



## •研究报告•

# 澜沧江流域水生昆虫群落分类多样性和功能多样性海拔格局的空间尺度依赖性

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**摘要:** 群落分类多样性和功能多样性的海拔格局研究, 是了解生物多样性空间分布现状、揭示多样性维持和变化机制的重要途径。当前对水生昆虫分类多样性和功能多样性沿海拔梯度分布格局, 及其尺度依赖性依旧缺乏深入研究。本文基于2013–2018年在云南澜沧江流域500–3,900 m海拔梯度共149个溪流点位的水生昆虫群落调查数据, 利用线性或二次回归模型探索并比较了局部尺度(点位尺度)和不同区域尺度(100 m、150 m、200 m、250 m海拔段)的分类多样性指数(物种丰富度指数、Simpson多样性指数和物种均匀度指数)和功能多样性指数(树状图功能多样性指数(dbFD)、Rao二次熵指数(RaoQ)和功能均匀度指数(FEve))的海拔格局。结果表明, 在局部尺度, 物种丰富度指数和dbFD指数沿海拔梯度均无显著分布特征, Simpson多样性指数、RaoQ指数、物种均匀度指数和FEve指数沿海拔梯度呈现U型或者单调递减趋势。在区域尺度, 随着区域海拔带宽度的增加, 物种丰富度指数沿海拔呈不显著的单调递减格局, 但dbFD指数沿海拔分布由U型转变为单调递减趋势; Simpson多样性指数和RaoQ指数沿海拔梯度由显著U型趋势转变为无显著分布特征; 物种均匀度指数沿海拔梯度无显著分布特征, 但FEve指数呈显著增加的海拔格局。综上, 群落分类多样性指数和功能多样性指数沿海拔梯度分布存在局部和区域尺度的空间差异, 但区域尺度下二者海拔格局随海拔带宽度的增加存在一定程度的一致性。

**关键词:** 生物多样性; 功能性状; 海拔梯度; 局部尺度; 区域尺度; 溪流; 生物地理学

## The spatial scale dependency of elevational patterns of taxonomic and functional diversity in aquatic insects in the Lancang River, Yunnan, China

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**Abstract:** Elevational patterns of taxonomic and functional diversity are important aspects of biodiversity maintenance and changes. However, the spatial scale dependency of elevational patterns on taxonomic and functional diversity of aquatic insect assemblages remains unclear. Using data collected from 149 stream sites along elevational gradients ranging between 500–3,900 m during 2013–2018 in the upper basin of Lancang River in Yunnan Province, China, we examined how elevational patterns of taxonomic and functional diversity of aquatic insect assemblages differed across local and regional scales among multiple elevational bands (i.e., 100, 150, 200, and 250 m). We used linear or quadratic regression models to explore the elevational patterns of taxonomic richness index, Simpson diversity index, evenness index, dendrogram-based functional diversity index (dbFD), Rao's Quadratic index (RaoQ), and functional evenness index (FEve). At the local scale, taxonomic richness index and dbFD index show no significant elevational patterns; while Simpson diversity index, RaoQ index, evenness index, and FEve index show either U-shaped or monotonically decreasing trends along elevation gradients. At the regional scale with increasing elevation, taxonomic richness index decreases (NS) while dbFD index changes from U-shaped to a monotonically decreasing trend along the elevational gradient. Both Simpson diversity index and RaoQ index change from a significant U-shaped to no significant regional elevational patterns. Taxonomic evenness index and FEve

index have no significant relationship with and significantly increased with regional elevations, respectively. Our results show that aquatic insect taxonomic and functional diversity are scale dependent across elevations. However, we observed a degree of consistency in elevational patterns for each taxonomic and functional diversity index across elevational bands at regional scales.

**Key words:** biodiversity; functional traits; elevation gradients; local scale; regional scale; stream; biogeography

海拔梯度综合了多种环境因子(如温度、降水、光照等)的梯度效应(Gaston, 2000; 唐志尧和方精云, 2004), 是影响物种组成、生物群落构建和多样性空间格局的重要因素(Sundqvist et al, 2013; 卢孟孟等, 2014)。物种多样性的海拔格局研究有助于揭示全球生物多样性现状及其维持和变化机制(李巧燕和王襄平, 2013; Laiolo et al, 2018)。作用于不同空间尺度(例如局部和区域)的多重生态学过程和空间距离等因素, 共同决定了物种沿海拔梯度的分布特征(Laiolo et al, 2017), 物种多样性海拔格局因此可能存在空间尺度依赖性(Rahbek, 2005)。分类多样性和功能多样性是物种多样性的重要组成: 分类多样性是基本组成, 描述群落物种组成、结构和多样性特征(宋普庆等, 2015); 功能多样性基于功能性状描述群落组成物种对生态过程的需求和响应及其生态功能等特征(Villéger et al, 2010)。已有研究对物种多样性海拔格局的空间尺度依赖性仍旧缺乏深入的认识; 同时探索分类多样性和功能多样性沿海拔梯度分布的空间尺度差异性, 对全面理解物种多样性的海拔格局具有重要价值。

