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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November 8, 2021

Abstract

As a rapidly growing field of community ecology, the study of meta-communities provides an effective framework to unravel community assembly mechanisms by focusing on the relative contributions of environmental screening and spatial processes. While macroinvertebrates have been extensively investigated in many river ecosystems, meta-community ecology perspectives in high mountain stream networks are very limited. In this study, we assessed the role of ecological determinants and temporal dynamics in the macroinvertebrate meta-community assembly of an alpine stream situated in a dry-hot valley of Baima Snow Mountain, Northwest Yunnan. Our results show significant differences in the macroinvertebrate community composition across time periods. Spatial structuring and environmental filtering jointly drive the configuration of macroinvertebrate meta-community, with relative contributions to the variance in community composition varying over time. Redundancy Analysis (RDA) 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 indicators 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 in such a specific environment of the stream. 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 locations. Thereby, we inferred that the 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.

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 an area, community ecology is concerned to explain the patterns of distribution, abundance, and archetype species interactions with each other (Leibold et al., 2004). Community ecologists proposed two key processes in order to describe the mechanisms that drive ecological communities (Tonkin et al., 2016). The deterministic, niche-based processes presume that species co-existence is based on ecological niche differentiation (Keddy, 1992). In this scenario, species that share identical functional characteristics should inhabit similar environments (Carvalho et al., 2020). Apart from this, stochastic processes presume that there is no ecological differentiation among species, and spatial characteristics are considered essential in constructing community assembly (Hubbell, 2004). 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 (Chase et al., 2020). This points to the fact that local communities are driven not only by local-scale environmental variables but also by regional-scale spatial factors (Mathew A Leibold & Chase, 2017).

As reported by earlier works, environmental and spatial structuring both lead to change in an ecological community, yet their relative role varies depending on ecosystem types (Logue et al., 2011), seasonal changes (Chen et al., 2019), focal organisms' dispersal ability (Gray & Arnott, 2011; Wang et al., 2020), and regional connectivity (Jamoneau et al., 2018). 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 (Westveer et al., 2018). 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 (Helsen et al., 2013). The above conclusions indicated that biological communities are not at equipoise, 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 extended timescales (Chang & HilleRisLambers, 2016), from years to decades (Alexander et al., 2012; Helsen et al., 2013). 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 (Li et al., 2020). 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 on this planet, with considerable regional and temporal variation (Beche et al., 2006), and this variation is driven by both environmental and spatial components (Jiang et al., 2017). Thus, we selected a stream, notably in the dry-hot valley in order to quantify its specific environmental condition and macroinvertebrate communities. 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. Moreover, the prevailing environmental heterogeneity in a study area is an important element that affects the meta-community assembly (Bini et al., 2014). In particular, the relevance of environmental filtering is likely to vary among locations with varying degrees of environmental variability (M. A. Leibold et al., 2004). 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 (Heino et al., 2015). The mechanisms of community assembly have been investigated in rivers and lowland streams ecosystem, but little is known about high mountain streams.

We collected macroinvertebrates and local environmental drivers from a stream, located in the unique environment of the Baima Snow Mountain (BSM). In the present study, we aimed to concentrate on stream benthic macroinvertebrates to better comprehend the community assembly mechanisms and the temporal changes of the mechanisms involved. 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 (Chen et al., 2019; Csercsa et al., 2019). Particularly, we predicted that in such a specific environment of dry hot valley, assembly of macroinvertebrate communities would be primarily driven by environmental filtering, because strong stressors can compose a stringent environmental filter to select specific organisms (Chase, 2007). We also projected that increased bio-diversity and stronger environmental filtring determine community assembly across periods because more habitat variability would offer more niches for macroinvertebrates

(Sarremejane et al., 2017), in such dry hot regions of BSM.

2.0 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°24–28°36' N, 98deg57'–99deg25' E), which is the core part of the Hengduan Mountains, at heights extending from 2040 to 5429 meters. The Hengduan Mountains are one of the biodiversity hotspots in the world, 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 environment of the research area can be found in the work of Wen et al. (2014) and Wu et al. (2013).

