

Article

The Joint Contributions of Environmental Filtering and Spatial Processes to Macroinvertebrate Metacommunity Dynamics in the Alpine Stream Environment of Baima Snow Mountain, Southwest China

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Abstract: While macroinvertebrates are extensively investigated in many river ecosystems, meta-community ecology perspectives in alpine streams are very limited. We assessed the role of ecological factors and temporal dynamics in the macroinvertebrate meta-community assembly of an alpine stream situated in a dry-hot valley of Baima Snow Mountain, China. We found that spatial structuring and environmental filtering jointly drive the structure of macroinvertebrate meta-community, with relative contributions to the variance in community composition changing over time. RDA ordination and variation partitioning indicate that environmental variables are the most important predictors of community organization in most scenarios, whereas spatial determinants also play a significant role. Moreover, the explanatory power, identity, and the relative significance of ecological factors change over time. Particularly, in the years 2018 and 2019, stronger environmental filtering was found shaping community assembly, suggesting that deterministic mechanisms predominated in driving community dynamics. However, spatial factors had a stronger predictive power on meta-community structures in 2017, implying conspicuous dispersal mechanisms which may be owing to increased connectivity amongst sites. Thereby, we inferred that the alpine stream macroinvertebrate metacommunity composition can be regulated by the interaction of both spatial processes and environmental filtering, with relative contributions varying over time. Based on these findings, we suggest that community ecology studies in aquatic systems should be designed beyond single snapshot investigations.

Keywords: macroinvertebrate metacommunity; temporal variation; environmental filtering; spatial processes; alpine stream; dry-hot valley

1. Introduction

Understanding the fundamental processes that drive spatio-temporal changes in biological communities is one of the most pressing topics in community ecology. As a field, community ecology is concerned to explain the patterns of distribution, abundance, and archetype species interactions with each other [1]. Community ecologists proposed two key processes in order to describe the mechanisms that drive ecological communities [2]. The deterministic, niche-based processes presume that species co-existence is based on

ecological niche differentiation [3]. In this scenario, species that share identical functional characteristics should inhabit similar environments [4]. Apart from this, stochastic processes presume that there is no ecological differentiation among species, and spatial characteristics are considered essential in constructing community assembly [5]. Meta-community ecology is one of the most intensively growing fields of community ecology, which provides an effective framework for studying community assembly mechanisms by integrating numerous ecological events, such as dispersal-linked and niche-based processes [6]. This points to the fact that local communities are driven not only by local-scale environmental variables but also by regional-scale spatial factors [7].

Environmental and spatial structuring both lead to change in an ecological community, yet their relative role varies depending on ecosystem types [8], seasonal changes [9], organisms' dispersal ability [10,11], regional connectivity [12], and spatial scale. Although the community assembly mechanisms have mostly been measured up across various spatial scales, only a few studies have focused on how these mechanisms change temporally [13]. In general, due to the time lag in species colonization, spatial processes are highly significant during the early stages of community formation, while environmental processes take place in the later phases [14,15]. These insights indicated that biological communities are not at equilibrium, but are on the short-term course of advancing it, and are crucial to a comprehensive understanding of the processes that determine community organization over long timescales [16], from years to decades [14,15]. Besides, most previous studies based on snapshot sampling design, which may misrepresent the relative contribution of particular community-building processes, because they surmised that the mechanism regulating community variation remains constant over time [17]. Consequently, separating the temporal changes of these core processes will present more specific knowledge to better understand the community assembly mechanisms.

Streams are very dynamic ecosystems, with considerable regional and temporal variation [18], and are driven by both environmental and spatial components [19]. Thus, we selected an alpine stream, notably in the dry-hot valley in order to quantify its specific environmental condition and macroinvertebrate communities. Moreover, the prevailing environmental heterogeneity in a study area is an important element that affects the meta-community assembly [20]. In particular, the relevance of environmental filtering is likely to vary among locations with varying degrees of environmental variability [1]. The environmental variability in which the alpine streams flow is attributable to nature (mountainous environment, elevation, climate), as well as human land use activities that are highly determined by the environment. The role of environmental filtering on community structure is supposed to be greater within locations with higher environmental variability, although empirical support for this hypothesis is limited, particularly in stream ecosystems [21].

This research was carried out across a broad mountainous landscape (average altitude 4000 m), where the mountain landforms make the studied stream a relatively isolated system. To our knowledge, community assembly processes are well established in temperate river ecosystems [22]. Nonetheless, this knowledge is currently lacking for the alpine stream. Moreover, there is still a need to examine the temporal differences of these processes in alpine stream systems. We collected macroinvertebrates and local environmental factors from an alpine stream, located in the environment of the Baima Snow Mountain (BSM). The macroinvertebrates were chosen as research organisms because they are useful indicators of stream integrity since they are affected by the stream's physicochemical and biological characteristics, as well as being relatively easy to sample and identify. In this study, we aimed to concentrate on stream communities to better comprehend the community assembly mechanisms and the temporal changes of the mechanisms involved by using the classical framework of meta-community research. Researchers have also started to analyze potential temporal fluctuation in the strength of assembly mechanisms using meta-community approaches [23,24]. Studies addressing temporal patterns of change in species compositions, as well as their interactions with environmental and spatial factors, may help researchers better comprehend meta-community structure patterns [7]. Based

on preceding knowledge of meta-community ecology in mountain freshwater bodies, we anticipated that both spatial structuring and environmental filtering induce variation in macroinvertebrate community composition, although their relative contributions would change over time [9,25]. Particularly, we hypothesized that in a dry-hot region alpine stream, macroinvertebrate community structure would be primarily driven by environmental filtering across time, because of habitat variability along the length of the stream and throughout the time [26].