水生昆虫是河流生态系统具有重要生态功能的组成类群(Covich et al, 1999; Mermillod-Blondin, 2011), 对自然环境和人类干扰梯度的响应敏感(Dohet et al, 2015), 可综合反映时空尺度环境作用下水生生态系统的动态变化。已有研究发现, 水生昆虫分类多样性海拔格局在局部和区域尺度主要符合单峰模型(Füreder et al, 2006; Wang et al, 2011; de Mendoza et al, 2017)和单调递减(Jacobsen, 2004; Castro et al, 2019)分布, Jacobsen (2004)发现溪流无脊椎动物丰富度沿海拔降低的分布格局呈现局部和区域尺度差异性。目前仅有部分研究探索了水生昆虫功能多样性的海拔格局, 如Lafferty<sup>①</sup>发现落基山脉水生昆虫功能丰富度与沿海拔梯度变化的溪流大小

和流量稳定性呈正相关关系。当前依旧缺乏对水生昆虫分类多样性和功能多样性海拔格局的局部和区域尺度空间差异的探索研究。

澜沧江流域海拔高差显著, 生物多样性丰富, 是世界生物多样性研究的热点地区(王川等, 2013; 程豹等, 2018), 也是开展空间尺度影响物种多样性海拔格局研究的重要区域。本研究通过系统分析澜沧江流域云南段的水生昆虫数据, 探索和比较局部和区域尺度的分类多样性和功能多样性指数海拔格局, 探讨多重空间尺度下水生昆虫物种多样性沿海拔梯度的分布规律; 以期为澜沧江水生昆虫多样性研究提供数据积累, 并为探讨水生昆虫海拔格局的空间尺度效应等研究奠定一定基础。

## 1 材料与方法

### 1.1 研究区域概况

澜沧江流域云南段由北向南从迪庆藏族自治州至西双版纳勐腊县出境口, 全长910 km (冯建孟等, 2012), 海拔高差超过6,500 m (胡波等, 2006), 澜沧江河谷海拔1,200–2,000 m (杨阳等, 2016)。流域地表形态复杂且特殊, 相对高差显著, 生物多样性丰富(王川等, 2013)。该流域纵跨热带、亚热带和大陆性高寒气候带, 气温和降水随海拔升高均表现出下降趋势(何云玲和张一平, 2004)。流域由北至南土地利用垂直分带明显, 上游地区人口较少, 主要以林地灌木为主; 中下游人口密集, 主要以耕地和人工经济林为主(姜昀等, 2006)。

参照Jacobsen (2004)的方法, 沿海拔梯度在2–4级溪流分别采集56、53和40个样点, 共149个溪流样点(图1)。于2013年3月、2016年3月和10月、2018年10月雨季前后的水文平稳期共进行4次野外样品采集, 所有采样点位海拔范围介于500–3,900 m, 采样点位覆盖研究区域的典型气候特征和土地利用类型。方差分析结果表明, 除水温外, 不同溪流等级采样点位的海拔、土地利用、底质组成及其他环境变量均无显著性差异(表1)。

<sup>①</sup> Lafferty MH (2018) Changes in Taxonomic and Functional Diversity of Aquatic Macroinvertebrates Along a Gradient of Stream Size and Flow Stability in the Northeastern Colorado Rocky Mountains. Master thesis, Colorado State University, Colorado.

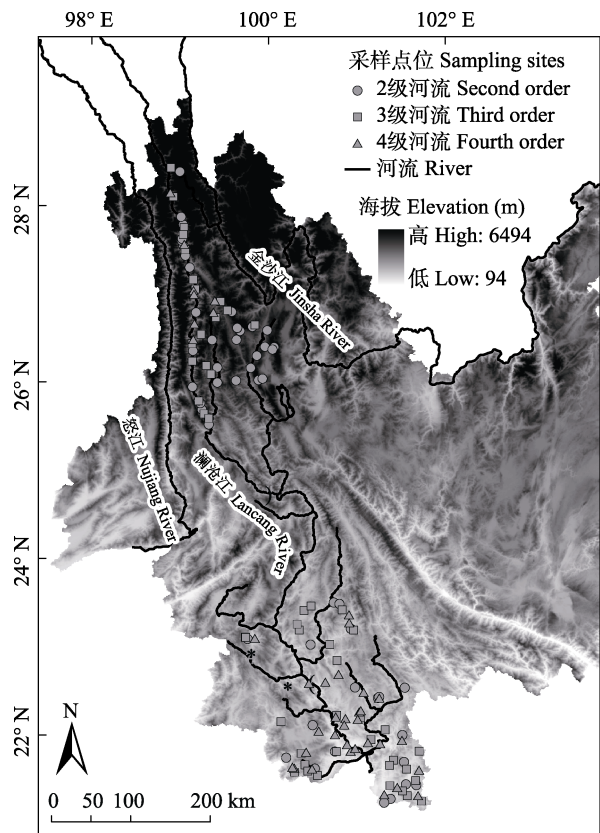


图1 澜沧江流域云南段溪流采样点位分布图  
Fig. 1 Locations of sampling sites in the Lancang River in Yunnan Province, China

