



•研究报告•

人为干扰对溪流鱼类功能多样性及其纵向梯度格局的影响

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摘要: 溪流鱼类多样性沿着河流纵向梯度的空间分布规律已得到大量报道, 但这些研究大多聚焦基于物种组成的分类 α 多样性, 而有关分类 β 多样性和功能多样性的纵向梯度分布规律及其对人类干扰的响应研究较少。本文以青弋江上游3条人为干扰程度不同的河源溪流为研究区域, 比较研究了人为干扰对溪流鱼类功能 α 和 β 多样性及其纵向梯度分布格局的影响。结果显示, 人类干扰改变了河源溪流鱼类功能多样性的纵向梯度格局——由线性变化变为二项式分布。此外, 我们发现, 人为干扰导致土著种被本地入侵种取代, 且较强的土地利用和水污染排放可能增大环境的不连续性, 而群落周转和嵌套变化往往取决于环境的变化。尽管功能 β 多样性由嵌套成分主导, 但周转成分占比相对于人为干扰较小的溪流而言明显增加。人为干扰显著改变了受干扰溪流鱼类的物种组成和功能多样性, 且功能多样性的纵向梯度格局在不同的多样性指标上存在差异。本研究强调, 在评估人为干扰下多样性的变化时, 需要从多方面考虑, 包括空间尺度和多样性指标等。

关键词: 河流连续体; 功能多样性; 物种周转; 物种嵌套; 人为干扰

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Anthropogenic disturbances affect the functional diversity of stream fishes and its longitudinal patterns in China

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ABSTRACT

Aims: The distribution and abundance of stream fishes are influenced by historical events as well as abiotic and biotic factors. Due to the high spatial heterogeneity and temporal differentiation of stream environmental characteristics, the composition and abundance of stream fish communities vary on spatial and temporal scales. On this basis, longitudinal patterns in the diversity and distribution of stream fish along upstream-downstream gradients have garnered the widespread attention of ecologists. Previous studies relevant to the longitudinal patterns in stream fish diversity along the upstream-downstream gradient mostly focused on taxonomic α diversity, while taxonomic β diversity and functional diversity have been given less attention. Therefore, this study aimed to (1) determine the effects of anthropogenic disturbances on species composition of fishes by comparing diversity across three streams, and determine the key species contributing to the between-stream variation in fish assemblages; (2) examine the influences of anthropogenic disturbances on functional diversity, and examine if differences in functional diversity relate to α and β diversity; (3) to assess whether the between-stream variations in functional diversity show dependence on the spatial positions along the river continuum or not, and further assess the effects of anthropogenic disturbances on the longitudinal patterns in the

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functional α and β diversities of stream fishes.

Methods: In this study, we focused on the functional diversity of fishes, which is an effective measure for assessing the response of communities to environmental changes and predicting changes in ecosystem functioning. Using data collected in three headwater streams of the Qingyi River, China, that experience different extents of anthropogenic disturbances, we examined the effects of anthropogenic disturbances on the longitudinal patterns in the functional α and β diversities of stream fishes. We considered multiple metrics of the α diversity, including the functional richness, evenness and divergence, which measure different aspects of functional space and abundance distribution. This work also analyzed β diversity, including its turnover and nestedness components, which can provide additional insights into the processes of community changing.

Results: We found that in the less disturbed stream, functional richness increased but divergence decreased downstream, and functional β diversity decreased downstream. On the other hand, in heavily disturbed streams functional richness was higher in the upstream-midstream but lower in the downstream, and functional divergence decreased in the upstream-midstream and β diversity increased in the downstream. Anthropogenic disturbances significantly altered species compositions and functional diversity of fishes in the heavily disturbed streams, and the mode and degree to which functional diversity varied related to both the metrics of functional diversity and the spatial position along river continuum. As a result, anthropogenic disturbances caused a shift in the longitudinal patterns of functional diversity, from linear variation in less disturbed streams to unimodal distribution in heavily disturbed streams. Similarly, variations in the functional β diversity of fishes mainly occurred in the lower segments, but not in the upper segments, and were derived by the turnover component. We found anthropogenic disturbances caused the endemic species to be replaced by the native-invasive species. Heavy land use and polluting emission could increase the environmental discontinuity, leading to community turnover and nestedness changing. Although functional β diversity was dominated by the nestedness component, the proportion of the turnover component increased significantly compared with less disturbed streams.

Conclusion: Our results highlight the need for a multifaceted approach, including spatial scale and diversity metrics, in assessing the diversity changes of stream fishes under anthropogenic pressure.

Key words: river continuum; functional diversity; community turnover; community nestedness; anthropogenic disturbance

人类活动改变了溪流中的理化条件和生态过程,引起鱼类群落物种组成和数量的变化,表现为土著物种丢失和广布物种获得两个过程(Allan, 2004),物种取代过程不仅改变了局域群落的物种多寡(Sax & Gaines, 2003),也引起区域群落的物种不相似性变化(Villéger et al, 2014),进而对溪流鱼类多样性构成严重威胁(张东等, 2018)。研究溪流鱼类多样性对人类活动的响应,是溪流生态系统及其鱼类多样性保护和管理的科学基础,也是淡水生态学领域的一个重要研究课题(Dudgeon et al, 2006)。

沿着“上游-下游”的河流纵向梯度,水文、水流流态、能量输入等系列环境因子呈现出显著的空间异质性(Poff & Ward, 1990),进而引起溪流鱼类群落物种组成和数量特征的变化(Wang et al, 2001)。溪流鱼类的物种丰富度从源头至河口,其变化模式大多为钟形,即物种数从上游至中游逐渐上升,在中游或中下游河段达到最大值,至下游相对下降(Sui et al, 2014)。人类干扰改变了鱼类局域群落的物种丰富度,因而也可能会引起物种丰富度纵向梯度分