2.2 Environmental factors and Benthic Macroinvertebrates

The sampling was carried out over three years periods (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 meters. Along the altitudinal gradient, different types of vegetation were present within the region surrounding the sampling sites. 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 specific environment of the dry-hot valley. A Surber net (30 X 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 randomly taken at each sampling point to cover multiple habitat types. 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 Orthocladiiae, Tanypodinae, Chironominae, Chironomidae, Dolichopodidae, and Elmidae were classified to family level using relevant taxonomic reference books (Dudgeon, 1999; Morse et al., 1994), literature in the lab (Jacobus, 2008; Jacobus, 2009; Shi & Tong, 2015), and online assets (https://www.freshwaterecology.info). 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, U.S.A) in the field. The geographical coordinates and altitude (ALT-m) of the sampling points were determined using a GPS device (Garmin eTrex20, China). 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 (Heino et al., 2017). 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 (Pierre Legendre & Legendre, 2012). Further, we retained the PCNM vectors with positive eigenvalues as dispersal-related components (spatial factors) (Gilbert & Bennett, 2010), based on overland distance. Since they indicate a possible positive auto-correlation between spatial sites at multiple scales (Dray & Legendre, 2008). 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 these vectors were then used as explanatory factors in multivariate ordination. The PCNM vectors (spatial factors) were retrieved using the function pcnm in the R vegan package (P Legendre et al., 2013).

2.4 Data Analysis

All biological and environmental data from the different periods were pooled 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 differences across periods. In addition, we conducted Principal Coordinates Analysis (PCoA) to portray differences in community structure across periods with the Bray-Curtis Index as a distance measurement. The nonparametric multivariate statistical test (PERMANOVA; adonis) and pairwise (adonis) tests were employed 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. RDA ordination was carried out to assess the connections between benthic macroinvertebrate community composition and local environmental and spatial determinants, accordingly. 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 (Dray et al., 2017). 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 R^2 values were used to present the results since they represent unbiased measures of explicated variance (Peres-Neto et al., 2006). Moreover, the PERMDISP analysis was used to evaluate if there were discrepancies in biological and environmental heterogeneity across periods. We selected to utilize 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 (R Development Core Team, 2018), while the map was created by using QGIS 3.8.

3.0 RESULTS

3.1 Environmental conditions

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

Moreover, except for pH, DO, and ORP, the remaining environmental components were not significantly different across periods such as WT, ALT, TDS, COND, and Sal (Appendix 1). Particularly, the 2017 period had higher values of WT and pH, while the DO concentration was found to be higher in the 2019 sampling time, and the remaining factors had nearly equal values across the periods. 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 flexible than both 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 (Appendix 2). 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 the period 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 Orthocladiiae (10.88%) were dominant in the period 2018. Similarly, *B. marginata* (24.15%),*Limnodrilus* sp. (14.39%), and *Prosimulium* sp. (12.16%) were dominant in the period 2019 (Appendix 2). 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. These results of principal coordinates analysis are further supported by the ANOSIM test (P = 0.001, R2 = 0.6).

Further the PERMANOVA and pairwise.adonis 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) respectively. However, PERMDISP found no 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 (e.g., PERMANOVA output) The Rank Abundance Curves (RAC) showed that *B. marginata* (Sp45) were among the most present taxa in both 2018 and 2019 sampling time, while *Baetis* sp1. was the most prevalent in 2017 (Figure 4).

Other characteristic taxa were *Rhithrogena* sp1. (Sp54), *B. marginata, and Limnodrilus* sp. (Sp65) for the period 2017; and in the period 2018, *Limnodrilus* sp. , Orthocladiiae (Sp31), and *Baetis* sp1. (Sp42), while *Limnodrilus* sp.,*Prosimulium* sp. (Sp39), and *Amphinemura* sp1. (Sp8) for the period 2019.

Only richness differed significantly across time, with higher species richness in the period 2019 (Figure 5). In contrast, Simpson index, Shannon index, and Evenness were not significantly different across time, and slightly higher diversity values were observed in the 2019 sampling period, followed by 2017.

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), hydrogen ion concentration (pH), 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).

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 1).

3.4 Relative roles of environmental and spatial components

As evidenced by the outputs of the variation partitioning approach, environmental variables 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).

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 determinants 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

Our findings present the first concise picture of macroinvertebrate community structure and temporal dynamics in the Sharong stream of Baima Snow Mountain. There was a marked shift of macroinvertebrates community structure across time. Also, significant variation in macroinvertebrate communities was explained by both environmental and spatial determinants, 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 (Leibold et al., 2004), and also a vast number of empirical research conducted in both aquatic (Heino et al., 2012; Kärnä et al., 2015) and terrestrial environments (Reinhardt et al., 2005; Tsang & Bonebrake, 2017). Mainly, our study revealed that the explanatory rate and identity of spatial and environmental components change over time. This result highlighted the necessity of studying assembly mechanisms over time (Vidal et al., 2014), as well as implied that the results from snapshot sampling design may not provide a complete picture (Vidal et al., 2014; Zhang et al., 2019). The spatially structured environmental factors also contributed significantly to the macroinvertebrate's meta-community. The shared effects of environmental and spatial elements, on the other hand, are difficult to interpret. Usually, in studies of aquatic meta-communities, such shared effects are rather typical (Vilmi et al., 2016).

