

• 研究报告 •

云南哀牢山常绿阔叶林的空间分异及其影响因素

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摘要: 理解物种丰富度在空间上的变化, 阐明植物群落组成对生境异质性的响应是群落生态学研究的核心议题之一。与生境异质性有关的生态位分化对植物群落的多样性格局和物种分布具有重要影响。本文以分布在云南哀牢山的4种常绿阔叶林为研究对象, 通过对42个森林样地的调查取样, 探讨了常绿阔叶林的群落分布和树种丰富度在地形和土壤环境梯度上的变异。结果表明: 4种常绿阔叶林的树种组成有显著的差异。季风常绿阔叶林的树种丰富度极显著地高于其他3种类型; 中山湿性常绿阔叶林极显著地高于半湿润常绿阔叶林; 其他类型之间的差异不显著。非度量多维尺度分析显示, 海拔、坡度、土壤含水率及有机质等9个环境梯度是控制森林群落结构和树种分布的主要因素。土壤有效硼、海拔、全钾和凹凸度为树种丰富度的最佳预测变量, 累积解释了树种丰富度63.2%的变异。地形和土壤因子一起能够解释哀牢山常绿阔叶林的群落组成和树种丰富度的大部分变异。

关键词: 生境异质性; 群落组成; 树种丰富度; 常绿阔叶林; 哀牢山

Spatial heterogeneity and its causes in evergreen broad-leaved forests in the Ailao Mountains, Yunnan Province

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Abstract: Understanding the variation of species richness over spatial scales, and elucidating the response of plant community composition to habitat heterogeneity has been one of the major topics in the study of community ecology. Niche differentiation related to habitat heterogeneity plays an important role in shaping diversity levels and species distribution patterns of plant communities. Based on a survey of 42 plots of four types of evergreen broad-leaved forests in the Ailao Mountains of Yunnan Province, this paper explored how community distribution and tree species richness of such forests changed along topographic and edaphic gradients. We found significant differences in community composition among the four types of evergreen broad-leaved forests. Tree species richness of monsoon evergreen broad-leaved forests was significantly higher than that of the other forest types. Tree species richness of mid-montane moist evergreen broad-leaved forests was significantly higher than that of semi-humid evergreen broad-leaved forests, whereas no significant difference was observed among the other forest types. Non-metric multidimensional scaling (NMDS) revealed that nine environmental gradients, including elevation, slope, soil water content, soil organic matter, were the determinants of forest community composition and tree distribution patterns. As the best predictors of tree species richness, soil available boron, elevation, soil total potassium and convexity together explained 63.2% of the variance of tree species richness. The combination of topographic and edaphic factors explained most of the variance of community composition and tree species richness of the evergreen broad leaved forests in the Ailao Mountains.

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Key words: habitat heterogeneity; community composition; tree species richness; evergreen broad-leaved forests; the Ailao Mountains

局地环境条件和生态系统过程对树种分布和丰富度格局的影响是植物生态学和生物地理学的核心议题之一(Poulos & Camp, 2010), 森林群落中树种的分布和多度格局反映着树种生态位需求和种群动态与生境的时空变化相互作用的结果(Urban et al, 2000)。物理环境的空间异质性造成资源可利用性的水平(如土壤养分和水分)和垂直(如林冠层和根系区域)方向上的差异(Oliveira-Filho et al, 2001; Pinto et al, 2005), 从而可导致树种的生态位分化, 形成特定的空间分布格局(Palmiotto et al, 2004; Russo et al, 2005)。除了对森林群落结构和树种组成复杂性产生影响(Pinto et al, 2005)外, 许多研究还表明生境异质性与树种多样性之间存在正相关关系(Balvanera & Aguirre, 2006; Pereira et al, 2007; Lundholm, 2009; Homeier et al, 2010)。多样化的生境能够支持较高的物种多样性, 这是因为树种资源利用策略的差异抑制了群落的竞争排除效应(Balvanera & Aguirre, 2006), 促成了更大范围的树种共存(Oliveira-Filho et al, 1994; Itoh et al, 2003; Yasuhiro et al, 2004)。

地形特征及土壤属性是环境异质性的主要决定因素(Ferreira-Júnior et al, 2007), 对树种多样性和群落结构具有重要的影响(Potts et al, 2002; Jones et al, 2008; Baldeck et al, 2013)。地形因素是为植物群落提供生境多样性最重要的环境梯度(Takyu et al, 2002), 森林树种与基于地形属性划分的生境类型之间存在普遍的关联(Chuyong et al, 2011), 随土壤养分的变化呈现出非随机分布格局(Baldeck et al, 2013)。局地尺度的研究常以地形变异替代生境异质性(Baldeck et al, 2013), 这是因为通过调节土壤养分和水分有效性(Tsui et al, 2004; Yimer et al, 2006; Engelbrecht et al, 2007), 地形因素对树木个体生长、死亡、更新的动态过程产生影响(Tateno & Takeda, 2003; Yasuhiro et al, 2004; de Toledo et al, 2011)。土壤属性对森林的群落结构和树种分布格局起实质性的作用(Budke et al, 2007; Pinto et al, 2005)。在树种极其丰富的森林群落中, 超过1/3的树种分布受到土壤养分资源的影响(John et al, 2007), 土壤质