布规律的变化(Li et al, 2018),然而,基于物种丰富度(即分类 α 多样性)无法解释生物群落与环境特征之间的关系(Zhang et al, 2020)。因此,基于特征的测量作为一种有前景的淡水生物评价方法受到了越来越多的关注,如功能群多样性(张东等, 2018)和功能多样性(Ding et al, 2017; Li et al, 2019)。尽管功能群多样性在鱼类生态学中得到了广泛应用,但其测度的功能性状较少,呈现的功能多样性实际上是功能群的数量,无法呈现同一功能类型不同物种间、尤其是同一物种不同种群间的功能特征差异,进而导致其研究结果所反映的生态系统功能等信息不完整(张东等, 2018)。功能多样性在评价群落对环境变化的响应和预测生态系统功能变化方面可能更好(Tolonen et al, 2017; Göthe et al, 2017),同时作为生物多样性的一个关键指标,功能多样性有助于跨环境梯度或空间尺度解析群落构建机制(Swenson et al, 2011; Münkemüller et al, 2012)。另外,功能多样性的多种度量指数可以描述局域群落功能属性的不同方面,如功能丰富度描述物种在群落中所占据

的功能空间的大小, 功能均匀度衡量物种功能性状在已占据的空间内分布是否均匀, 功能离散度衡量群落中功能性状多度分布的最大离散程度(Petchey & Gaston, 2006)。

与 α 多样性(量化局域群落的物种多寡)不同, β 多样性量化的是群落间的物种变化幅度(Whittaker, 1960)。群落间的物种组成变化无外乎物种丢失与物种获得(Villéger et al, 2014)。当只有物种丢失或物种获得时, 小群落是大群落的一个子集, 其群落变化呈嵌套模式; 若兼有物种丢失和获得, 则表现为群落周转格局(Leprieur et al, 2011)。可见, β 多样性可被分解为嵌套和周转2个组分(Baselga, 2010), 前者一般发生于连续性环境变化(Taylor & Warren, 2001), 后者则多见于间断性环境变化(Mazzoni & Lobón-Cerviá, 2008), 这表明 β 多样性分解有助于认识生物群落空间变异的生态过程(Soininen et al, 2018)。

先前有关溪流鱼类多样性的纵向梯度格局及其对人类干扰的响应研究大多聚焦于基于物种组成的局域多样性(物种 α 多样性), 对功能 β 多样性的纵向梯度格局及其如何响应人类干扰尚不清楚。本研究以我国亚热带地区青弋江流域上游3条人为干扰强度不同的河源溪流为研究区域, 自上游至下游连续设置研究样点进行取样; 基于采集到的渔获物, 结合鱼类功能特征, 着重比较研究人类干扰对溪流鱼类的功能 α 多样性和 β 多样性及其纵向梯度格局的影响。具体目标包括: (1)确定人为干扰强度不同的溪流鱼类物种组成的差异, 以及影响溪流间鱼类群落组成差异的关键种; (2)溪流间的功能 α 和 β 多样性沿河流纵向梯度是否表现出不同的变化规律; (3)人为干扰如何影响功能 α 和 β 多样性及其纵向分布规律。

1 材料与方法

1.1 研究区域

青弋江发源于黄山北麓, 呈东北流向汇入长江。属亚热带湿润季风气候, 全年四季分明; 年均气温 17.8°C (-2.1°C – 27.5°C), 年降水量约2,000 mm, 主要集中在4–9月, 占全年降水量的79%。舒溪、麻溪和浦溪是该流域的河源溪流, 受到不同程度的人为干扰, 其中麻溪每年排放的污染物, 如化学需氧量(COD)、氨氮($\text{NH}_3\text{-N}$)和总磷(TP)最高, 约为舒溪

的4倍, 浦溪是舒溪的2倍多。另外, 浦溪的城镇和农田土地利用比例最高(超过20%), 麻溪其次(超过10%), 舒溪最低(少于5%) (附录1)。此外, 土地利用比例沿坡度变化较大, 从高坡度至低坡度, 3条研究河流均呈现出上升趋势(附录2)。

1.2 样点设置与鱼类采集

基于栖息地的可达性和可操作性, 3条研究河流均间隔2–3 km连续设置采样点。选择的采样点均可涉水(水深小于1 m), 各样点采样河长为50 m, 且都包含两种栖息地斑块类型(急滩和深潭)。于2011年5月和10月对样点各进行1次鱼类采集, 舒溪、麻溪和浦溪样点数分别是11个、12个和9个(图1)。采用背式电鱼器(CWB-2000 P, China; 12 V import, 250 V export)直接涉水取样(经安徽省渔业渔政管理局批准), 采样时间30 min。依据Nelson (2006)和陈小勇(2013)的目科级分类系统, 在鱼类新鲜状态下进行鉴定(吻虾虎鱼(*Rhinogobius* sp.)仅鉴定至属的水平)、计数, 疑难种保存在8%的甲醛溶液中带回实验室做进一步的鉴定。

1.3 物种特征测量

参照Villéger等(2008)的方法, 针对栖息地利用、运动以及摄食等3方面, 测量体长、眼径、头长等功能特征。采集到的渔获物按每种30尾成鱼进行

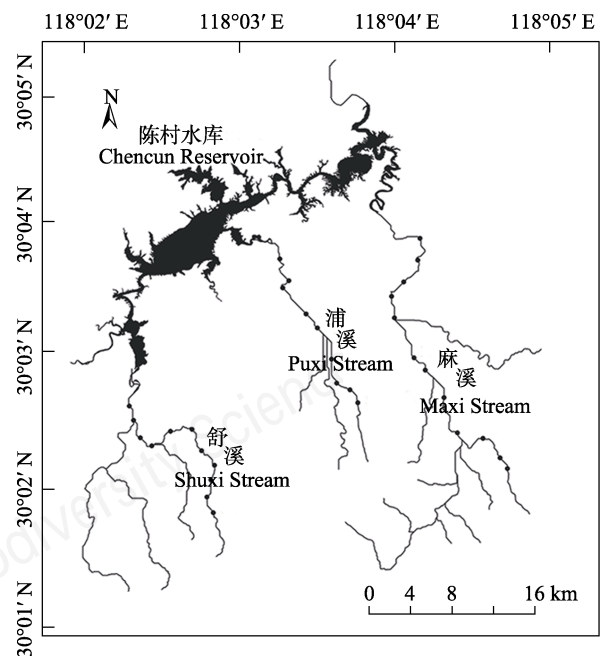


图1 青弋江舒溪、麻溪、浦溪鱼类采样点

Fig. 1 Fish samplings sites of Shuxi, Maxi and Puxi Stream, Qingyi River, Anhui

功能特征测量, 不足30尾的物种则测量全部成鱼。平均性状值是根据个体测量计算的, 假设每个物种的种内变异小于种间变异(Dumay et al, 2004) (表1)。