Earlier studies on the comparative role of spatial and environmental processes in determining aquatic organism structure have given inconsistent findings. For instance, Heino & MYKRÄ (2008), in their study 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. (Vanschoenwinkel et al., 2007) indicated that local environmental components were more important than spatial determinants 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 (Castillo-Escrivà et al., 2017; Li et al., 2020; Vanschoenwinkel et al., 2007, 2010).

In our study, spatial determinants also accounted for a significant proportion of variance in stream macroinvertebrate communities, implying that dispersal constraint and mass effects may influence meta-community structure (Cottenie, 2005; Heino, 2013), 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 (Raitif et al., 2018). The apparent temporal trends of abundance and occurrence were determined for the majority of macroinvertebrates, containing the four utmost abundant taxa in each period (Figure 3 and Appendix 2). 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 components and environmental factors changed over time, we did find that the explanatory rate and identity of both environmental factors and spatial determinants 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 (Li et al., 2020).

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) (Sarremejane et al., 2017). In our study, several environmental factors such as water temperature (WT), total dissolved solids (TDS), dissolved oxygen (DO), conductivity (COND) oxidation-reduction potential (ORP) hydrogen ion concentration (pH), salinity (Sal), and significantly elucidated 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 fairly 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. According to Datry et al. (2016), the relative contribution of dispersal-linked processes on biotic communities was likely affected by rapid recolonization after a flood event. One factor that cannot be overlooked is that spatial signal could be amplified by the enormous fly of fully adult insects. 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 (Cid et al., 2020) 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 (Heino et al., 2017). 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.

5. CONCLUSION

Our research contributed to the meta-community studies in the high-mountain 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, maybe 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.

FUNDING STATEMENT

This research was funded by the National Natural Science Foundation Program of P.R. China [31760126, U1602262, 31960255], supported by the Second Tibetan Plateau Scientific Expedition and Research Program (STEP), Grant No. SQ2019QZKK2002, the provincial innovation team of biodiversity conservation and utility of the three parallel rivers region from Dali University and the "Key Laboratory of Yunnan State Education Department on Erhai Lake Basin Protection and the Sustainable Development Research".

CONFLICTS OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Muhammad Farooq: Conceptualization (equal); formal analysis (equal); writing-original draft (equal); writing-review and editing (equal); visualization (equal); Validation (equal). **Xianfu Li:** Field sampling (equal); methodology (equal); visualization (equal); Validation (equal). **Zhengfei Li:** Conceptualization (equal); writing-review and editing (equal); visualization (equal); Validation (equal). **Ronglong Yang:** Field sampling (equal); methodology (equal). **Zhen Tian:** Field sampling (equal); methodology (equal). **Lu Tan:** Methodology (equal); visualization (equal); Validation (equal). **Davide Fornacca** : Writing-review and editing (equal); visualization (equal); Validation (equal). **Yanpeng Li:** Field sampling (equal); visualization (equal); Validation (equal). **Nima Cili:** Field sampling (equal); methodology (equal). **Zhongyong Ciren:** Field sampling (equal); methodology (equal). **Shuoran Liu:** Conceptualization (equal); methodology (equal); writing-review and editing (equal); supervision (equal); Validation (equal). **Wen Xiao:** Conceptualization (equal); Validation (equal); Validation (equal); visualization (equal); funding acquisition (equal).

DATA AVAILABILITY STATEMENT

Macroinvertebrates and explanatory data would be deposited in the Dryad Digital Repository, XXX.