2. Materials and Methods

2.1. Study Area

The study region is located in the Baima Snow Mountain (BSM) Nature Reserve (Figure 1), Southwest China ($27^{\circ}24'–28^{\circ}36' N$, $98^{\circ}57'–99^{\circ}25' E$), which is the core part of the Hengduan Mountains, at elevations extending from 2040 to 5429 m. The Hengduan Mountains are one of the biodiversity hotspots in the world [27], located in a biogeographic transition zone between the Paleo-arctic and Oriental regions. This region has a cold temperate climate influenced by the monsoon, resulting in distinct wet (May to October) and dry (November to April) seasons, with rising altitude, the weather regime shifts, resulting in deep valleys dry and hot, whereas mountain summits are typically cold. The combination of altitude and climate gradient enables a reasonably distinct differentiation of main mountain forest types by altitudinal belts. Additional details on the research area can be found in [28,29].

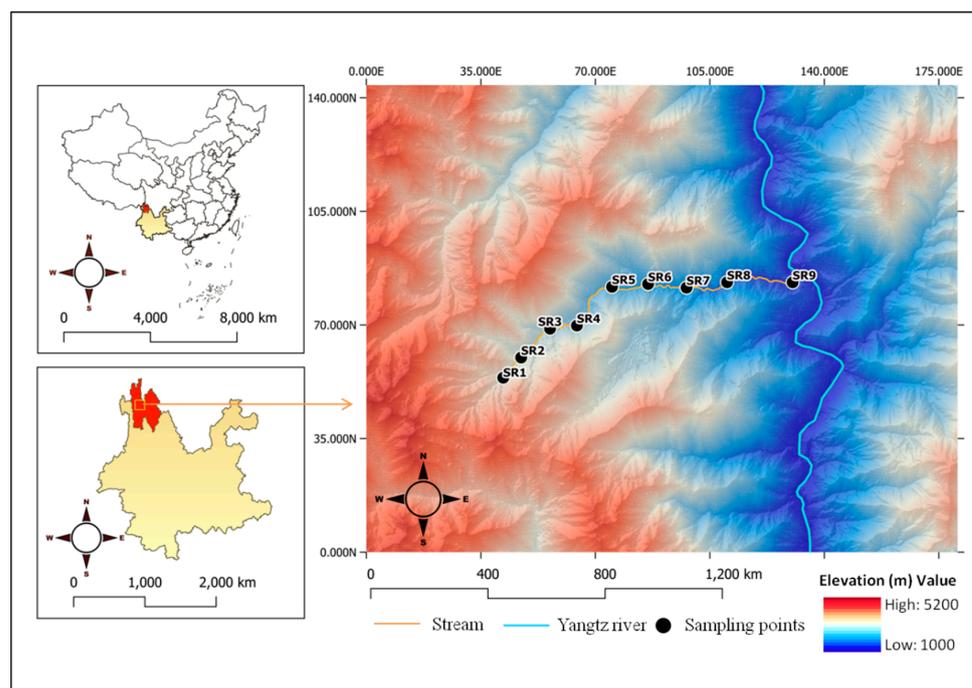


Figure 1. Map of the study region and sampling sites of an alpine stream namely Sharong (SR) situated in Baima Snow Mountain, Northwest Yunnan.

2.2. Environmental Factors and Benthic Macroinvertebrates

The sampling was carried out over three years periods (October 2017, 2018, and 2019). We sampled a total of 9 sites following the altitudinal gradient along the Sharong (SR) stream, located in the specific environment of BSM. The stream was shallow and long, with cobble, pebbles and, gravel beds, with a maximum width of 2 m. Along the altitudinal gradient, different types of vegetation were present within the region surrounding the sampling sites, with a maximum distance between sites 2228 m and a minimum distance of 1134 m. The sites further upstream were generally devoid of human activities, as located farther away from human settlements, whereas agricultural practices occurred around the

middle area of the sampling sites., however, the downstream sites ($n = 3$) were located in the dry-hot valley.

A Surber net (30 × 30 cm, 500 μm, mesh size) was used to collect macroinvertebrate samples, and the items that remained on the net were carefully picked and stored in 75 percent ethanol for preservation purposes. Five replicates were taken at each sampling site to cover multiple habitat types. The Surber net frame remained at the predetermined sampling site in water, by means of hands, the stones and sediments within the sampling frame were agitated for approximately 1–2 min to drain the organisms. To prevent disturbing the water, the downstream site was sampled first, followed by a 100 m walk upstream to the next sites (for microhabitats). The five replicates of macroinvertebrate specimen samples were then pooled to illustrate the community composition of each site. All the sampled specimens were then classified to the lowest taxonomic level (usually to genus and possibly to morphospecies level) except Orthoclaadiinae, Tanypodinae, Chironomidae, Dolichopodidae, and Elmidae were classified to family level using relevant taxonomic reference books [30,31], literature in the lab [32–34], and online assets (<https://www.freshwaterecology.info> (12 August 2021)).

The environmental factors were measured three times as the study was conducted over three years periods. We assessed the effect of the subsequent set of local environmental factors on benthic communities, including conductivity (COND-μS/cm), total dissolved solids (TDS-mg/L), dissolved oxygen (DO-mg/L), salinity (Sal), water temperature (WT-°C), oxidation-reduction potential (ORP-mV), and hydrogen ion concentration (pH) were quantified using a portable multi-parameter probe (YSI Professional plus, Yellow Springs, OH, USA) in the field. The geographical coordinates and altitude (ALT-m) of the sampling sites were determined using a GPS device (Garmin eTrex20, Lenexa, KS, USA). These factors were measured at each sampling site after macroinvertebrate sampling.