1.4 多样性计算

我们选取3个多样性指数计算功能 α 多样性: 功能丰富度($FRic$)、功能离散度($FDiv$)以及功能均匀度($FEve$) (Mason et al, 2005; Villéger et al, 2008) (附录3)。利用R 3.4.1中“FD”软件包进行计算(Laliberte & Legendre, 2010)。

参照Villéger等(2013)的方法, 根据每个群落中所有物种的特征性状所占的空间体积以及两两样点间的分类/功能组成, 计算功能 β 多样性($\beta_{s\phi r}$), 并参照Baselga (2010)的方法, 将其分解为周转(β_{tur})和嵌套(β_{nes}) 2个组分(附录3)。

1.5 数据分析

根据距河源距离将3条研究河流分成上(0–15 km)、中(15–25 km)、下(25–40 km) 3个河段, 采用多元统计分析方法检验溪流和河段对物种组成和功能多样性的影响。首先, 在Primer 7.0软件中, 对鱼类物种组成数据进行 $Lg(1+x)$ 转换, 运用双因素交互相似性分析(two-way crossed ANOSIM)检验溪流和河段对群落结构空间变化的影响, 并运用非度量多维标度法(non-metric multidimensional scaling, nMDS)构建鱼类群落物种组成的二维双标图, 将其空间变化进行直观化。其次, 运用相似百分比分析(similarity percentages, SIMPER)确定物种组成中对河流间的差异有贡献的关键物种。在SPSS 22.0软件中, 使用双因素方差分析(two-way ANOVA)分别检验溪流和河段对功能多样性各个指

数的影响。此外, 考虑到纵向梯度下鱼类功能多样性的潜在空间格局, 采用线性模型和二次项模型检验距河源距离同功能多样性的关系。根据各模型的相关性 R 值和显著性 P 值, 确定解释这种关系的最优模型, 3条研究河流独立进行, 视 $P < 0.1$ 边缘显著差异有统计学意义(Lin et al, 2020; Mariani et al, 2021)。

2 结果

2.1 物种组成

32个采样点共采集到27种鱼类, 其中舒溪采集到23种, 麻溪24种, 浦溪22种。双因素交互相似性分析发现, 物种组成随溪流(Global $R = 0.36$, $P = 0.001$)与河段(Global $R = 0.37$, $P = 0.001$)显著变化。就溪流间物种组成变化而言, 舒溪与麻溪和浦溪间均具有显著差异(舒溪 \times 麻溪: $R = 0.31$, $P = 0.035$; 舒溪 \times 浦溪: $R = 0.62$, $P = 0.001$), 而后两者间无显著差异($R = 0.16$, $P = 0.15$)。由nMDS二维双标图可见, 舒溪鱼类群落明显区别于其他两条溪流, 尤其在中、下游河段(图2)。根据SIMPER结果, 光唇鱼(*Acrossocheilus fasciatus*)、原缨口鳅(*Vanmanenia stenosoma*)、稀有花鳅(*Cobitis rarus*)在舒溪中的多度较高, 但在麻溪和浦溪中多度明显下降; 相反, 河川沙塘鳢(*Odontobutis obscurus*)、麦穗鱼(*Pseudorasbora parva*)等物种在麻溪和浦溪中的多度较高, 而在舒溪中较低(表2)。

2.2 功能 α 多样性

双因素方差分析显示: $FRic$ 和 $FDiv$ 随溪流显著变化, $FRic$ 在舒溪(3.73 ± 1.23)显著低于麻溪($9.13 \pm$

表1 本研究所使用的鱼类功能特征

Table 1 The functional traits measured for each fish species in this study

功能特征 Functional traits	计算方法 Measure	生态学意义 Ecological meaning	参考文献 Reference
眼睛相对大小 Relative eye size	眼径/头长 Ed/Hd	对食物的可视范围 Visual scope to food	Boyle & Horn, 2006
眼睛相对位置 Relative eye position	眼位/头高 Eh/Hd	在水体中的垂直位置 Vertical position in water	Gatz, 1979
口裂位置 Mouth gape position	口位/头高 Mo/Hd	在水中的生活位置 Living position in water	Sibbing & Nagelkerke, 2000
相对肠长 Relative gut length	肠长/体长 Gl/Bl	食物消化能力 Ability to digest food	Kramer & Bryant, 1995
体型指标I Body shape I	体高/体宽 Bd/Bw	在水体中的栖息位置及游泳能力 Habitat location and swimming ability in water	Sibbing & Nagelkerke, 2000
体型指标II Body shape II	体高/体长 Bd/Bl	在水体中的栖息位置及游泳能力 Habitat location and swimming ability in water	Sibbing & Nagelkerke, 2000
尾柄对游泳的贡献 Contribution of caudal peduncle to the swimming capability	最大尾鳍高/最小尾柄宽 CFd/CPd	游泳持久性 Staying power to swimming	Webb, 1984

Ed , Eye diameter; Eh , Eye height; Hd , Head depth; Mo , Mouth orientation; Gl , Gut length; Bl , Body length; Bd , Body depth; Bw , Body width; CFd , Maximum caudal fin depth; CPd , Caudal peduncle depth.