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Table 1 Results of the forward selection method in the Redundancy Analysis for three years time periods

	2017 F-value P-value	2017 F-value P-value	2017 F-value P-value	2018 F-val
ALT(m)				

	2017 F-value P-value	2017 F-value P-value	2017 F-value P-value	2018 F-va
COND (μs/cm)	2.224		0.04	0.04
Sal (ppt)				
TDS (mg/L)				
WT (°C)	3.584		0.05	0.05
DO (mg/L)				
pH				
ORP (mV) PCNM1 PCNM2 PCNM3	4.128 8.489 3.957 3.273		0.01 <0.01 0.01 0.02	0.01 <0.0

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

	2017 Max Min Mean	2017 Max Min Mean	2017 Max Min Mean	2018 Max Min Mean	2018 Ma
ALT(m) ^{ns}	3769	2417	3041	3041	3800
COND (μs/cm) ^{ns}	286.4	172	246.54	246.54	259
Sal (ppt) ^{ns}	0.19	0.12	0.16	0.16	0.18
TDS (mg/L) ^{ns}	250.9	167.7	217.89	217.89	239.85
WT (°C) ^{ns}	13.7	7.5	10.88	10.88	13
DO (mg/L) ***	7.87	6.94	7.4	7.4	8.12
pH ***	8.96	8.62	8.86	8.86	8.56
ORP (mV) ***	138.1	80.6	110.96	110.96	236.9

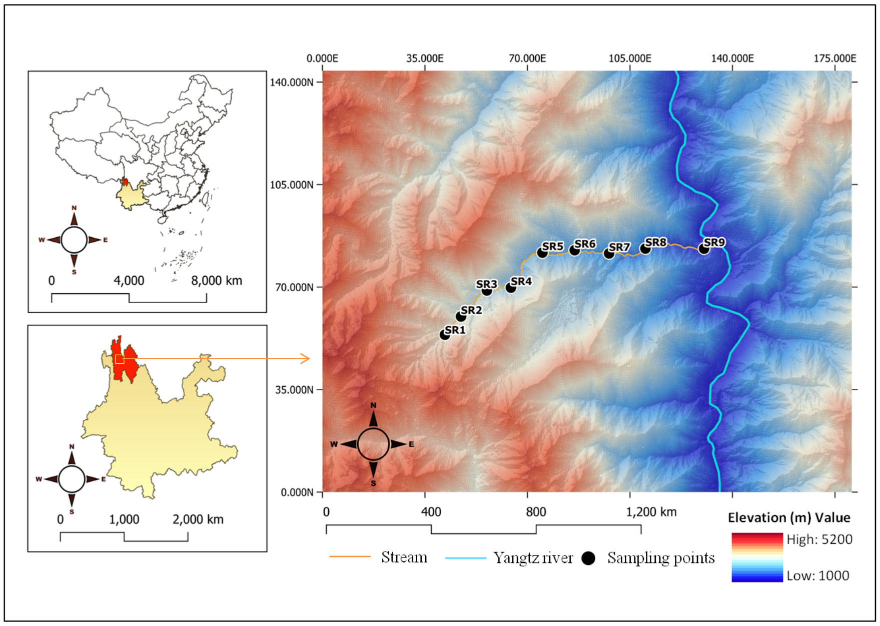
Appendix 2 Identified taxa of macroinvertebrates found in the Sharong stream of Baima Snow Mountain. Abund refers to abundance and Prop refers to proportions of each taxon in different years. The top 3 dominant species have shown in bold in the table for each year.