2.3. Spatial Factors

In a multi-species metacommunity, dispersal is a complex and convoluted ecological process that is hard to measure. As a result, ecologists are compelled to exploit proxies, such as spatial eigenfunction analysis, to indirectly determine an organism's dispersal process [35]. In order to simulate the spatial linkages of community composition between sampling points at different levels, the principal coordinates of neighbor matrices (PCNM) method were employed to generate spatial components based on geographic coordinates between sampling sites for additional analysis. The PCNM method is frequently used in biological communities for simulating spatial structures [36]. Further, we retained the PCNM vectors with positive eigenvalues as dispersal-related components (spatial factors) [37], based on overland distance because they indicate a possible positive autocorrelation between spatial sites at multiple scales [38]. The first PCNM vectors represent large-scale spatial linkages between locations, whereas the latter spatial vectors demonstrate smaller-scale differences between sites. Finally, we retrieved 6 PCNM vectors and used them as explanatory factors in multivariate ordination. The PCNM vectors (spatial factors) were retrieved using the function 'pcnm' in the R 'vegan' package [39].

2.4. Data Analysis

All biological and environmental data from the different periods were summarized and analyzed with various descriptive and inferential statistics. Prior to statistical analysis, environmental factors were z-score standardized and the community matrix was transformed by $\log(x + 1)$ to improve normality. The nonparametric Kruskal–Wallis test was used to examine potential environmental and biodiversity indices differences across periods. Principal component analysis (PCA) was carried out using the R 'ggord' package [40], in order to identify the main gradient of environmental factors in the data of study sites. In addition, we conducted Principal Coordinates Analysis (PCoA) to portray differences in community structure across periods using the Bray–Curtis Index as a distance measurement. We used the nonparametric multivariate statistical test (PERMANOVA; adonis)

and pairwise (adonis) tests to further corroborate the divergence in community composition. The Rank Abundance Curve (RAC) was plotted to illustrate the most dominant macroinvertebrate taxa for each period.

Redundancy analysis (RDA) and the associated variation partitioning algorithm were employed to illuminate the relative roles of local environmental and spatial determinants in shaping macroinvertebrate communities. The environmental variables were z-scored standardized, whereas the community data was Hellinger transformed as needed by the RDA model prior analysis. Further, a forward selection approach was used to screen both environmental and spatial elements to identify a set of significant components in the R package ‘adespatial’ [41]. To show the relative contributions of environmental variables and spatial determinants to change in community composition, the variation partitioning analysis was employed to derive the pure environmental variables, pure spatial factors, their shared fractions, and unexplained fractions in the R ‘vegan’ package using the function ‘varpart’. Adjusted R² values were used to present the results since they represent unbiased measures of explicated variance [42]. Moreover, the PERMDISP analysis was used to evaluate if there were discrepancies in biological and environmental heterogeneity across periods. We selected to exploit Euclidean distance on z-scored standardized environmental factors and Bray–Curtis distance on community abundance data. All statistical analyses were carried out in the R-statistic environment [43], while the map was created by using QGIS 3.8.

3. Results

3.1. Environmental Conditions

In general, the first three principal components (PC) explained 91.53% of the variation, the local environmental factors such as conductivity, water temperature, dissolved oxygen, hydrogen ion concentration, salinity, and total dissolved solids were positively correlated on the first principle component, while altitude and oxidation-reduction potential were negatively correlated. The first axis (PC1) explained 49.98% variation (Figure 2), which was primarily related to the factors altitude, conductivity, salinity, and total dissolved solids. The second axis (PC2) explained 31.21% of the variation was mainly associated with water temperature, dissolved oxygen, and hydrogen ion concentration. Overall, the PCA biplot showed water temperature, dissolved oxygen, and altitude gradients along with the sites. The key indicators that contributed greatly to the total variations in the first six principal components were altitude, dissolved oxygen, water temperature, oxidation-reduction potential, and hydrogen ion concentration.

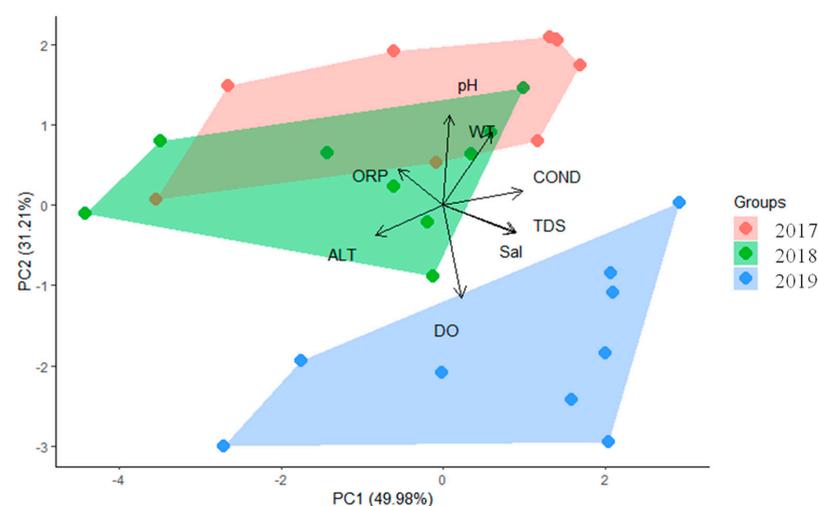


Figure 2. PCA biplot of environmental components based on the euclidean distance for three analyzed periods. Abbreviation: altitude (ALT), conductivity (COND), dissolved oxygen (DO), total dissolved solids (TDS), salinity (Sal), water temperature (WT), hydrogen ion concentration (pH), and oxidation-reduction potential (ORP).