1.2 水生昆虫的采集与鉴定

根据多生境采样原则，在100 m长的溪流河段内根据栖境类型的出现比例分配样方数，使用D型网(直径30 cm、60目孔径)采集水生昆虫(Hughes & Peck, 2008)。每个样点共采集8–10个样方，混合成为1个样点样本后，使用60目分样筛筛洗，加入分析纯乙醇溶液固定。实验室内挑拣、鉴定和计数水生昆虫所有个体，根据已有可靠的形态学资料鉴定至可能的最低分类单元，通常为属级；其中，仅鞘翅目、半翅目和双翅目的部分类群鉴定至科级。

1.3 数据分析

1.3.1 空间尺度

首先从中国科学院国际科学数据服务平台(<http://www.resdc.cn>)下载精度为30 m的数字高程模型(DEM)数据，通过ArcGIS 10.2软件对所有野外获得的海拔数据进行校正。局部尺度，即每个采样点的点位尺度；区域尺度，共划分4个海拔段大小，分别以100 m (即500–599 m、600–699 m，以此类推)，150 m (即500–649 m、650–799 m，以此类推)，200 m (即500–699 m、700–899 m，以此类推)，250 m (即500–749 m、750–999 m，以此类推)为单位划分海拔段(Gill et al, 2014; Carvajal-Quintero et al, 2015;

表1 不同溪流等级采样点位环境因子概况

Table 1 Summary of environmental variables across sampling sites collected from second-, third-, and fourth-order streams

环境变量 Environmental variables	2级 Second order		3级 Third order		4级 Fourth order	
	平均值 ± 标准差 Mean ± SD	范围 Range	平均值 ± 标准差 Mean ± SD	范围 Range	平均值 ± 标准差 Mean ± SD	范围 Range
海拔 Elevation (m)	1,392 ± 719	528–3,146	1,451 ± 721	502–3,935	1,311 ± 569	595–2,899
水温 Water temperature (°C)*	15.46 ± 4.69	1.10–26.10	16.63 ± 5.05	6.80–28.00	19.33 ± 4.30	10.30–26.00
泥沙含量百分比 Percent of sand (%)	8.61 ± 16.20	0.00–100.00	7.62 ± 10.79	0.00–60.00	14.09 ± 16.69	0.00–70.00
碎石含量百分比 Percent of gravel (%)	32.49 ± 24.41	0.00–100.00	30.15 ± 20.38	5.08–87.93	36.71 ± 18.25	2.78–85.00
鹅卵石含量百分比 Percent of cobbles (%)	42.82 ± 21.40	0.00–81.82	45.52 ± 17.98	0.00–72.37	39.10 ± 19.30	0.00–68.06
大石块含量百分比 Percent of boulders (%)	16.08 ± 14.53	0.00–55.00	16.71 ± 14.25	0.00–60.00	10.10 ± 11.17	0.00–45.71
农业用地占比 Percent of agricultural land (%)	1.61 ± 4.73	0.00–32.01	0.91 ± 1.51	0.00–8.44	3.11 ± 3.49	0.02–15.90
森林用地占比 Percent of forest land (%)	82.32 ± 17.73	21.58–100.00	85.89 ± 12.33	41.38–100.00	83.77 ± 11.27	54.20–96.86

\*  $P < 0.05$ .



Laiolo et al, 2018; Castro et al, 2019)。

1.3.2 多样性指数计算

分别计算局部和区域尺度水生昆虫群落的分类多样性和功能多样性指数, 然后对多样性指数的海拔格局进行分析。点位多样性指数即为局部尺度多样性指数; 综合每个海拔段所有点位的水生昆虫组成为海拔段物种组成, 计算区域尺度多样性指数。