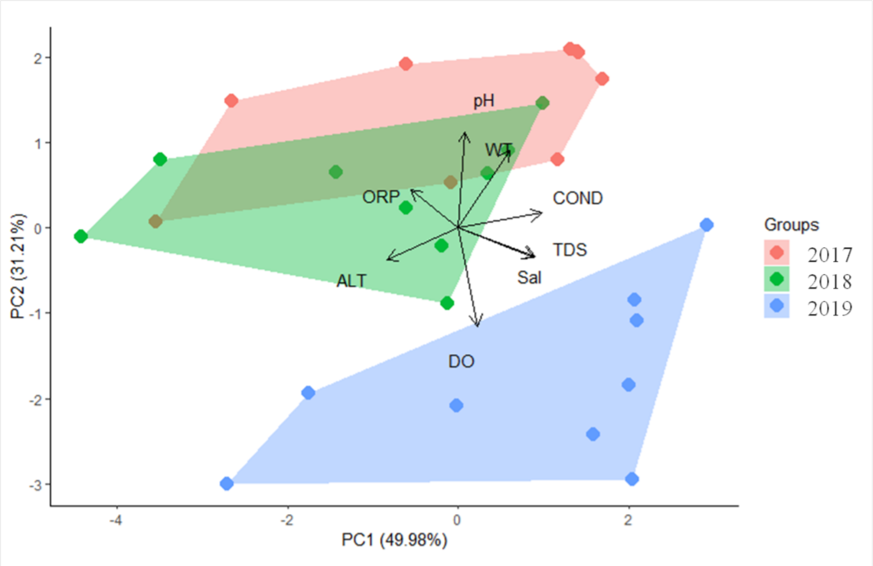
Phyla	Classes	Families	Orders	Genus/Taxa	id	2017 Abund	Prop	2018 Abund	Prop	2019 Abund
Arthropoda	Insecta	Perlidae	Plecoptera	*Kamimuria* sp.	Sp1	2	0.04	2	0.05	7
Arthropoda	Insecta	Perlidae	Plecoptera	*Neoperla* sp.	Sp2	1	0.02	0	0	0
Arthropoda	Insecta	Perlodidae	Plecoptera	*Paracapnia* sp.	Sp3	57	1.36	12	0.34	57
Arthropoda	Insecta	Perlodidae	Plecoptera	*Isoperla* sp.	Sp4	25	0.59	4	0.11	13
Arthropoda	Insecta	Peltoperlidae	Plecoptera	*Cryptoterla* sp.	Sp5	27	0.64	20	0.56	25
Arthropoda	Insecta	Chloroperlidae	Plecoptera	*Sweltsa* sp.	Sp6	12	0.28	0	0	67
Arthropoda	Insecta	Capniidae	Plecoptera	*Eucapnopsis* sp.	Sp7	113	2.70	260	7.40	364
Arthropoda	Insecta	Nemouridae	Plecoptera	*Amphinemura* sp1.	Sp8	119	2.84	136	3.87	1050
Arthropoda	Insecta	Nemouridae	Plecoptera	*Amphinemura* sp2.	Sp9	38	0.90	0	0	2

Phyla	Classes	Families	Orders	Genus/Taxa	id	2017 Abund	Prop	2018 Abund	Prop	2019 Abund
Arthropoda	Insecta	Nemouridae	Plecoptera	*Nemoura* sp.	Sp10	0	0	0	0	1
Arthropoda	Insecta	Rhyacophilidae	Trichoptera	*Rhyacophila* **sp1.**	Sp11	18	0.43	16	0.45	90
Arthropoda	Insecta	Rhyacophilidae	Trichoptera	*Rhyacophila* sp2.	Sp12	1	0.02	0	0	0
Arthropoda	Insecta	Stenopsychidae	Trichoptera	*Stenopsyche* sp.	Sp13	122	2.91	24	0.68	35
Arthropoda	Insecta	Rhyacophilidae	Trichoptera	*Himalopsyche* sp1.	Sp14	1	0.02	1	0.02	4
Arthropoda	Insecta	Rhyacophilidae	Trichoptera	*Himalopsyche* sp2.	Sp15	0	0	0	0	6
Arthropoda	Insecta	Hydropsychidae	Trichoptera	*Hydropsyche* sp.	Sp16	15	0.35	14	0.39	52
Arthropoda	Insecta	Hydropsychidae	Trichoptera	*Macrostemum* sp.	Sp17	0	0	0	0	1
Arthropoda	Insecta	Lepidostomatidae	Trichoptera	*Lepidostoma* sp1.	Sp18	5	0.11	7	0.19	0
Arthropoda	Insecta	Lepidostomatidae	Trichoptera	*Lepidostoma* sp2.	Sp19	44	1.05	17	0.48	0
Arthropoda	Insecta	Limnephilidae	Trichoptera	*Phylloicus* sp.	Sp20	15	0.35	25	0.71	35
Arthropoda	Insecta	Leptocerdae	Trichoptera	*Nectopsyche* sp.	Sp21	3	0.07	0	0	19
Arthropoda	Insecta	Glossosomatidae	Trichoptera	*Glossosoma* sp.	Sp22	3	0.07	2	0.05	77
Arthropoda	Insecta	Philopotamidae	Trichoptera	*Chimarra* sp.	Sp23	0	0	1	0.02	13
Arthropoda	Insecta	Athericidae	Diptera	*Suragina* sp.	Sp24	6	0.14	19	0.54	31
Arthropoda	Insecta	Tipulidae	Diptera	*Tipula* sp.	Sp25	1	0.02	2	0.05	7
Arthropoda	Insecta	Limoniidae	Diptera	*Hexatoma* sp.	Sp26	15	0.35	10	0.28	38
Arthropoda	Insecta	Tipulidae	Diptera	*Antocha* sp.	Sp27	23	0.54	1	0.02	58
Arthropoda	Insecta	Tabanidae	Diptera	*Tabanus* sp.	Sp28	0	0	0	0	1
Arthropoda	Insecta	Tipulidae	Diptera	*Dicranota* sp.	Sp29	19	0.45	23	0.65	50
Arthropoda	Insecta	Ceratopogonidae	Diptera	*Bezzia* sp.	Sp30	1	0.02	2	0.05	11
Arthropoda	Insecta	Orthocladiinae	Diptera	**Orthocladiinae**	Sp31	62	1.48	382	**10.88**	521
Arthropoda	Insecta	Tanypodinae	Diptera	Tanypodinae	Sp32	0	0	0	0	3
Arthropoda	Insecta	Chironominae	Diptera	Chironominae	Sp33	25	0.59	19	0.54	101
Arthropoda	Insecta	Chironomidae	Diptera	Chironomidae	Sp34	9	0.21	8	0.22	36
Arthropoda	Insecta	Dixidae	Diptera	*Dixella* sp	Sp35	2	0.04	0	0	11