1.74)和浦溪(10.57 ± 2.55) ($P < 0.05$), 而 $FDiv$ 在舒溪(0.82 ± 0.11)中显著高于麻溪(0.75 ± 0.01)和浦溪(0.76 ± 0.01) ($P < 0.05$); 仅 $FRic$ 随河段显著变化, 上游的 $FRic$ 显著低于中游和下游; $FRic$ 和 $FDiv$ 受河流和河段的显著性交互影响, $FEve$ 不随河流和河段显著变化(表3)。

在SPSS软件中运用曲线估计解析鱼类功能多样性与距河源距离的关系, 结果显示: 舒溪中 $FRic$ 与距河源距离呈显著线性相关, 从上游至下游逐渐增大($P < 0.05$); $FRic$ 在麻溪和浦溪中与距河源距离呈二项式关系, 从上游至下游先增大后减小, 呈钟形分布($P < 0.05$); $FEve$ 仅在麻溪中与距河源距离显著相关(正线性关系) ($P < 0.1$); 舒溪中 $FDiv$ 与距河源距离呈显著线性相关, 从上游至下游逐渐减小, $FDiv$ 在浦溪中与距河源距离呈显著的二项式关系, 从上游先降低后上升($P < 0.1$) (图3, 表4)。

2.3 功能β多样性

3条溪流的功能β多样性平均值分别为 0.53 ± 0.03 (舒溪)、 0.75 ± 0.03 (麻溪)和 0.71 ± 0.05 (浦溪), 其中, 舒溪的功能β多样性主要由嵌套成分贡献, 占比高达75.47%, 而在麻溪和浦溪中, 嵌套与周转成分对功能β多样性的贡献相对接近(麻溪: 嵌套和周转分别占45.33%和54.37%; 浦溪: 嵌套和周转分别占57.75%和42.25%)。

根据双因素方差分析, 功能β多样性在溪流间

有显著差异($P < 0.05$), 舒溪的 $\beta_{s\phi r}$ 显著低于浦溪和麻溪($P < 0.05$); 尽管嵌套成分 β_{nes} 不随溪流显著变化, 但周转成分 β_{tur} 在舒溪中显著低于浦溪和麻溪($P < 0.05$)。功能β多样性及其成分均不随河段显著变化($P > 0.1$)。此外, $\beta_{s\phi r}$ 和 β_{tur} 受溪流与河段的交互影响($P < 0.1$) (表3)。

曲线估计显示, 仅 $\beta_{s\phi r}$ 与距河源距离显著相关($P < 0.1$), 其中在舒溪中呈线性相关, 从上游至下游呈下降趋势; 在麻溪中呈二项式U型分布, 从上游至下游先下降后上升, 但在浦溪中与距河源距离

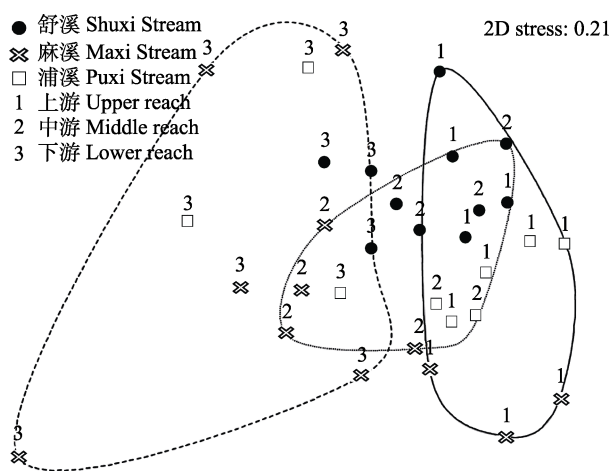


图2 溪流间鱼类物种组成结构的非度量多维标度法双标图
Fig. 2 Spatial variations in species composition of fishes across streams and reaches based on nMDS

表2 基于相似百分比分析得到的溪流间物种组成差异的鱼类关键种

Table 2 The key fish species contributing the between-stream composition difference based on similarity percentages

物种 Species	平均多度 Average abundance			舒溪 vs. 麻溪 Shuxi vs. Maxi		舒溪 vs. 浦溪 Shuxi vs. Puxi	
	舒溪 Shuxi	麻溪 Maxi	浦溪 Puxi	平均不相似性 Average dissimilarity	贡献率 Contribution (%)	平均不相似性 Average dissimilarity	贡献率 Contribution (%)
光唇鱼 <i>Acrossocheilus fasciatus</i>	0.91	0.17		4.69	8.27		
原缨口鳅 <i>Vanmanenia stenosoma</i>	0.91	0.33	0	4.01	7.08	5.09	10.33
稀有花鳅 <i>Cobitis rarus</i>	0.73	0.17	0.11	3.95	6.96	3.74	7.59
河川沙塘鳢 <i>Odontobutis obscurus</i>	0	0.58		3.34	5.89		
麦穗鱼 <i>Pseudorasbora parva</i>	0.27		0.56			2.84	5.77
中华花鳅 <i>Cobitis sinensis</i>	0.55	0.17	0.56	3.28	5.79	2.83	5.75
高体鲮鱼 <i>Rhodeus ocellatus</i>	0.55	0.58	0.56	3.05	5.37	2.82	5.72
花斑副沙鳅 <i>Parabotia fasciata</i>	0.27		0.44			2.75	5.58
似鲮 <i>Belligobio nummifer</i>	0.45	0.33	0.33	2.93	5.17	2.73	5.54
泥鳅 <i>Misgurnus anguillicaudatus</i>	0.64	0.67		2.87	5.07		
银鲃 <i>Squalidus argentatus</i>	0.36	0.17	0.44	2.54	4.47	2.73	5.54

表3 溪流和河段对鱼类功能 α 多样性和 β 多样性的影响

Table 3 Effect of streams and segments on the functional α and β diversity of fish assemblages