Moreover, except for hydrogen ion concentration, dissolved oxygen, and oxidation-reduction potential, the remaining environmental factors were not significantly different across periods such as water temperature, altitude, total dissolved solids, conductivity, and Salinity (Table 1). Particularly, the 2017 period had higher values of water temperature and hydrogen ion concentration, while the dissolved oxygen concentration was found to be higher in the 2019 sampling time, and the remaining environmental factors had nearly equal values throughout the periods. Information on the correlation between environmental factors for the studied stream can be found in the Supplementary of Table S1.

Table 1. General statistics of local environmental variables and results of the Kruskal-Wallis test for three periods. “****” denote significant differences at $p < 0.05$ and $p < 0.001$, respectively, whereas “ns” denotes non-significant differences.

	2017			2018			2019		
	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean
ALT(m) ^{ns}	2417	3769	3041	2200	3800	3000	2158	3773	3005
COND ($\mu\text{s}/\text{cm}$) ^{ns}	172	286.4	246.54	159.7	259	226.94	176	298.2	252.72
Sal (ppt) ^{ns}	0.12	0.19	0.16	0.12	0.18	0.15	0.14	0.2	0.17
TDS (mg/L) ^{ns}	167.7	250.9	217.89	163.15	239.85	214.35	193.7	265.2	240.35
WT ($^{\circ}\text{C}$) ^{ns}	7.5	13.7	10.88	6	13	8.63	3.6	13.4	8.26
DO (mg/L) ^{***}	6.94	7.87	7.4	7.26	8.12	7.59	7.86	8.81	8.22
pH ^{***}	8.62	8.96	8.86	8.26	8.56	8.48	8.02	8.31	8.18
ORP (mV) ^{***}	80.6	138.1	110.96	125.3	236.9	195.13	25.1	63.1	46.88

PERMANOVA implied that mean environmental conditions differed significantly between time ($F = 7.144$, $p = 0.001$). However, PERMDISP analysis indicated no significant effect in the variance of the environmental heterogeneity across periods ($F = 0.010$; $p > 0.05$). In the context of the variation of the environmental heterogeneity, the 2019 period (mean Euclidean distance: 3.05), was quite variable than both the 2017 (average Euclidean distance: 2.94), and 2018 periods (average Euclidean distance: 2.93)

3.2. Macroinvertebrates Composition

A total of 17,823 individuals of macroinvertebrates were collected during the entire sampling period, representing 73 taxa, corresponding to 3 phyla, 6 classes, 12 orders, 47 families, and 61 genera (Table S2). Freshwater insects accounted for 86.05% (65 taxa), followed by Clitellata (2 taxa, 13.28%), Malacostraca (1 taxon, 0.39%), Rhabditophora and Arachnida (both 1 taxon 0.10%), and Entognatha (1 taxon, 0.04%). Macroinvertebrate species with maximum existence frequency were *Baetiella marginata*, *Limnodrilus* sp., *Baetis* sp1., *Prosimulium* sp., and *Amphinemura* sp1.

As a whole, 53, 52, and 59 macroinvertebrates taxa were sampled across three years periods (2017, 2018, and 2019). In terms of relative abundance, the top three dominant species in 2017 were *Baetis* sp1. (23.32%), *Rhithrogena* sp1. (19.55%), and *B. marginata* (12.93%), whereas *B. marginata* (21.45%), *Limnodrilus* sp. (17.06%), and Orthocladidae (10.88%) were dominant in 2018. Similarly, *B. marginata* (24.15%), *Limnodrilus* sp. (14.39%), and *Prosimulium* sp. (12.16%) were dominant in 2019 (Table S2). Moreover, Principal Coordinates Analysis (PCoA) visualized notable differences in community composition between the three periods. The first axis of PCoA explained 24.51% of the variation in macroinvertebrate communities composition, whereas the second axis accounted for 15.89% of the variation (Figure 3), in total 40.40%. In addition, the variance of the first six PCoA axes explained 74.43% of the variation in community composition.

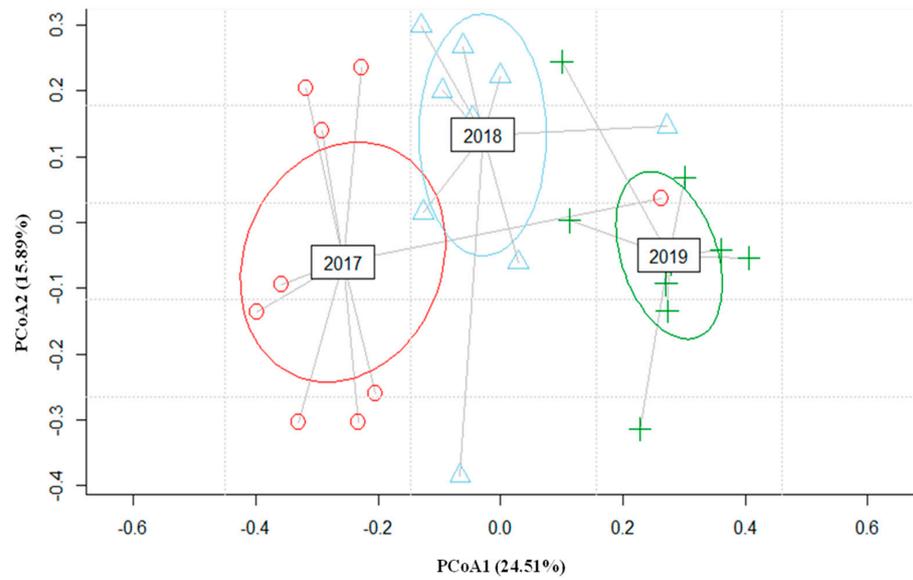


Figure 3. NMDS biplot based on Bray–Curtis dissimilarity index for three periods, shown by different colors and symbols.