(1)分类多样性指数

分类多样性指数基于群落分类特征测定群落分类组成和结构。采用物种丰富度指数(*S*)、Simpson多样性指数(*D*)和物种均匀度指数(*J*)综合表征局部和区域尺度的群落分类多样性特征。物种丰富度指数即群落内记录的物种总数; Simpson多样性指数(Simpson, 1949)和物种均匀度指数(Pielou, 1966)计算公式如下:

$$D = -\left(\sum_{i=1}^S \frac{N_i}{N}\right) N^2 \tag{1}$$

$$J = -\frac{\sum (N_i / N) \ln(N_i / N)}{\ln(S)} \tag{2}$$

式中, *S*为水生昆虫物种数, *N<sub>i</sub>*为第*i*个物种的个体数, *N*为水生昆虫个体总数。

(2)功能多样性指数

选择外骨骼保护状况、体型、呼吸方式、营养习性、亲流性、生活习性和个体大小共7个对环境变化响应敏感连续型和离散型生物性状(Ding et al, 2017; 李胜利等, 2018)。参照Colzani等(2013)使用离散数字1、2、3……对每个性状进行赋值, 将所有性状划分为共25个离散类别(表2), 用于功能多样性指数计算。所有生物学性状及其赋值主要从已发表文献资料获取(Morse et al, 1994; Usseglio-Polatera et al, 2000; Poff et al, 2006; Ding et al, 2017)。

功能多样性指数表征群落物种功能性状组成和结构特征(Villéger et al, 2008), 本文选用以下3个指数: (1)树状图功能多样性指数(dendrogram-based functional diversity, dbFD)。根据功能性状矩阵构建群落性状树状图, 树状图所有分支长度的总和即为dbFD指数; 该指数结合了物种丰富度、群落组成和功能性状数量(Petchey & Gaston, 2002), 通过估算物种在性状空间的分布, 衡量物种性状的互补程度(Petchey & Gaston, 2002), 与物种多度无关(González-Maya et al, 2016)。(2) Rao二次熵指数(Rao's Quadratic,

表2 水生昆虫功能性状类别及其赋值  
Table 2 Functional trait states and scores of aquatic insects

性状类别	Trait state	赋值	Score
外骨骼保护状况 Exoskeleton or external protection			
虫体柔软	Soft-bodied forms	1	
轻微骨化	Lightly sclerotized	2	
骨化良好	Heavily sclerotized	3	
体型 Body shape			
流线型	Streamlined	1	
非流线型	Not streamlined	2	
呼吸方式 Respiration			
体壁呼吸	Tegument	1	
鳃呼吸	Gills	2	
气氧呼吸(呼吸管、气泡、气盾)	Air (spiracles, tracheae, plastrons)	3	
营养习性 Trophic habit			
集食者	Collector-gatherer	1	
滤食者	Collector-filterer	2	
刮食者	Scraper	3	
捕食者	Predator	4	
撕食者	Shredder	5	
亲流性 Rheophily			
沉积型	Only depositional	1	
沉积型和冲刷型	Depositional and erosional	2	
冲刷型	Erosional	3	
生活习性 Habit			
掘穴者	Burrowers	1	
攀爬者	Climbers	2	
匍匐者	Sprawlers	3	
附着者	Clingers	4	
游泳者	Swimmers	5	
滑行者	Skaters	6	
个体大小 Body size			
小	Small (< 9 mm)	1	
中等	Medium (9–16 mm)	2	
大	Large (> 16 mm)	3	

RaoQ)。RaoQ指数结合了物种相对多度和物种间的成对功能差异性, 表达两个随机选择个体间的性状平均差异性(Laliberté & Legendre, 2010); RaoQ指数可视为Simpson多样性指数在功能多样性维度的扩展(Shimatani, 2001), 当所有物种间无共享性状时, Simpson多样性指数值即代表了RaoQ指数能达到的最大值(de Bello et al, 2006)。(3)功能均匀度指数(functional evenness, FEve)。FEve指数测量了物种性状在性状空间的分布规律, 值越高意味着物种性状的分布越均匀(Mason et al, 2005); FEve指数与物种均匀度指数相似, 两者分别从功能性状和分类维度

描述了物种分布规律。

### 1.3.3 多样性海拔格局分析

应用线性模型和二次回归模型拟合局部和区域尺度多样性指数的海拔梯度格局;局部尺度海拔格局即点位多样性指数对点位海拔的响应,区域尺度海拔格局即区域尺度多样性指数对区域海拔段中点的响应。选择赤池系数(Akaike's Information Criterion, AICc)较小且 $F$ 检验显著( $P < 0.1$ )的模型为最佳拟合模型(Yamaoka et al, 1978; Mayor et al, 2017)。分析前使用广义线性模型(generalized linear models, GLM)拟合区域尺度多样性指数对海拔段采样点位数量、平均空间距离和平均纬度的响应,综合分析区域海拔段采样强度和纬度梯度对生物多样性海拔格局的影响。其中,采样点位数量即每个海拔段的采样点位数,点位平均空间距离为海拔段内所有点位欧几里得距离(Euclidean distance)的平均值,平均纬度为海拔段内所有点位的纬度平均值。使用Poisson分布拟合分类多样性指数,使用高斯分布拟合功能多样性指数(Jyväsjärvi et al, 2018)。当GLM呈显著水平( $P < 0.05$ )时,说明海拔段间的采样点位数量、平均空间距离和平均纬度对多样性指数影响显著,进一步计算多样性指数残差用于后续分析;当GLM呈现非显著水平( $P > 0.05$ )时,说明以上因素对多样性指数无显著影响,则使用原始多样性指数用于海拔格局分析。

