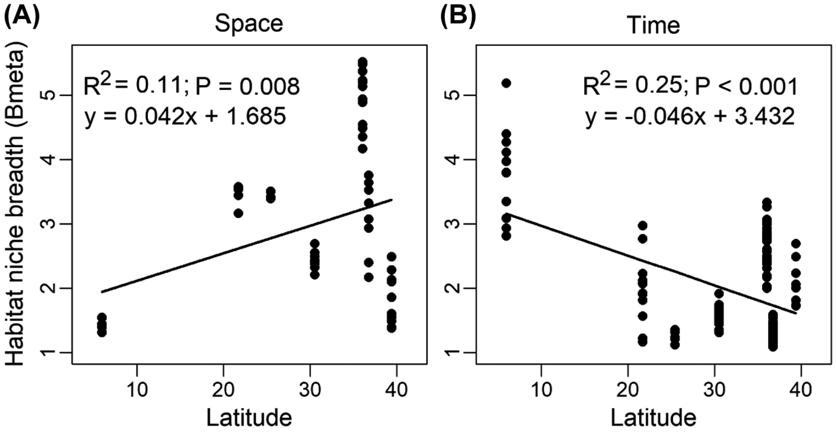

Figure 2. The relationships of bulk metacommunity habitat niche breadth (Bmeta) in space (A) and time (B) with latitude.

tropical and subtropical communities contain more functionally unique taxa (e.g. more environmentally specialized taxa) in space relative to time than communities at higher latitudes.

Quantifying the role of environmental factors (P_1)

In the subtropical TR and LR regions, the environmental predictors were more important in determining β-diversity in space (Coeff-I: 0.407–0.635, TR; 0.178–1.096, LR) than in time (0.199–0.425, TR; 0.067–0.534, LR) (Supporting information). Conversely, in the temperate HR region, the environmental predictors were more important in determining β-diversity in time (Coeff-I: 1.702–3.196) than in space (0.673–1.222) (Supporting information). We thus found a higher spatial/temporal SS ratio in the subtropical TR and LR regions than in the temperate HR region (Fig. 3A).

β-diversity patterns (P_2)

β-diversity partitioning

We observed that the average contribution of β_{space} to β_{total} was higher than the average contribution of β_{time} in the subtropical TR and LR regions (Supporting information). Conversely, the average contribution of β_{space} to β_{total} was lower than the average contribution of β_{time} in the temperate HR region (Supporting information). We thus found a higher average $\beta_{space}/\beta_{time}$ ratio in the subtropical TR and LR regions than in the temperate HR region (Fig. 3B).