Further the PERMANOVA and pairwise tests supported the findings of principal coordinates analysis that the macroinvertebrate community composition differed significantly across time, 2017–2018 ($F = 3.200, p = 0.001$), 2017–2019 ($F = 7.163, p = 0.002$), and 2018–2019 ($F = 4.014, p = 0.002$). However, we did not find significant variations in macroinvertebrate community heterogeneity (or beta diversity) among periods ($F = 1.706, p = 0.2$). The findings demonstrated a location effect, not a dispersion effect on the community composition of macroinvertebrates between periods (e.g., PERMANOVA output). The Rank Abundance Curves (RAC) showed that *B. marginata* (Sp45) was among the most present taxa in both 2018 and 2019 sampling time, while *Baetis* sp1. was the most prevalent in 2017 (Figure 4).

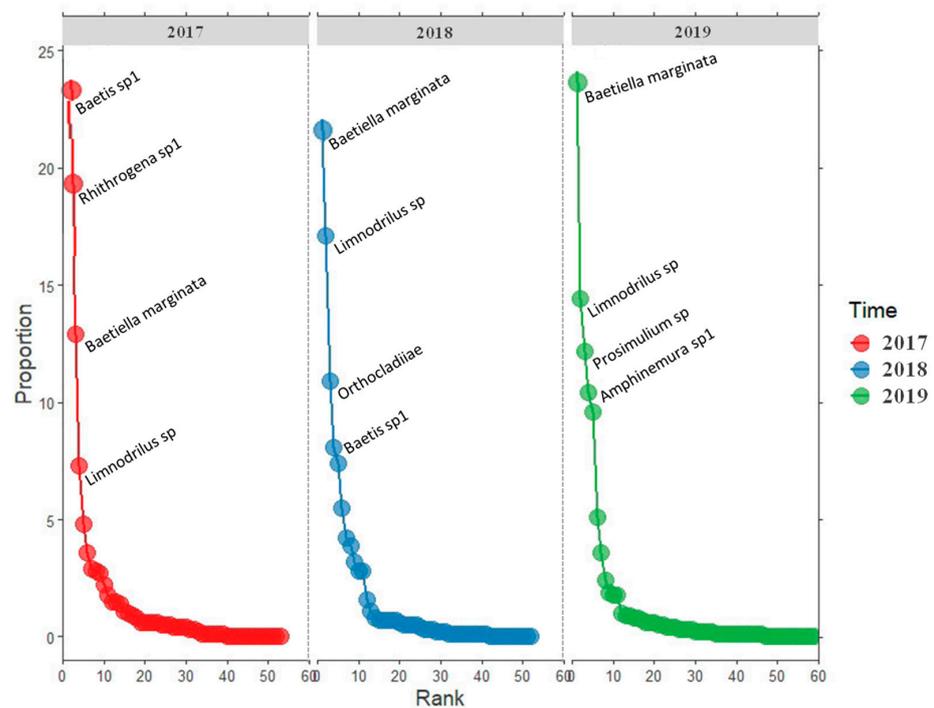


Figure 4. Rank Abundance Curves (RAC) for each of the three analyzed periods represent the most dominant macroinvertebrate taxa. The species name with the codes mentioned in the main text.

Other characteristic taxa were *Rhithrogena* sp1., *B. marginata*, and *Limnodrilus* sp., for the period 2017; and in the period 2018, *Limnodrilus* sp., Orthocladidae, and *Baetis* sp1., while *Limnodrilus* sp., *Prosimulium* sp., and *Amphinemura* sp1., for the period 2019.

Only species richness differed significantly throughout time, with higher species richness recorded in the period 2019 (Figure 5). In contrast, Simpson index, Shannon index, and Evenness were non-significantly different across time, and slightly higher diversity values were observed in the 2019 sampling period, followed by 2017.