功能多样性 Functional diversity	多样性指数 Diversity index	分类变量 Factors	T-III SS	F	P	组间比较 S-N-K
α 多样性 α diversity	功能丰富度 Functional richness	溪流 Stream	268.569	5.629	0.010	舒溪 < 麻溪 = 浦溪 $SS < MS = PS$
		河段 Segment	173.811	3.643	0.042	上游 < 中游 = 下游 $Up < Mi = Lo$
		溪流 \times 河段 Stream \times Segment	300.09	3.145	0.034	
	功能均匀度 Functional evenness	溪流 Stream	0.003	1.444	0.256	
		河段 Segment	0.002	1.033	0.372	
		溪流 \times 河段 Stream \times Segment	0.007	1.485	0.239	
	功能离散度 Functional divergence	溪流 Stream	0.029	14.189	0.000	舒溪 > 浦溪 = 麻溪 $SS > PS = MS$
		河段 Segment	0.001	0.658	0.527	
		溪流 \times 河段 Stream \times Segment	0.011	2.595	0.063	
β 多样性 β diversity	功能 β 多样性 Functional β_{sor} diversity	溪流 Stream	0.328	13.749	0.000	舒溪 < 浦溪 = 麻溪 $SS < PS = MS$
		河段 Segment	0.003	0.125	0.883	
		溪流 \times 河段 Stream \times Segment	0.086	1.804	0.063	
	功能嵌套 Functional β_{nes} diversity	溪流 Stream	0.029	1.661	0.212	
		河段 Segment	0.007	0.385	0.685	
		溪流 \times 河段 Stream \times Segment	0.014	0.385	0.817	
	功能周转 Functional β_{tur} diversity	溪流 Stream	0.477	25.032	0.000	舒溪 < 浦溪 < 麻溪 $SS < PS < MS$
		河段 Segment	0.013	0.695	0.509	
		溪流 \times 河段 Stream \times Segment	0.091	2.400	0.079	

SS, MS and PS represent Shuxi, Maxi and Puxi Stream, respectively. Up, Mi and Lo represent the upper, middle and lower segments, respectively.

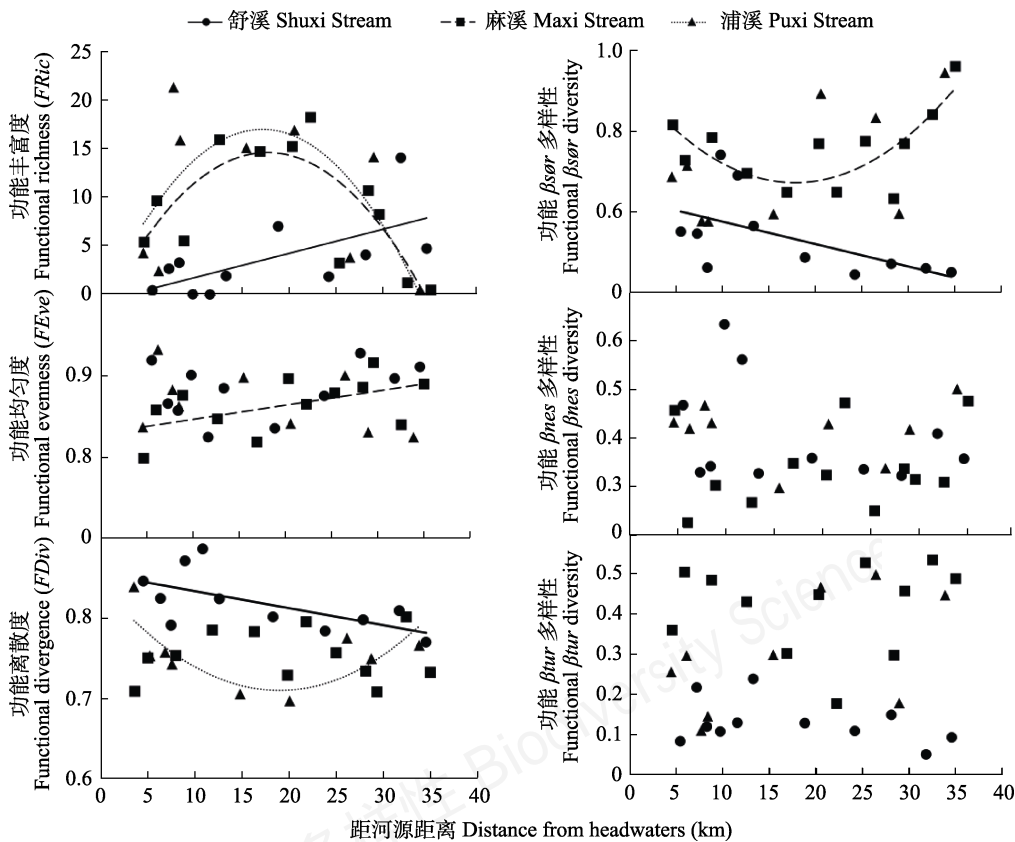


图3 功能多样性与距河源距离的关系

Fig. 3 Relationship between the functional diversity and the distance from headwaters

表4 功能α和β多样性与距河源距离的线性和二次项模型的统计数据

Table 4 Summary statistic for the linear and quadratic models explaining the correlations between functional diversities and distance from headwaters