采用R 3.6.1软件vegan功能包的diversity函数计算分类多样性指数,通过FD功能包的dbFD函数计算功能多样性指数,使用MuMIn功能包计算AICc值,应用ggplot2程序包绘图。

## 2 结果

### 2.1 水生昆虫物种组成

共鉴定水生昆虫277个分类单元,隶属10目102科;其中,双翅目(23科51分类单元)、鞘翅目(16科50分类单元)、毛翅目(20科48分类单元)、蜉蝣目(13科46分类单元)和蜻蜓目(12科46分类单元)为丰富度较高的优势类群,分别占总分类单元数的18.4%、18.1%、17.3%、16.6%和16.6%。所有2–4级溪流水生昆虫群落结构间无显著差异(附录1)。

### 2.2 分类多样性指数的海拔分布格局

区域尺度下,仅物种丰富度指数对海拔段间的采样点位数量、平均空间距离和平均纬度的响应关

系显著(附录2)。所有分类多样性指数中,仅Simpson多样性指数同时在局部和部分区域尺度呈现显著海拔分布特征,所有分类多样性指数在不同区域尺度下沿海拔梯度分布存在一致性(表3, 图2)。物种丰富度指数在所有空间尺度均无显著的海拔分布特征,海拔格局从局部尺度的弱“U”型,变化为区域尺度下不显著单调递减趋势。Simpson多样性指数在局部和区域(除250 m海拔段)尺度沿海拔梯度变化均表现出“U”型趋势,在中海拔部分局部尺度的指数值较低,最低值出现在1,500–2,500 m海拔范围内;随着空间尺度增大, SImpson多样性指数与海拔间的显著关系逐渐降低。物种均匀度指数在局部尺度下随海拔梯度的变化表现出显著单调递减趋势,而区域尺度下均未表现出显著的变化趋势。

### 2.3 功能多样性指数海拔分布格局

区域尺度下,所有功能多样性指数对海拔段采样点位数量、平均空间距离和平均纬度均无显著响应关系(附录2)。所有功能多样性指数的海拔格局在局部和区域尺度均存在差异性,但所有功能多样性指数在区域尺度下沿海拔梯度分布存在一致性(表3, 图2)。局部尺度dbFD指数沿海拔梯度表现出不显著的单调递增趋势;在区域尺度对海拔梯度变化存在显著响应关系,随海拔带宽度的增加,由近单调递减趋势的“U”型关系转变为单调递减的趋势。RaoQ指数沿海拔梯度由局部尺度的单调递减趋势,变化为100 m和150 m海拔带区域尺度的显著“U”型趋势,到200 m和250 m海拔带区域尺度的不显著“U”型趋势。FEve指数在所有空间尺度沿海拔梯度均呈现显著分布特征,在局部尺度沿海拔梯度呈现单调递减趋势,但在所有区域尺度下沿海拔梯度表现为单调递增趋势。

## 3 讨论

当前对水生昆虫群落多样性海拔格局的研究多集中在单一尺度的分类多样性(例如Wang et al, 2011; Castro et al, 2019)、或单个类群的个体大小性状分布(例如Vamosi et al, 2007; Cressa et al, 2008)等方面,对群落分类多样性和功能多样性海拔分布格局的空间差异研究缺乏深入的认识。了解生物多样性对空间尺度的响应,有助于更清晰地认识群落结构、格局、构建过程及其组织方式,为探究物种共存或物种多样性的形成和维持机制提供重要基础

(Rahbek, 2005)。本研究对云南澜沧江流域水生昆虫群落分类多样性和功能多样性海拔格局的空间差异研究表明, 水生昆虫群落多样性指数海拔格局对局部和区域尺度存在空间依赖性(Jacobsen, 2004; Rahbek, 2005); 在区域尺度下, 分类多样性和功能多样性指数的海拔格局存在一定程度的一致性。

局部尺度水生昆虫物种丰富度指数对海拔梯度无显著响应关系(Flowers, 1991), 但区域尺度物种丰富度指数沿海拔递减的格局特征在水生昆虫中较为普遍(Jacobsen, 2003; Cárcamo et al, 2019)。已

表3 不同空间尺度下水生昆虫群落多样性指数与海拔的线性和二次回归模型  
Table 3 Linear and quadratic model fitting relationships of diversity indices and elevation at different spatial scales