Phyla	Classes	Families	Orders	Genus/Taxa	id	2017 Abund	Prop	2018 Abund	Prop	2019 Abund
Arthropoda	Insecta	Deuterophlebiidae	Diptera	*Deuterophlebia* sp.	Sp36	6	0.14	6	0.17	63
Arthropoda	Insecta	Deuterophlebiidae	Diptera	*Deuterophlebia* sp.	Sp37	0	0	1	0.02	0
Arthropoda	Insecta	Dolichopodidae	Diptera	Dolichopodidae	Sp38	0	0	3	0.08	9
Arthropoda	Insecta	Simulidae	Diptera	*Prosimulium* **sp.**	Sp39	151	3.60	100	2.84	1232
Arthropoda	Insecta	Psychodidae	Diptera	*Pericoma* sp.	Sp40	64	1.52	112	3.19	193
Arthropoda	Insecta	Psychodidae	Diptera	*Maruina* sp.	Sp41	0	0	0	0	1
Arthropoda	Insecta	Baetidae	Ephemeroptera	*Baetis* **sp1**.	Sp42	976	**23.32**	283	**8.06**	968
Arthropoda	Insecta	Baetidae	Ephemeroptera	*Baetis* sp2.	Sp43	2	0.04	0	0	0
Arthropoda	Insecta	Baetidae	Ephemeroptera	*Alainites* sp.	Sp44	200	4.78	193	5.49	181
Arthropoda	Insecta	Baetidae	Ephemeroptera	*Baetiella* ***marginata.***	Sp45	541	**12.93**	753	**21.45**	2447
Arthropoda	Insecta	Baetidae	Ephemeroptera	*Baetiella sexta.*	Sp46	25	0.59	0	0	8
Arthropoda	Insecta	Siphlonuridae	Ephemeroptera	*Ameletus* sp.	Sp47	1	0.02	5	0.14	3
Arthropoda	Insecta	Leptophlebiidae	Ephemeroptera	*Habrophlebiodes* sp.	Sp48	1	0.02	0	0	42
Arthropoda	Insecta	Caenidae	Ephemeroptera	*Caenis* sp.	Sp49	1	0.02	0	0	0
Arthropoda	Insecta	Heptageniidae	Ephemeroptera	*Iron* sp1.	Sp50	13	0.31	1	0.02	0
Arthropoda	Insecta	Heptageniidae	Ephemeroptera	*Epeorus* sp.	Sp51	94	2.24	99	2.82	248
Arthropoda	Insecta	Heptageniidae	Ephemeroptera	*Iron* sp2.	Sp52	0	0	11	0.31	15
Arthropoda	Insecta	Heptageniidae	Ephemeroptera	*Ecdyonurus* sp.	Sp53	33	0.78	147	4.18	181
Arthropoda	Insecta	Heptageniidae	Ephemeroptera	*Rhithrogena* sp1.	Sp54	818	**19.55**	57	1.62	18
Arthropoda	Insecta	Heptageniidae	Ephemeroptera	*Rhithrogena* sp2.	Sp55	1	0.02	0	0	0
Arthropoda	Insecta	Ephemera	Ephemeroptera	*Ephemera* sp.	Sp56	0	0	1	0.02	1
Arthropoda	Insecta	Ephemera	Ephemeroptera	*Ephemera* hsui	Sp57	0	0	1	0.02	0
Arthropoda	Insecta	Psephenidae	Coleoptera	*Nipponeubria* sp.	Sp58	0	0	0	0	1
Arthropoda	Insecta	Scirtidae	Coleoptera	*Hydrocyphon* sp.	Sp59	42	1.00	40	1.13	82
Arthropoda	Insecta	Elmidae	Coleoptera	Elmidae	Sp60	26	0.62	29	0.82	13