功能多样性 Functional diversity	多样性指数 Diversity index	溪流 Stream	模型 Models	R^2	F	P
α多样性 α diversity	功能丰富度 Functional richness	舒溪 Shuxi	线性 Linear	0.410	6.310	0.033*#
			二次项 Quadratic	0.418	2.870	0.115
		麻溪 Maxi	线性 Linear	0.092	1.013	0.338
			二次项 Quadratic	0.648	8.288	0.009*
		浦溪 Puxi	线性 Linear	0.052	0.387	0.554
			二次项 Quadratic	0.434	2.304	0.081
	功能均匀度 Functional evenness	舒溪 Shuxi	线性 Linear	0.120	1.210	0.300
			二次项 Quadratic	0.350	2.180	0.175
		麻溪 Maxi	线性 Linear	0.288	4.045	0.072#
			二次项 Quadratic	0.317	2.091	0.182
		浦溪 Puxi	线性 Linear	0.183	1.571	0.250
			二次项 Quadratic	0.274	1.132	0.383
	功能离散度 Functional divergence	舒溪 Shuxi	线性 Linear	0.395	5.880	0.038*#
			二次项 Quadratic	0.398	2.640	0.132
		麻溪 Maxi	线性 Linear	0.003	0.029	0.868
			二次项 Quadratic	0.132	0.682	0.530
		浦溪 Puxi	线性 Linear	0.045	0.328	0.585
			二次项 Quadratic	0.578	4.104	0.075
β多样性 β diversity	功能βsor多样性 Functional βsor diversity	舒溪 Shuxi	线性 Linear	0.339	4.624	0.060#
			二次项 Quadratic	0.347	2.123	0.182
		麻溪 Maxi	线性 Linear	0.080	0.865	0.374
			二次项 Quadratic	0.598	6.700	0.017*
		浦溪 Puxi	线性 Linear	0.324	3.356	0.110
			二次项 Quadratic	0.352	1.632	0.272
	功能βnes多样性 Functional βnes diversity	舒溪 Shuxi	线性 Linear	0.124	1.278	0.287
			二次项 Quadratic	0.132	0.610	0.567
		麻溪 Maxi	线性 Linear	0.039	0.407	0.538
			二次项 Quadratic	0.102	0.508	0.618
		浦溪 Puxi	线性 Linear	0.000	0.002	0.962
			二次项 Quadratic	0.477	2.737	0.431
	功能βtur多样性 Functional βtur diversity	舒溪 Shuxi	线性 Linear	0.147	1.551	0.244
			二次项 Quadratic	0.255	1.368	0.308
		麻溪 Maxi	线性 Linear	0.008	0.079	0.785
			二次项 Quadratic	0.186	1.029	0.396
		浦溪 Puxi	线性 Linear	0.322	3.320	0.111
			二次项 Quadratic	0.338	1.533	0.290

* $P < 0.05$; # 线性关系 Linear relationship

无显著相关。 βnes 和 βtur 与距河源距离无显著的线性或二项式关系($P > 0.10$) (表3, 图3)。

3 讨论

沿着上游-下游的纵向梯度, 溪流系统存在显著的空间异质性, 栖息地多样化且具有一定的复杂性, 进而影响鱼类物种组成及其数量的分布 (Suvarnaraksha et al, 2012)。此外, 在河流网络结构

中, 不同河段在河网中的空间位置不同, 其鱼类的迁入迁出速率也存在差异, 因而其鱼类多样性也可能存在差异(Yan et al, 2011)。本研究发现, 在人类干扰程度较轻的舒溪中, 鱼类功能丰富度与距河源距离呈线性正相关, 反映了功能丰富度从上游至下游呈线性上升趋势, 该结果与Li等(2018)所观察到的物种丰富度的纵向梯度规律一致。关于生物多样性和生态系统功能的经典研究表明, 高物种多样性往

往产生高功能多样性(Tilman et al, 1997); 同时, 本研究结果也进一步证实了河流连续体(The River Continuum Concept)的预期, 即: 从河流上游至下游, 随着资源多样性的增加, 鱼类营养多样性上升, 最终流域下游的功能多样性增加(Thorp et al, 2006)。但是, 本研究也发现, 舒溪鱼类功能离散度(*FDiv*)的纵向梯度分布规律与*FRic*相反——从上游至下游呈线性下降趋势。*FDiv*衡量群落功能性状多度分布的最大离散程度, 离散度高表明物种间的生态位分化程度高、资源竞争程度低(Mason et al, 2005)。有研究表明, 溪流系统的栖息地多样性、复杂性和稳定性从上游至下游显著变化。同溪流下游相比, 上游河段的水文和栖息地条件的季节变化非常大, 因而鱼类的种群数量波动较大, 通常达不到形成种间甚至种内竞争的种群数量; 相反, 下游河段的水文和栖息地条件的稳定性较高, 鱼类的种群数量也相应较大, 种内竞争激烈(Horwitz, 1978)。据此, 我们推测, 溪流环境稳定性的空间变化可能影响了溪流鱼类的种群数量及种间资源竞争强度变化, 进而可能促进了鱼类功能离散度由上游至下游逐渐减小这一空间格局。

本研究还发现, 在受干扰程度较低的舒溪, 从上游至下游, 鱼类功能 β 多样性(*βsør*)呈线性下降趋势, 该空间格局与功能丰富度正好相反。类似结果也见于Li等(2018)针对物种多样性的研究结果。众所周知, α 多样性和 β 多样性的内涵不同(Kessler et al, 2009), 正因为两者的生物学意义差异, α 多样性和 β 多样性沿着环境梯度的空间格局可能不一致甚至相反(Tylianakis et al, 2005)。同中下游河段相比, 上游河段的环境条件苛刻(如低营养、低温、急流等), 尽管鱼类物种较少但其特有性较高, 因而具有极高的 β 多样性(Li et al, 2018; 张东等, 2018)。因此, 有理由相信, 若上游河段特有鱼类物种也具有特殊的功能特征, 那么, 上游河段的鱼类功能 β 多样性也就相对较高, 这在一定程度上能够解释本研究所观察到的舒溪鱼类功能 β 多样性为何从上游至下游呈下降趋势。此外, 本研究还发现, 在舒溪中, 鱼类功能 β 多样性主要由嵌套成分贡献, 其比例超过3/4。从一个群落落到另一个群落, 其物种/功能的变化模式包括物种/功能丢失与物种/功能获得(Villéger et al, 2014), 若丢失和获得过程两者兼有则呈群落周转格局, 若仅含丢失或获得1个过程则呈群落嵌套格