空间尺度 Spatial scale		多样性指数 Diversity index	线性模型 Linear model (L)			二次回归模型 Quadratic model (Q)			选择模型 Model selection
			解释量 Adjusted R <sup>2</sup>	P	赤池系数 AICc	解释量 Adjusted R <sup>2</sup>	P	赤池系数 AICc	
局部尺度 Local scale									
	物种丰富度指数	Species richness index	<0.001	0.418	1,218.2	0.01	0.166	1,217.2	NS
	Simpson多样性指数	Simpson diversity index	0.04	0.010	-136.6	0.05	0.001	-137.4	Q
	物种均匀度指数	Species evenness index	0.06	0.001	-152.6	0.07	0.002	-152.0	L
	树状图功能多样性指数	Dendrogram-based functional diversity index (dbFD)	<0.001	0.633	364.0	<0.001	0.477	364.7	NS
	Rao二次熵指数	Rao's Quadratic index (RaoQ)	0.02	0.057	-516.4	0.02	0.074	-516.0	L
	功能均匀度指数	Functional evenness index (FEve)	0.01	0.079	-284.8	0.01	0.136	-283.7	L
区域尺度 Regional scale									
100 m	物种丰富度指数	Species richness index	<0.001	0.68	218.7	<0.001	0.50	219.3	NS
	Simpson多样性指数	Simpson diversity index	0.20	0.015	-56.6	0.28	0.011	-58.3	Q
	物种均匀度指数	Species evenness index	<0.001	0.450	-53.2	0.01	0.355	-52.9	NS
	树状图功能多样性指数	Dendrogram-based functional diversity index (dbFD)	0.52	<0.001	70.6	0.57	<0.001	68.7	Q
	Rao二次熵指数	Rao's Quadratic index (RaoQ)	0.10	0.064	-120.5	0.24	0.020	-123.6	Q
	功能均匀度指数	Functional evenness index (FEve)	0.19	0.017	-73.6	0.17	0.048	-72.2	L
150 m	物种丰富度指数	Species richness index	<0.001	0.33	143.4	<0.001	0.53	145.0	NS
	Simpson多样性指数	Simpson diversity index	0.10	0.116	-35.9	0.29	0.035	-39.1	Q
	物种均匀度指数	Species evenness index	<0.001	0.512	-40.0	0.16	0.112	-42.8	NS
	树状图功能多样性指数	Dendrogram-based functional diversity index (dbFD)	0.76	<0.001	27.9	0.82	<0.001	23.8	Q
	Rao二次熵指数	Rao's Quadratic index (RaoQ)	<0.001	0.351	-82.0	0.20	0.081	-85.1	Q
	功能均匀度指数	Functional evenness index (FEve)	0.18	0.052	-55.2	0.12	0.153	-53.2	L
200 m	物种丰富度指数	Species richness index	<0.001	0.77	116.1	<0.001	0.92	118.0	NS
	Simpson多样性指数	Simpson diversity index	0.22	0.059	-27.8	0.34	0.051	-29.1	Q
	物种均匀度指数	Species evenness index	0.02	0.285	-30.2	0.14	0.191	-31.1	NS
	树状图功能多样性指数	Dendrogram-based functional diversity index (dbFD)	0.75	<0.001	26.4	0.80	<0.001	24.2	Q
	Rao二次熵指数	Rao's Quadratic index (RaoQ)	0.06	0.208	-62.9	0.22	0.114	-64.5	NS
	功能均匀度指数	Functional evenness index (FEve)	0.31	0.027	-42.4	0.25	0.099	-40.4	L
250 m	物种丰富度指数	Species richness index	<0.001	0.66	86.4	<0.001	0.91	88.4	NS
	Simpson多样性指数	Simpson diversity index	<0.001	0.455	-18.0	0.07	0.311	-18.5	NS
	物种均匀度指数	Species evenness index	<0.001	0.964	-21.1	0.02	0.381	-21.7	NS
	树状图功能多样性指数	Dendrogram-based functional diversity index (dbFD)	0.82	<0.001	20.1	0.82	<0.001	20.6	L
	Rao二次熵指数	Rao's Quadratic index (RaoQ)	<0.001	0.773	-49.9	0.04	0.351	-50.7	NS
	功能均匀度指数	Functional evenness index (FEve)	0.26	0.062	-35.8	0.19	0.181	-33.9	L

NS表示无显著解释模型。NS indicates non-significant model selected.