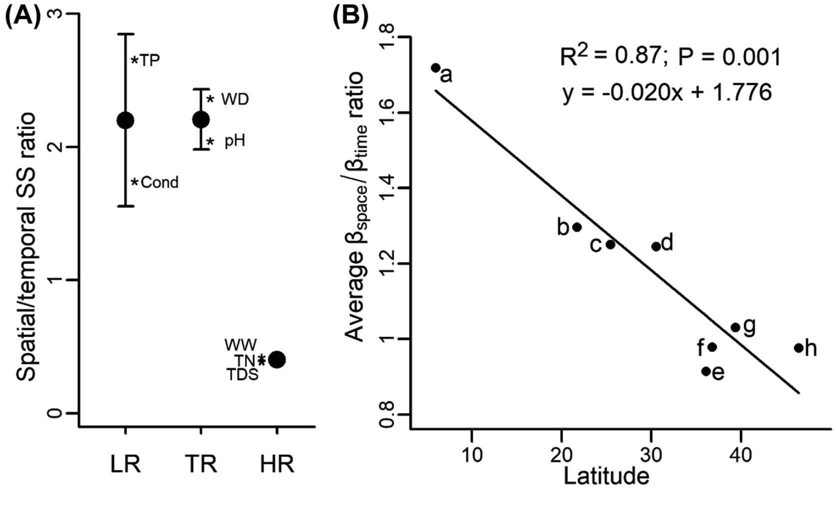

Figure 3. The spatial/temporal species –environment sorting (SS) ratio in the the Li River (LR) region, the Tiaoxi River (TR) region and Huangshui River (HR) region (A), and the average $\beta_{space}/\beta_{time}$ ratio against latitude in eight (a–h) regional datasets (B). Species–environment sorting was calculated by summing the coefficients of the I-splines from generalized dissimilarity model. Circular symbols represent averages and error bars denote the standard deviations. Stars represent individual environmental variables, only predictors found to be the first four environmental variables (TP, total phosphorus; Cond, conductivity; WD, water depth; WW, water width; TN, total nitrogen; TDS, total dissolved solids) in both spatial and temporal dimensions (see the Supporting information for more details) are included in the figure. The average $\beta_{space}/\beta_{time}$ ratio was calculated as the average contribution of β_{space} to β_{total} divided by the average contribution of β_{time} to β_{total}.

Moreover, the average $\beta_{space}/\beta_{time}$ ratio showed a significant negative relationship with latitude by our literature review analyses (Fig. 3B).

Distance decay of similarity

In the subtropical TR and LR regions, the environmental distance that halves the similarity from its value at one environmental distance ($d_{0.5}$) was much shorter in space and time; however, in the temperate HR region, the $d_{0.5}$ was slightly longer in space than in time (Table 3).

The similarity at one km distance (i.e. initial similarity in space) increased significantly with latitude (Fig. 4A), while the similarity at one day distance (i.e. initial similarity in time) decreased significantly with latitude (Fig. 4B). However, the spatial and temporal distance that halves the similarity from its value at one km and day distance (i.e. halving distance in space and time) were not related to latitude (Supporting information).

Discussion

In this study, we set out to compare spatial and temporal variations of macroinvertebrate β-diversity and their underlying drivers in distant biogeographic regions covering a substantial latitudinal gradient (subtropical versus temperate zones). We found that in the subtropics, β-diversity is shaped by SS more strongly in space than in time, likely due to the steeper environmental gradients in space than in time, leading β-diversity to vary more in space than in time. However, in the temperate zones, the opposite outcomes emerged, perhaps because β-diversity is shaped by SS more strongly in time than in space, likely due to the higher habitat specialization in time (e.g. caused by larger intra-annual differences among seasons distributed with different unique traits) than in space, leading β-diversity to vary more across years than in space.

Comparison of SS in space and time among HR, TR and LR

We detected higher spatial/temporal SS ratios in the subtropical TR and LR regions than in the temperate HR region, consistent with our $\mathbf{P}_1$. This finding suggests that subtropical macroinvertebrate β-diversity is shaped by SS more strongly in space relative to time than temperate macroinvertebrate β-diversity. Similarly, Khattar et al. (2021) found a stronger influence of SS on terrestrial insect β-diversity in space than in time in the low latitudes, whereas Mruzek et al. (2022) and Salinas-Ivanenko and Múrria (2021) found that the influence of SS on aquatic insect β-diversity in space was weak at the high latitudes. The finding of a stronger role of SS in space than in time in the subtropical TR and LR regions can be explained by the considerably faster change of environmental conditions in space than in time, as suggested by Khattar et al. (2021). Additionally, we found that environmental conditions in the temperate HR region have changed slightly faster in space than in time; however, this difference was not substantial, compared with the large differences in the subtropical region. Such findings suggest that the temperate macroinvertebrates may experience more temporal and/or less spatial environmental variation (MacArthur 1972, Zuloaga and Kerr 2017), and thus strengthen the role of SS in time and/or reduce the role of SS in space (Xing and He 2019, Zhang et al. 2020).

An alternative explanation for the latitudinal variation of SS in space and time may be related to niche specialization. We found that, in the temperate HR region, macroinvertebrates had narrower niche breadths in time than in space. Macroinvertebrate communities in the temperate streams are more likely to comprise abundant specialists in time (but not in space, Múrria et al. 2020, Grigoropoulou et al. 2022), whose presence can vary seasonally in response to variations in hydrological habitats (Sarremejane et al. 2017, Crabot et al. 2020). For example, Sarremejane et al.