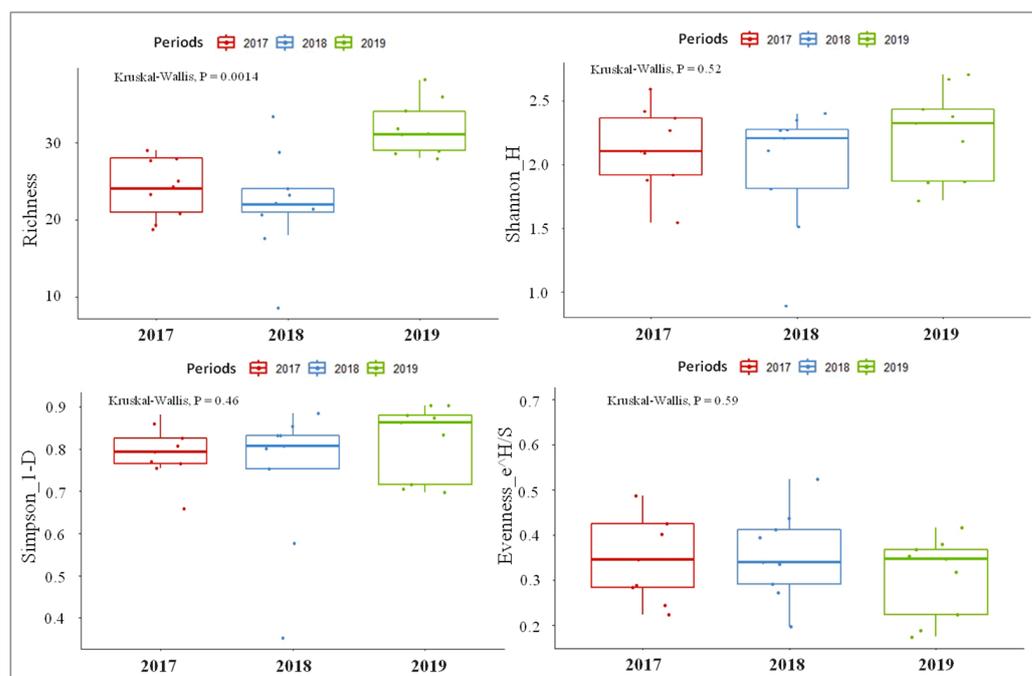


Figure 5. Species richness and Biodiversity indices (Shannon_H, Simpson_1-D, and Evenness_e^H/S) of macroinvertebrates were measured for each period of sampling. To facilitate the comparison of patterns in different diversity measures, parameter values are displayed in the Y-axes relative to the highest value for each period. Significance levels are also shown on the graphs for these different periods.

3.3. Important Local Environmental Variables and Spatial Components

The forward selection approach indicated that oxidation-reduction potential (ORP), water temperature (WT), and conductivity (COND) were significantly related with the macroinvertebrate communities in the 2017 sampling period, while total dissolved solids (TDS), altitude (ALT), salinity (Sal), and dissolved oxygen (DO) displayed to be imperative in determining macroinvertebrate communities in the period 2018. Similarly, in the 2019 sampling period, oxidation-reduction potential (ORP), water temperature (WT), and hydrogen ion concentration (pH) were found to be significantly structuring macroinvertebrate communities (Figure 6, Table 1).

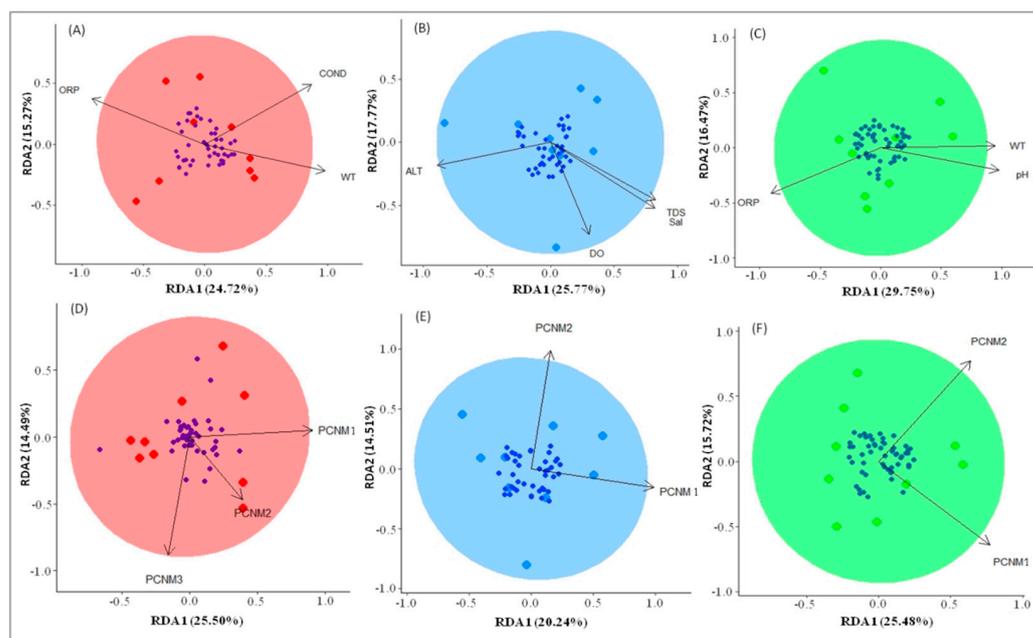


Figure 6. RDA model of the macroinvertebrate communities for environmental and spatial components of each period. The first three graphs represent the relationship between environmental variables and communities in each period i.e., (A) = 2017, (B) = 2018, and (C) = 2019. The (D) = 2017, (E) = 2018, and (F) = 2019, represent the relationship between spatial factors and communities. The significant spatial and environmental factors were selected based on the forward selection procedure ($p < 0.05$).

Based on the forward selection approach, spatial factors analysis revealed that PCNM1, PCNM2, and PCNM3 were maintained in the period 2017, while PCNM1, and PCNM2, were retained in the period 2018. Similarly, in the 2019 sampling period, PCNM1 and PCNM2 were selected (Figure 6, Table 2).

Table 2. Results of the forward selection method in the Redundancy Analysis for three years time periods.

	2017		2018		2019	
	F-Value	p-Value	F-Value	p-Value	F-Value	p-Value
ALT(m)	3.712	>0.05	2.001	>0.05	2.800	>0.05
COND (µs/cm)	2.224	0.04	2.172	>0.05	2.038	>0.05
Sal (ppt)	1.489	>0.05	2.201	0.03	1.692	>0.05
TDS (mg/L)	1.590	>0.05	2.262	0.02	1.692	>0.05
WT (°C)	3.584	0.05	1.635	>0.05	2.643	0.01
DO (mg/L)	0.663	>0.05	1.701	0.09	0.755	>0.05
pH	1.443	>0.05	2.427	0.01	2.549	<0.01
ORP (mV)	4.128	0.01	1.315	>0.05	2.927	0.01
PCNM1	8.489	<0.01	2.326	0.02	3.145	0.03
PCNM2	3.957	0.01	2.282	0.02	3.108	0.01
PCNM3	3.273	0.02	2.282	>0.05	1.883	>0.05

3.4. Relative Roles of Environmental and Spatial Components

As evidenced by the outputs of the variation partitioning approach, environmental factors and spatial determinants all played potentially key roles in organizing macroinvertebrate communities relying on both unique (individual) and joint fractions. Overall, the variation partitioning approach showed that pure environmental factors, spatial determinants, and their shared effects combined elucidated 65% of the community change in the period 2017, 53% in 2018, and 24% of community variation in the period 2019, respectively (Figure 7).