局(Leprieur et al, 2011)。有研究发现, 沿着特定的环境梯度, 周转和嵌套成分对 β 多样性的贡献大小, 会随物种和功能多样性而变化——物种 β 多样性主要由周转主导, 而功能 β 多样性由嵌套主导(Bishop et al, 2014; 张东等, 2018)。


本研究中的3条河源溪流的人为干扰强度不同, 同舒溪相比, 麻溪和浦溪的人为干扰强度明显较重(附录1), 且同一溪流内人为扰动强度由上游(高坡)向下游(低坡)逐渐增大(附录2)。*FRic*和*FDiv*两个指数受溪流和河段2个因素的交互影响, 这反映了人类干扰对鱼类功能 α 多样性的影响视不同河段而变化。我们发现, 同舒溪相比, 麻溪和浦溪的鱼类物种组成发生了显著变化, 主要表现为光唇鱼、原缨口鳅、稀有花鳅等物种的减少或丢失以及河川沙塘鳢和麦穗鱼等物种的增多或获得。根据Chu等(2015)和Liu等(2019), 上述丢失的光唇鱼、原缨口鳅和稀有花鳅为研究区域内河源溪流中的土著种, 而获得的河川沙塘鳢和麦穗鱼原生活于研究区域内的低地水体, 故在河源溪流中隶属本地入侵种。溪流间各个河段的物种组成均有差异, 尤其是以下游更为明显(图2), 这也意味着上述土著物种丢失和本地入侵种获得过程在各个河段均有发生。麻溪和浦溪的中上游河段的*FRic*高于舒溪, 但其下游的*FRic*却低于舒溪(图3)。我们认为, 因中上游河段的人为干扰强度相对较小, 麻溪和浦溪中上游河段的鱼类物种组成变化可能是以本地入侵种的获得为主导(较轻的人为干扰可能没有导致土著种的大量丢失), 那么, 当获得的本地入侵种带来一定的新功能特征时, 将提高麻溪和浦溪中上游河段的功能丰富度。但是, 在下游河段, 因人为干扰强度较大, 其物种组成变化不仅体现在本地入侵种的获得, 也表现为很多土著种的丢失, 那么, 当获得物种所带来的新功能特征远少于丢失物种所具有的功能特征时, 将导致麻溪和浦溪下游河段功能丰富度的下降。我们还发现, 在麻溪和浦溪上中游, 随着人为干扰增大, 功能离散度逐渐降低。我们认为, 在人类活动的影响下, 浦溪和麻溪中上游河段获得了一些本地入侵种, 这些本地入侵种在食物等资源利用上与土著鱼类存在较高的重叠。朱仁等(2012)通过胃含物分析发现, 在青弋江陈村水库上游河源溪流中, 以本地入侵种麦穗鱼为例, 其与光唇鱼、宽鳍鱲(*Zacco platypus*)等土著种的食物重叠系数超过90%; 相反, 以土著


物种吻虾虎鱼为例, 其与光唇鱼、宽鳍鱲等其他土著种的食物重叠系数低于50%。这可能意味着, 在浦溪和麻溪中上游河段, 因本地入侵种获得所带来的种间资源分化下降、种间竞争加剧, 导致了其鱼类功能离散度相对下降。

物种取代过程既能够驱动基于物种组成的分类同质化/异质化过程, 也能够带来基于物种特征的功能同质化/异质化变化(Su et al, 2015)。同舒溪相比, 麻溪和浦溪的平均功能 β 多样性($\beta_{s\phi r}$)显著上升, 由此可见, 人类干扰促进了溪流鱼类群落趋于功能异质化。考虑到同一溪流不同河段间人类干扰强度存在差异, 当土著种和本地入侵种存在功能特征上的差异时, 该物种异质化也将引起鱼类群落在功能特征上趋于异质化。本研究还发现, 功能 $\beta_{s\phi r}$ 受溪流与河段的交互影响, 这意味着溪流间的 $\beta_{s\phi r}$ 变化视河段而不同。在下游, 麻溪和浦溪的功能 β 多样性相对于舒溪而言, 其变化程度增大, 这可以通过人为干扰强度(如城市用地比例)沿纵向梯度的空间分布来解释。尽管舒溪功能 β 多样性主要由嵌套成分组成(占比超过75%), 麻溪和浦溪中嵌套成分所占比例明显下降(麻溪: 57.75%; 浦溪: 45.33%)。若环境变化具有连续性, 则多为嵌套模式; 相反, 若环境变化呈间断性, 则主要表现为周转模式(Roberts & Hitt, 2010)。根据“河流连续体概念”, 河流系统具有连续性、等级性和异质性等多重属性; 从河源至河口, 其非生物因子及生物成分的空间变化具有连续性特点(Vannote et al, 1980)。但是, 受水坝、土地利用等人类活动的影响, 很多河流的空间连续性被打断, 呈现为“序列不连续”特点(Ward & Stanford, 1983)。因此, 同舒溪相比, 麻溪和浦溪中较强的土地利用(陆君等, 2014)和水污染排放(李响等, 2014)可能增大了其序列不连续, 进而导致鱼类群落及其功能特征的周转率上升。

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附录 Supplementary Material

附录1 青弋江3条河源溪流每年排放的污染及不同土地利用比例的差异

Appendix 1 Differences in the pollution emitted yearly and the proportions of land use across three headwaters of Qingyi River
<https://www.biodiversity-science.net/fileup/PDF/2020434-1.pdf>

附录2 不同坡度土地利用比例的变化

Appendix 2 The variations in the proportion of land use across the areas of different slopes
<https://www.biodiversity-science.net/fileup/PDF/2020434-2.pdf>

附录3 本研究功能 α 和 β 多样性指数的计算公式

Appendix 3 The formulas of the functional α and β diversity indices calculated in this study
<https://www.biodiversity-science.net/fileup/PDF/2020434-3.pdf>

贺佳云, 张东, 储玲, 严云志 (2021) 人为干扰对溪流鱼类功能多样性及其纵向梯度格局的影响. 生物多样性, 29, 927–937. <https://www.biodiversity-science.net/CN/10.17520/biods.2020434>