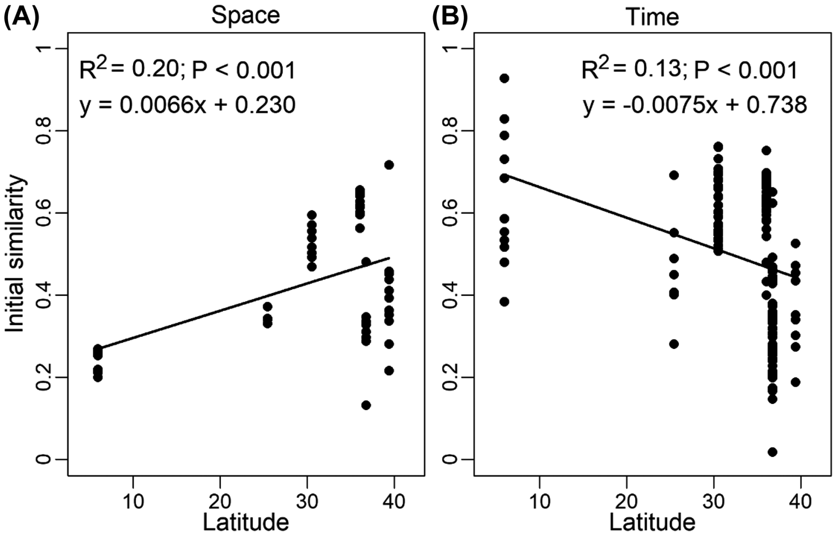

Figure 4. The relationships of initial similarity in space (A) and time (B) (i.e. similarity at one km and day distance) with latitude.

(2017) found that some unique traits (e.g. multivoltinism) dominated during the rewetting period, whereas some other unique traits (e.g. respiration through spiracles) dominated during the dry period. Community variation of habitat specialists with narrow niches are more influenced by SS than that of habitat generalists with wide niches (Pandit et al. 2009, Wu et al. 2018). Thus, macroinvertebrate β-diversity would be shaped by SS more strongly in time than in space in the temperate HR region. However, when latitude decreases, different outcomes may emerge as the relative importance of SS shaping β-diversity in space may increase, while the relative importance of SS shaping β-diversity in time may decrease. This is because we found that in space, macroinvertebrates had wider niche breadths at the higher latitudes, which aligns with previous work, showing the classical latitude–niche breadth gradient in terrestrial tree (Xing and He 2019, Cao et al. 2021) and in freshwater fish (Mruzek et al. 2022). By contrast, in time, the pattern was reversed, which to the best of our knowledge has not previously been found.

Latitudinal patterns and drivers in spatiotemporal β-diversity

As predicted ($\mathbf{P_2}$), we observed that 1) the spatial β/temporal β ratio was higher in the subtropics than in the temperate zone, indicating that subtropical β-diversity varied more in space relative to time than temperate β-diversity ($\mathbf{P_{2a}}$); and 2) the subtropical community similarity was decreasing with environmental distance faster (i.e. indicated by shorter halving distance) in space relative to time than temperate community similarity ($\mathbf{P_{2b}}$). Such patterns can be explained by the latitudinal gradient in the relative importance of SS underpinned by differences in the spatiotemporal structure of environmental condition and niche specialization. At low latitudes (e.g. tropics and subtropics) where 1) environmental gradients are likely steeper in space than in time (Fig. 1A) (Ghalambor et al. 2006, Zuloaga and Kerr 2017, Khattar et al. 2021) and 2) niche specialization is relatively high in space (Fig. 1C) (Brown 2014, Cao et al. 2021) and low in time (Fig. 1E), species may be sorted along environmental gradients more effectively in space than in time (Thompson et al. 2020), hence producing greater variation in species composition among local communities (i.e. higher β-diversity) in space than in time (Fig. 1A). However, at middle latitudes (e.g. temperate zone), opposite outcomes may emerge, as species may be sorted along environmental gradients more effectively in time than in space, leading to higher β-diversity in time than in space (Fig. 1B). This is because when latitude increases, 1) the relative steepness of environmental gradients across space compared with over time should decrease (Fig. 1A–B) (Zuloaga and Kerr 2017, Khattar et al. 2021), and 2) niche specialization should decrease in space (Fig. 1C–D) and increase in time (Fig. 1E–F), as in this study. Beyond SS, some other factors such as phenological changes could drive temporal β-diversity variations. However, we found a relatively much higher explanatory power of environmental distance than temporal distance on temporal β-diversity in the LR, TR and HR regions (Supporting information). We thus believe that our results may have been only little affected by phenology.