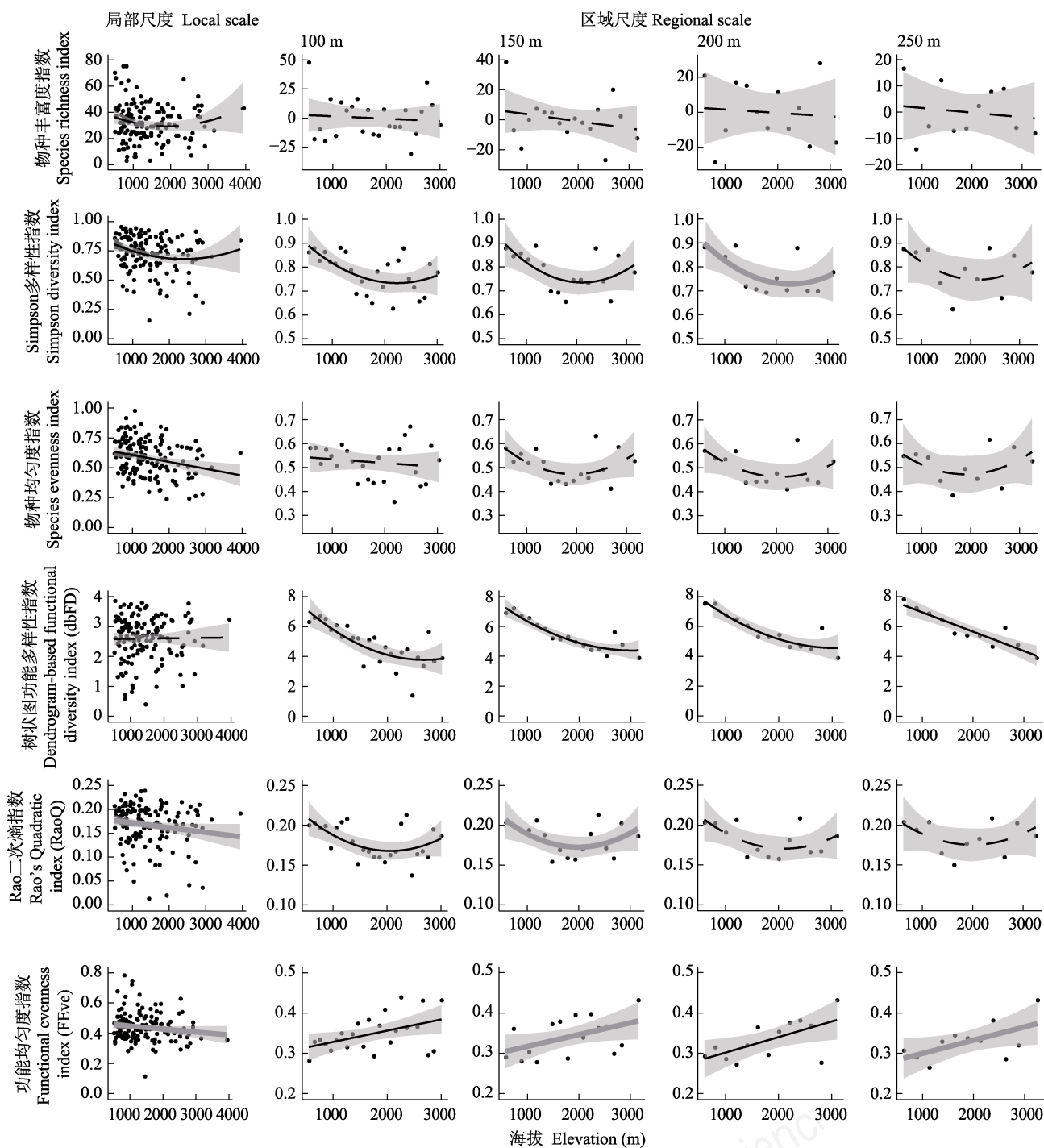


图2 局部尺度和区域尺度(100 m、150 m、200 m和250 m海拔段)水生昆虫群落分类多样性和功能多样性指数的海拔格局。黑色实线表示多样性指数对海拔梯度存在极显著( $P < 0.01$ )和显著( $P < 0.05$ )的线性或二次响应关系,灰色实线表示轻微显著( $P < 0.1$ )的线性或二次响应关系,黑色虚线表示无显著( $P > 0.1$ )的线性或二次响应关系。

Fig. 2 The relationship between taxonomic and functional diversity indices and elevation at local and regional (elevational band across 100 m, 150 m, 200 m, and 250 m) scales. Black solid line indicates highly significant ( $P < 0.01$ ) and significant ( $P < 0.05$ ) linear or quadratic relationships, grey solid line indicates marginally significant ( $P < 0.1$ ) linear or quadratic relationships, and black dotted line indicates non-significant ( $P > 0.1$ ) linear or quadratic relationships.