Phyla	Classes	Families	Orders	Genus/Taxa	id	2017 Abund	Prop	2018 Abund	Prop	2019 Abund
Arthropoda	Insecta	Elmidae	Coleoptera	*Stenelmis* sp.	Sp61	3	0.07	25	0.71	93
Arthropoda	Insecta	Elmidae	Coleoptera	*Oulimnius* sp.	Sp62	75	1.79	1	0.02	18
Arthropoda	Insecta	Dytiscidae	Coleoptera	*Hydaticus* sp.	Sp63	0	0	1	0.02	0
Arthropoda	Insecta	Hydrophilidae	Coleoptera	*Berosus* sp.	Sp64	0	0	1	0.02	0
Annelida	Clitellata	Tubificidae	Tubificida	*Limnodrilus* **sp.**	Sp65	304	**7.26**	599	**17.06**	1458
Platyhelminthes	Rhabditophora	Planariidae	Tricladida	*Planaria* sp.	Sp66	0	0	4	0.11	15
Annelida	Clitellata	Glossiphoniidae	Arhynchobdellida	*Erpobdella* sp.	Sp67	1	0.02	2	0.05	4
Arthropoda	Arachnida	Hydrachnidae	Trombidiformes	water mites	Sp68	1	0.02	1	0.02	17
Arthropoda	Entognatha	Poduridae	Poduromorpha	*Podura* sp.	Sp69	0	0	4	0.11	4
Arthropoda	Malacostraca	Gammaridae	Amphipoda	*Gammarus* sp.	Sp70	21	0.50	23	0.65	27
Arthropoda	Insecta	Osmylidae	Neuroptera	*Osmylus* sp.	Sp71	0	0	0	0	1