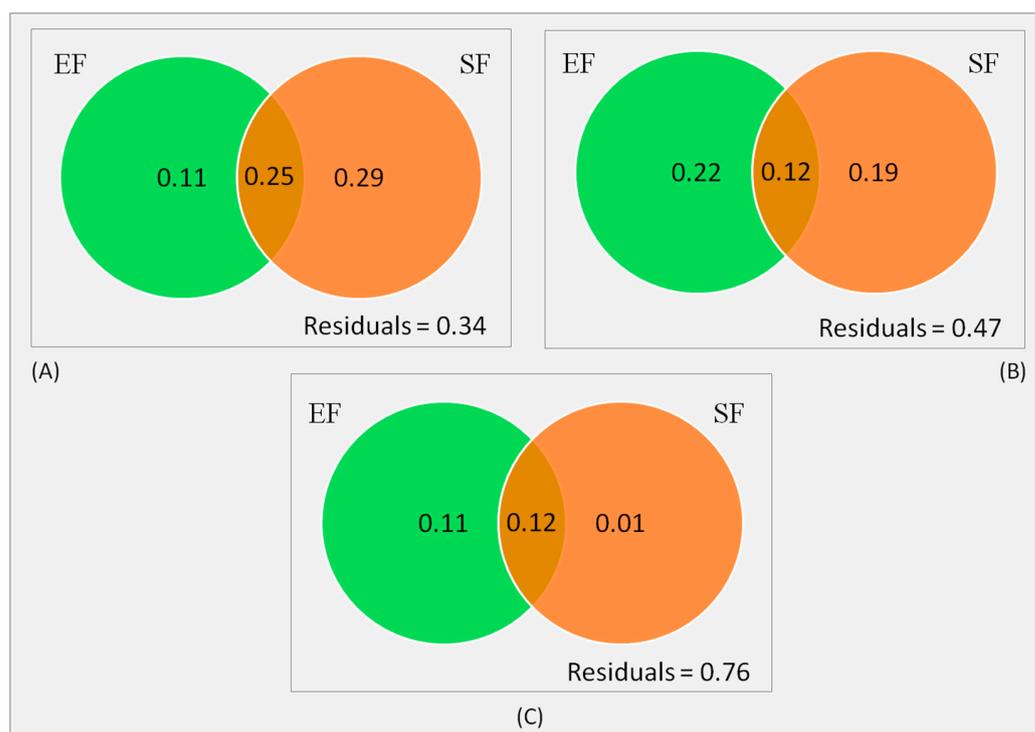


Figure 7. Results of the variation partitioning for metacommunity of macroinvertebrates into pure environmental factors (EF), pure spatial factors (SF), and their shared fractions for each period, (A) = 2017, (B) = 2018, and (C) = 2019. The entire fractions are based on R^2 adjusted values indicated as proportions of the overall variation. The residuals (unexplained variance) are displayed in the lower right corner.

Throughout the three periods, the relative strength of local environmental variables and spatial determinants were considerably different. The environmental factors elucidated more variation than spatial components. Particularly, only in the period 2017, spatial factors explained more of the variations (29%) compared to environmental variables (11%). On the other hand, in the period 2018 environmental factors accounted for 22% of the community variation than spatial components (19%). Similarly, in the period 2019, environmental factors accounted for 11% of the community changes compared to spatial factors (1%). Conversely, the shared fractions that are described collectively by both environmental and spatial factors are also considered for significant variations, with 25% of community variations explained in 2017, and 12% in both the 2018 and 2019 periods, correspondingly.

4. Discussion

The main objective of this study was to determine the relative role of environmental and spatial factors that influence macroinvertebrates, as well as to unravel temporal changes in meta-community structuring. Local environmental and spatial factors determined macroinvertebrate community structure variably in the alpine stream of Baima Snow Mountain throughout time, suggesting a temporal dynamic in the assembly processes of the macroinvertebrate meta-community composition. There was a marked shift in macroinvertebrates' community composition across periods. Also, significant variation in macroinvertebrate communities was explained by both environmental and spatial factors, showing that dispersal-linked and niche-based mechanisms were both crucial for macroinvertebrate's community assembly. Such finding corroborated meta-community ecology's key ideas [1], and also a vast number of empirical research conducted in both aquatic [44,45] and terrestrial environments [46,47]. Mainly, our study revealed that the explanatory rate and identity of spatial and environmental factors change over time. This result highlighted the necessity of studying assembly mechanisms over time [48], as well

as implied that the results from snapshot sampling design may not provide a complete picture [48,49]. The spatially structured environmental factors also contributed significantly to the macroinvertebrate's meta-community. The shared effects of environmental and spatial factors, on the other hand, are difficult to interpret. Usually, in studies of aquatic meta-communities, such shared effects are rather typical [50].

Earlier studies on the comparative role of spatial and environmental processes in determining aquatic organism structure have given inconsistent findings. For instance, Heino & Mykra [51], found no spatial location effects on stream macroinvertebrates assemblages, given that these assemblages were not highly dispersal constrained over the study drainage system. On the other hand, Vanschoenwinkel et al. [52] indicated that local environmental components were more important than spatial factors in predicting invertebrate community composition and that both these factors acted nearly independently. Thus, in most scenarios, an RDA-based variation partitioning approach in our study revealed that environmental filtering predominated in governing macroinvertebrate meta-communities, corroborating the notion that species sorting is usually the primary mechanism shaping benthic macroinvertebrate communities. These findings are consistent with other studies conducted in various water bodies [24,52–54].