有研究表明物种丰富度和功能丰富度存在一定程度的相关关系(例如Edie et al, 2018),当物种丰富度

和dbFD指数相关性较高时表明群落间物种功能冗余度较低(Natalia et al, 2019)。本研究发现物种丰富



度指数和dbFD指数在局部尺度沿海拔梯度分别呈现弱“U”型和并不显著的单调递增趋势,但随区域尺度海拔带宽度的增加,物种丰富度指数和dbFD指数的区域尺度海拔格局呈现递减趋势;可能表明澜沧江流域区域尺度间溪流水生昆虫类群功能冗余度较低,即区域尺度下不同物种扮演较为独立的生态功能(Mouchet et al, 2010)。物种组成通常反映了区域过程(物种扩散)和局部过程(竞争、生境异质性)相互作用的结果(Szava-Kovats et al, 2013)。沿海拔梯度升高,区域尺度下水温(Vinson & Hawkins, 2003)和降水(张景华等, 2015)等因素急剧变化(Wang et al, 2011),环境过滤作用导致适宜生态位减少,群落生物性状组成逐渐同质化(Poff et al, 2006),引起区域尺度丰富度和dbFD指数沿海拔梯度呈降低趋势。但局部尺度下,溪流生态系统提供的生物栖境异质性(如底质、水文条件和水体理化性质等)(Li FQ et al, 2012; Li ZF et al, 2019),可能在一定程度抵消了区域生态位减少的影响,因此局部尺度物种丰富度和dbFD指数的海拔格局并没有呈现显著变化趋势。

尽管当前水生昆虫多样性海拔格局的研究较少涉及Simpson多样性和RaoQ指数,但其他类群已有相关报道;如Carvajal-Quintero等(2015)对安第斯山脉鱼类多样性研究发现,250–500 m区域尺度Simpson多样性指数呈单调递减趋势。本研究发现Simpson多样性指数和RaoQ指数的区域尺度海拔格局呈现一定程度的一致性;同时,随区域尺度海拔带宽度增加,海拔格局均转变为不显著,这种一致性可能来源于Simpson多样性指数与RaoQ指数的高相关关系(Wong & Dowd, 2015)。然而,Simpson多样性指数在局部尺度的海拔格局最为显著,RaoQ指数则在100 m海拔带区域尺度呈现显著的海拔分布格局,这种差异性可能源于分类多样性和功能多样性指数对环境因子过滤作用和空间距离的响应差异性(McConkey & O’Farrill, 2015)。如Tinoco等(2018)研究发现,景观尺度下蜂鸟的RaoQ指数对土地利用变化的敏感程度高于Simpson多样性指数。对淡水大型底栖动物来说,Simpson多样性指数和RaoQ指数均对物理栖境(如底质组成)和水体理化环境(如溶解氧)呈显著的响应关系,但空间距离同时也是影响RaoQ指数空间分布的重要因素(Wang et al, 2018; Li ZF et al, 2019)。

本文发现局部尺度物种均匀度指数沿海拔呈现单调递减趋势(Mejias, 2011),FEve指数也呈现单调递减的海拔格局,可能是由于局部尺度FEve与物种均匀度指数呈显著正相关关系所致(陈静等, 2018);但Wang等(2011)研究发现局部尺度下底栖动物物种均匀度指数沿海拔梯度呈现上升趋势。区域尺度下FEve指数表现出显著的单调递增趋势,但物种均匀度指数未表现出显著的海拔分布格局,表明水生昆虫群落组成在区域海拔段的分布均匀程度较为相似。FEve指数衡量物种性状在已占据生态位空间的分布均匀程度,值越高表明物种对环境资源的利用越充分(Mason et al, 2005)。伴随着海拔梯度上升,环境过滤作用持续增强,导致适合物种生存的生态位减少,因此在局部尺度的水生昆虫空间分布均匀度持续降低;但区域尺度下物种性状对资源的利用更为充分,因此区域尺度FEve指数沿海拔梯度呈现递增趋势。

本研究定量分析了多重空间尺度下水生昆虫物种多样性的海拔格局,结果表明水生昆虫分类多样性和功能多样性海拔格局存在空间尺度依赖性。在不同空间尺度共同作用的多重生态学过程和环境因素(如环境过滤、扩散作用和物种相互作用等)(McGill, 2010; McGill et al, 2015),是影响物种多样性海拔格局空间尺度依赖性的可能原因;进一步分析不同空间尺度下分类多样性和功能多样性海拔格局的影响因素,是理解区域多样性现状,并制定生物多样性保护对策的重要基础。

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## 附录 Supplementary Material

### 附录1 澜沧江不同溪流等级采样点位的水生昆虫非参数多维尺度分析

Appendix 1 Nonparametric multidimensional scaling (NMDS) ordination of sampling sites collected from different stream orders using aquatic insect assemblages

<http://www.biodiversity-science.net/fileup/PDF/2019359-1.pdf>

附录2 基于广义线性模型(GLM)的区域尺度水生昆虫多样性指数响应海拔段采样点位数量、平均空间距离和平均纬度的P值

Appendix 2 The *P* values of generalized linear models (GLMs) regressing taxonomic and functional diversity indices against sampling site numbers, average Euclidean distances, and average latitude across elevational bands at regional scales

<http://www.biodiversity-science.net/fileup/PDF/2019359-2.pdf>