An alternative explanation for $\mathbf{P_{2a}}$ may be related to dispersal. Compared with temperate zones, subtropics typically show more stable environmental conditions, increasing the relative importance of dispersal limitation across space (Salinas-Ivanenko and Múrria 2021) and hence higher spatial β-diversity. However, a greater dispersal limitation should predict a relative higher explanatory power of geographical distance than environmental distance on spatial β-diversity at low latitudes (explained variation: space > environment) (Myers et al. 2013, Múrria et al. 2015). Our findings suggest the opposite in the subtropical TR (explained variation: 1.9%, space; 40.0% environment; Supporting information; indicating a much higher importance of SS than dispersal limitation) and LR regions (0.1%, space; 47.4% environment; Supporting information), and therefore this explanation might be unlikely in our study. Moreover, the effect of geographical distance on spatial β-diversity did not relate with latitude (Supporting information), concordant with the observations of Mruzek et al. (2022). This finding further indicates that dispersal limitation was only a weak driving force of spatial β-diversity along the latitudinal gradient. These patterns might arise because most macroinvertebrate taxa (> 65% of taxa) are active dispersers (i.e. aquatic insects with terrestrial winged adults), which can actively select environmentally suitable sites via dispersal (Grönroos et al. 2013), resulting in stronger SS than dispersal limitation on β-diversity (Mruzek et al. 2022).

Scale dependency

The latitudinal patterns in spatiotemporal β-diversity likely resulted from small-scale rather than large-scale influences of β-diversity. This is because we found that, in space, small-scale β-diversity was higher (i.e. indicated by lower initial similarity) at low latitudes; while in time, small-scale β-diversity was higher at higher latitudes. However, these patterns were not observed for large-scale β-diversity (i.e. halving distance) in both space and time. Similar scale dependency in the latitudinal gradient of β-diversity in space and time have been observed in earlier studies (Soininen et al. 2007, Korhonen et al. 2010, Xing and He 2019). For instance, Soininen et al. (2007) found that small-scale β-diversity decrease with latitudes, while such a pattern was not observed for large-scale β-diversity. Our results support the general idea that latitudinal β-diversity gradient is scale-dependent in both space and time (Soininen 2010).

Conclusions

We believe our research is an important step towards a more comprehensive understanding of the mechanisms that create β-diversity along latitudinal zones both in space and time. We suggest that spatiotemporal variation in β-diversity differs substantially between subtropical and temperate zones, as they have strikingly different spatiotemporal influence of SS most likely due to different level of habitat heterogeneity and species specialization. However, future studies should investigate comprehensive spatiotemporal datasets of taxon abundances and environmental variables from a broader range of latitudes (e.g. from tropical to arctic regions) and incorporate other diversity facets (e.g. functional and phylogenetic, which may tell us more about diversity patterns and species–environment associations in space and time (Heino and Tolonen 2017, Crabot et al. 2020)) than taxonomical to test whether spatiotemporal organization of β-diversity and the underlying drivers vary systematically along latitudinal gradient across the planet.

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Author contributions

Siwen He: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Funding acquisition (equal); Investigation (supporting); Methodology (equal); Project administration (equal); Resources (equal); Software (lead); Validation (equal); Visualization (equal); Writing – original draft (lead); Writing – review and editing (equal). **Beixin Wang**: Conceptualization (equal); Data curation (equal); Formal analysis (supporting); Funding acquisition (equal); Investigation (equal); Methodology (supporting); Project administration (lead); Resources (lead); Software (supporting); Supervision (lead); Validation (supporting); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Kai Chen**: Conceptualization (supporting); Data curation (supporting); Formal analysis (equal); Funding acquisition (supporting); Investigation (equal); Methodology (equal); Project administration (supporting); Software (supporting); Supervision (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Ning Li**: Conceptualization (supporting); Data curation (equal); Formal analysis (supporting); Funding acquisition (supporting); Investigation (supporting); Methodology (supporting); Project administration (supporting); Resources (supporting); Supervision (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Janne Soininen**: Conceptualization (equal); Data curation (supporting); Formal analysis (supporting); Project administration (supporting); Software (supporting); Supervision (equal); Writing – original draft (equal); Writing – review and editing (supporting).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.hdr7sqvpk (He et al. 2024b).

Supporting information

The Supporting information associated with this article is available with the online version.

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