附录1 青弋江3条河源溪流每年排放的污染及不同土地利用比例的差异
Appendix 1 Differences in the pollution emitted yearly and the proportions of land use across three headwaters of Qingyi River

人为干扰 Disturbance	变量类型 Variable	舒溪 Shuxi	麻溪 Maxi	浦溪 Puxi	参考文献 Reference
污染排放 Polluting emission (t/year)	化学需氧量 COD	332.22	1,246.39	998.41	李响等, 2014
	氨氮 NH ₃ -N	38.50	134.51	104.11	
	总磷 TP	5.27	17.04	10.59	
土地利用 Land use (%)	建筑用地 Urban land	0.63	3.13	9.32	
	耕地 Farmland	3.67	8.08	11.12	
	林草地 Forest-grass land	92.43	81.71	75.99	
	其他用地 Others	1.30	3.82	1.56	

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附录 2 不同坡度土地利用比例的变化(城市用地/农业用地)
Appendix 2 The variations in the proportion of land use across the areas of different slopes (urban land/farmland)

坡度 Slope	舒溪 Shuxi	麻溪 Maxi	浦溪 Puxi	参考文献 Reference
>25 °	0.03/0.13	0.13/0.10	0.08/0.08	陆君等, 2014
15 °-25 °	0.05/0.22	0.26/0.40	0.37/0.64	
6 °-15 °	0.12/0.69	0.60/1.69	1.53/2.47	
0 °-6 °	0.43/2.63	2.14/5.90	7.33/7.94	

Lu J, Liu YF, Huang HH, Qi K, Li X, Fan ZQ (2014) Correlation analysis between land use structure and water quality of the Taiping Lake watershed in Huangshan. Journal of Fudan University (Natural Science), 53, 731–736, 746. (in Chinese with English abstract)
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附录3 本研究功能 α 和 β 多样性指数的计算公式
Appendix 3 The formulas of the functional α and β diversity indices calculated in this study

多样性类型 Diversity type	多样性指标 Diversity index	计算公式 Calculation formula	参考文献 Reference
功能 α 多样性 Functional α diversity	功能丰富度 (<i>FRic</i>)	$FRic = \frac{SF_{ic}}{R_c}$	Mason et al, 2005; Villéger et al, 2008
	功能均匀度 (<i>FEve</i>)	$EW_l = \frac{dist(i,j)}{w_i + w_j}$ $PEW_l = \frac{EW_l}{\sum_{l=1}^{s-1} EW_l}$ $FE_{ve} = \frac{\sum \min(PEW_l, \frac{1}{s-1}) - \frac{1}{s-1}}{1 - \frac{1}{s-1}}$	
	功能离散度 (<i>FDiv</i>)	$g_k = \frac{1}{S} \cdot \sum_{i=1}^s x_{ik}$ $dG_i = \sqrt{\sum_{k=1}^T (x_{ik} - g_k)^2}$ $\overline{dG} = \frac{1}{S} \sum_{i=1}^s dG_i$ $\Delta d = \sum_{i=1}^s W_i$ $\Delta d = \sum_{i=1}^s W_i \times dG_i - \overline{dG} $ $FD_{iv} = \frac{\Delta d + \overline{dG}}{\Delta d + \overline{dG}}$	
功能 β 多样性 Functional β diversity	β_{sor}	$\beta_{sor} = \frac{V(C1) + V(C2) - 2 * V(C1 \cap C2)}{V(C1) + V(C2) - V(C1 \cap C2)}$	Villéger et al, 2013
	β_{nes}	$\beta_{nes} = \frac{ V(C1) - V(C2) }{V(C1) + V(C2) - V(C1 \cap C2)} * \frac{V(C1 \cap C2)}{2 * \min(V(C1), V(C2)) - V(C1 \cap C2)}$	
	β_{tur}	$\beta_{tur} = \frac{2 * \min(V(C1), V(C2)) - 2 * V(C1 \cap C2)}{2 * \min(V(C1), V(C2)) - V(C1 \cap C2)}$	

*SF_{ic}*指群落中物种所占据的生态位; *R_c*指特征值的绝对值; *dist*(*i*, *j*)为物种和的欧氏距离; *S*为物种数; *w_i*为物种*i*的相对丰富度; *l*为分支长; *PEW_l*为分支长权重; *x_{ik}*为物种*i*性状*k*的重心; *g_k*为性状*k*的重心; *dG_i*为到重心的欧氏距离; \overline{dG} 为物种到重心的平均距离; Δd 为丰度加权偏加的总和;

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Δ/d 为物种 i 与重心的平均距离。

$C1$ 和 $C2$ 代表两个群落, $V(C1)$ 和 $V(C2)$ 分别代表这两个群落中物种功能特征所占空间体积; $V(C1 \cap C2)$ 代表两个群落功能空间相交部分的体积。

SF_{ic} is the niche space filled by the species within the community; R_c is the absolute range of the character; $dist(i, j)$ is the Euclidean distance between species i and j ; S is species numbers; w_i is the relative abundance of species i ; l is the length of the branch; PEW_l is weight of branch length; x_{ik} is the coordinate of species i on trait k ; g_k is the center of gravity of trait k ; dG_i is the Euclidean distance to this center of gravity; \overline{dG} is the mean distance of the S species to the center of gravity; Δd is the sum of abundance-weighted deviances; Δ/d is the absolute abundance-weighted deviances for distances from the center of gravity.

$C1$ and $C2$ represent two communities, and $V(C1)$ and $V(C2)$ is the spatial volume occupied by the functional traits of species in these two communities respectively. $V(C1 \cap C2)$ is the volume of the intersection part of the functional space of two communities.

Mason NWH, Mouillot D, Lee WG, Wilson JB (2005) Functional richness, functional evenness and functional divergence: The primary components of functional diversity. *Oikos*, 111, 112–118.

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