In our study, spatial factors also accounted for a significant proportion of variance in alpine stream macroinvertebrate communities, implying that dispersal constraint and mass effects may influence meta-community structure [55,56], and should be considered in routine monitoring and evaluation efforts. Since our study was conducted in a mountainous region, we conclude that spatial signals in community structures are produced by dispersal constraints. Besides, based on the forward selection approach spatial components with larger eigenvalues, for example, PCNM1 and PCNM2 were chosen, implying that broad-scale spatial processes were essential in shaping the stream macroinvertebrates meta-community. In the present study, the macroinvertebrate community composition was significantly different across periods and most macroinvertebrates in the Sharong stream are generally small-sized and short-lived taxa, their life-history strategies, and phenology are highly associated with their reproduction, emergence, recruitment, and overwintering in time [57]. The apparent temporal trends of abundance and occurrence were determined for the majority of macroinvertebrates, containing the four most abundant taxa in each period (Figure 3 and Table S2). Thus, temporal dynamics in species abundance and identity, as well as the ecological circumstances may be related to the shifts in the comparative contribution of spatial structuring and environmental screening (filtering) temporally.

Despite the fact that the importance of spatial and environmental factors changed over time, we did find that the explanatory rate and identity of both environmental factors and spatial variables altered across periods. Thereby, our findings corroborate the prediction that community assembly processes exhibit temporal changes in the study region, emphasizing the need of investigating community assembly processes from a temporal viewpoint [17].

Our findings also revealed that both in the periods 2018 and 2019, stronger environmental filtering was found shaping community assembly, suggesting that deterministic mechanisms predominated in driving community dynamics in such a specific environment of the dry hot valley. This finding was reasonable since the roles of environmental filtering are anticipated to be robust with growing environmental stiffness throughout the period with low water current (flow) [26]. In our study, several environmental factors such as water temperature, total dissolved solids, dissolved oxygen, conductivity, salinity, oxidation-reduction potential, and hydrogen ion concentration significantly explained the changes in macroinvertebrate communities, thereby these factors act as environmental filters that select for the most adapted taxa in the regional species pool. In addition, the role of spatial factors was lower than that of environmental factors and was temporally variable. However, we also observed a strong predictive potential of spatial determinants over meta-community structures only in the period 2017. The relative contribution of dispersal-linked processes on biological communities was likely affected by rapid recolonization after a

high flow rate or flood event [58]. One factor that cannot be overlooked is that spatial signal could be amplified by the enormous fly of fully adult insects [59]. Conversely, in our study, we primarily examined stream macroinvertebrates larvae, which indicate we may have neglected dispersal patterns of fully adult insects, limiting the generalizability of our findings. Therefore, future research should take into account varied dispersal strategies of aquatic larvae and adults in such particular habitats of dry hot valleys. This study could have implications for biomonitoring in the context of a meta-community [60] when utilizing macroinvertebrate taxa as ecological indicators. For instance, biological monitoring programs may be less efficient in identifying degraded and impaired locations in the study region, owing to the substantial migration of individuals of these taxa from immaculate sites to adjacent impacted sites [35].

We assume that the most important environmental factors were assessed and comprised in this study; however, it remains to be evaluated that the pure spatial effects ascertained can be associated with the effect of certain unquantified environmental factors or demonstrate actual spatial constraints in functional assemblage composition. Besides, more comprehensive statistical methodology and experimental examination on a spatial-temporal scale are needed to better understand the important mechanisms driving macroinvertebrates' meta-community in alpine streams. A drawback of this study is that only one stream was sampled across the three-year study period, and while these were fairly indicative of typical weather conditions, more sampling would be required to confirm whether the stated dynamics are really widespread. It would also be useful to know how water quality responds to exceptionally dry or rainy years, as well as how agricultural runoff varies from year to year, and how this affects biological populations.

5. Conclusions

Our research contributed to the meta-community studies in the alpine freshwater system by combining different ecological processes driving variation in community structure. The results showed that both spatial structuring and environmental filtering jointly drive the structure of macroinvertebrate meta-community, although their relative contributions to variance in community composition varied in time. In general, our findings revealed that environmental variables were the most important predictors of community organization in most scenarios, whereas spatial determinants also played a significant role. Moreover, we found that the identity, explanatory rate, and relative significance of assembly processes changed over time. Thus, we assert that a single snapshot sampling design is inadequate for assessing these meta-community dynamics-influencing ecological processes. The findings also render implications for bioassessment programs, such programs, for example, may be extremely biased if we utilize organisms groups as bioindicators that imply a robust connection to dispersal-related mechanisms. These findings highlight the need of incorporating dispersal strategies in meta-community studies in terms of understanding the relative roles of environmental and spatial dynamics in time.

Supplementary Materials: The following are available online at <https://www.mdpi.com/article/10.3390/d14010028/s1>, Table S1: The correlation between environmental factors based on the Pearson correlation. Stars next to values stand for the level of significance: according to the code: (*) $0.05 \leq p\text{-values} < 0.01$; (**) $0.01 \leq p\text{-values} < 0.001$; (***) $p\text{-values} \leq 0.001$. Table S2: Identified taxa of macroinvertebrates found in the Sharong stream of Baima Snow Mountain, Yunnan, China. Abund refers to abundance and Prop refers to proportions of each taxon in different years. The top 3 dominant species have shown in bold in the table for each year.

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