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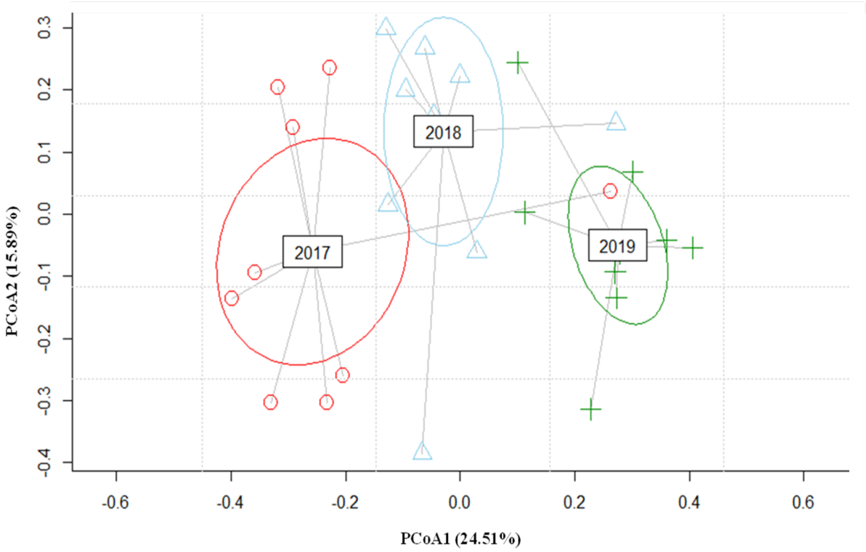
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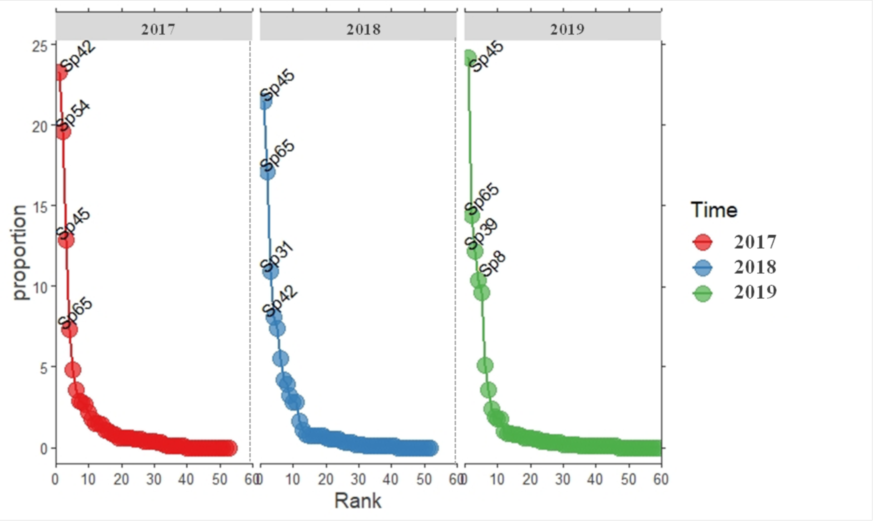
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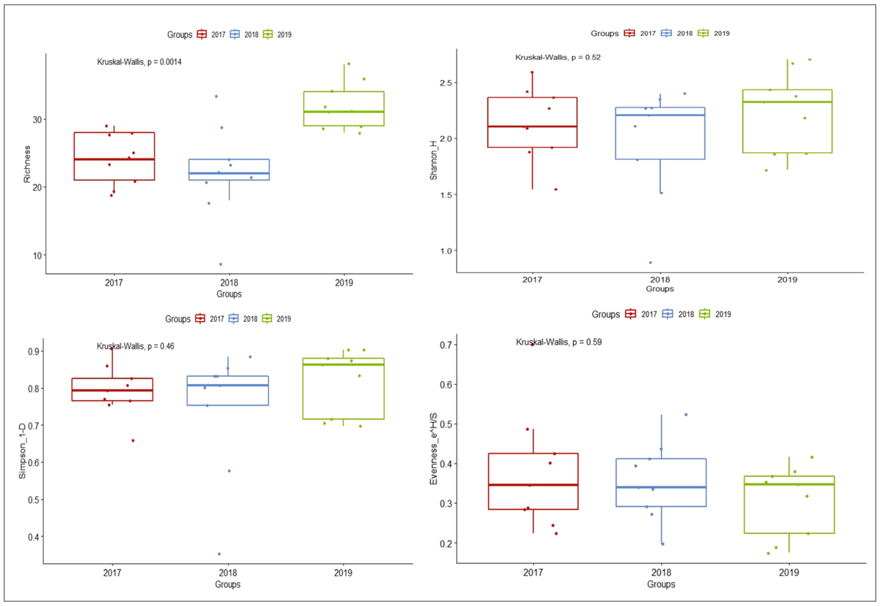
Groups 2017 2018 2019
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Richness
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Shannon_H
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Simpson_1-D
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Evenness_e^H/S
Groups
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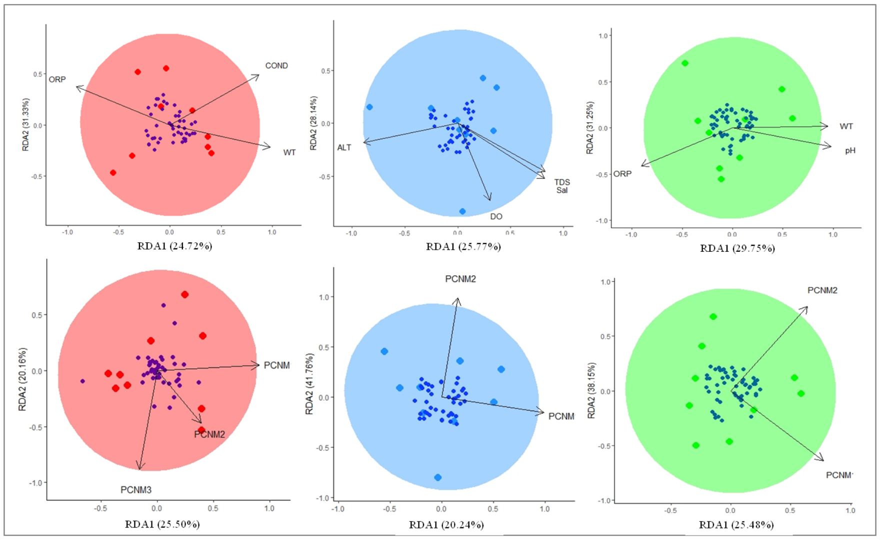
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RDA2 (28.14%)
RDA1 (25.77%)
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RDA2 (31.25%)
RDA1 (29.75%)
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RDA2 (20.16%)
RDA1 (25.50%)
PCNM2
PCNM
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RDA1 (20.24%)
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PCNM
RDA2 (38.15%)
RDA1 (25.48%)


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Residuals = 0.34
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0.11
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Residuals = 0.76
(C)