地、阳离子构成和碳氮比是森林树种组成的决定因素(Bohlman et al, 2008)。由于群落结构的复杂性以及环境因子间的交互作用, 树种分布及多样性格局沿环境梯度变化的机制尚不清楚(Engelbrecht et al, 2007; Homeier et al, 2010)。

常绿阔叶林是云南亚热带植被的优势类型, 有着极为广阔的分布地域, 其类型之多样和物种之丰富为该省多数植被类型所不及(云南植被编写组, 1987)。哀牢山纵贯云南中部, 位于我国云贵高原、横断山地和青藏高原三大自然区域的结合部, 是多种生物区系地理成分东西交汇、南北过渡之地, 保存着我国亚热带地区面积最大的山地常绿阔叶林(哀牢山自然保护区综合考察团, 1988)。本文以分布在哀牢山的4种常绿阔叶林植被亚型——山顶苔藓矮林、中山湿性、半湿润、季风常绿阔叶林为研究对象, 通过样地调查和取样分析, 拟探讨以下问题: (1)4种常绿阔叶林的群落组成和树种丰富度是否存在显著差异; (2)哪些环境因子与常绿阔叶林树种构成的空间分异之间存在密切联系; (3)树种丰富度格局能被哪些关键环境因子所解释。通过揭示常绿阔叶林群落分布及树种丰富度格局的变化规律, 以及关键环境梯度的作用和影响, 可为云南常绿阔叶林资源及其树种多样性的保护提供科学依据。

1 材料与方法

1.1 研究区概况

哀牢山属云岭山脉向南分支的余脉, 呈西北往东南走向, 纵贯云南省中部。根据哀牢山森林生态系统研究站的长期监测资料, 该区年平均降雨量为1,931 mm, 雨季(5–10月)降雨量占年降雨量的85%左右。年平均蒸发量为1,485 mm, 年平均温度为11.3℃, 最热月(7月)平均气温为16.4℃, 最冷月(1月)平均气温为5.4℃。哀牢山海拔高差达2,000 m以上, 气候、植被、土壤沿海拔梯度分异明显。森林类型丰富多样, 以云南特有种或以云南为分布中心的树种为优势; 常绿阔叶林有4个植被亚型, 即山顶苔藓矮林、中山湿性、半湿润和季风常绿阔叶林, 以山地黄棕壤和红壤为主要土壤类型(哀牢山自然

保护区综合考察团, 1988; 巩合德等, 2011)。

1.2 样地调查

野外调查取样路线的确定主要参考《云南植被》(云南植被编写组, 1987)对常绿阔叶林植被亚型的划分, 以及《哀牢山自然保护区综合考察报告集》(哀牢山自然保护区综合考察团, 1988)中对山地植被垂直带谱和常绿阔叶林分布状况的研究结果。山顶苔藓矮林和中山湿性常绿阔叶林样地设置在哀牢山森林生态系统研究站附近(24°32' N, 101°01' E), 海拔范围2,400–2,700 m; 季风常绿阔叶林样地设置在镇沅县恩乐镇民江村(24°03' N, 101°09' E), 海拔1,800–1,900 m; 半湿润常绿阔叶林样地设置在新平县大帽耳山(24°12' N, 101°25' E), 海拔2,100–2,200 m左右。由于中山湿性常绿阔叶林是哀牢山自然保护区的主体和精华, 分布最为广泛, 保存最为完整, 所以设置样地数目为24个, 其余植被亚型均为6个, 共计42个(图1)。样地投影面积为20 m×20 m, 借助于全站仪, 我们还测定了样地顶点及中心的相对高差, 用于计算地形因子(坡度、坡向、凹凸度)。用GPS记录每个样地的海拔和经纬度, 测量了样地内所有木本个体的胸径(≥1 cm)。调查时将样地划分为

4个象限, 在每个象限中心处对表层土(0–20 cm)取样, 混合均匀, 风干后以备实验分析。

1.3 环境因子的测定

样地海拔为4个顶点海拔的平均值; 坡度为样地任意3个顶点组成的平面与水平面夹角的平均值; 坡向为坡面法线在水平面上投影与正北方向的夹角; 凹凸度为样地中心的海拔减去4个顶点海拔的平均值, 详细算法参照Yamarura等(1995)和Lai等(2009)。数据分析时对坡度数值取正弦, 使之成为0–1之间的数值; 坡向的转换使用以下公式:

$$TRASP = \frac{1 - \cos[\pi (aspect - 30) / 180]}{2}$$

式中 $aspect$ 为坡向的角度数值, $TRASP$ 为转换后的坡向数值, 该值越大表明越向阳, 如1代表南偏西30°, 0代表北偏东30°(Xu et al, 2011)。

土壤样品在实验室内处理分析, 共获得10项理化指标。土壤含水量的测定用烘干法, pH值用电位测定法, 有机质用重铬酸钾容量-外加热法, 全氮用高氯酸-硫酸消化法, 全磷用酸溶-钼锑抗比色法, 全钾用酸溶-火焰光度法, 有效氮用碱解蒸馏法, 有效磷采用碳酸氢钠浸提-钼锑抗比色法, 有效钾用

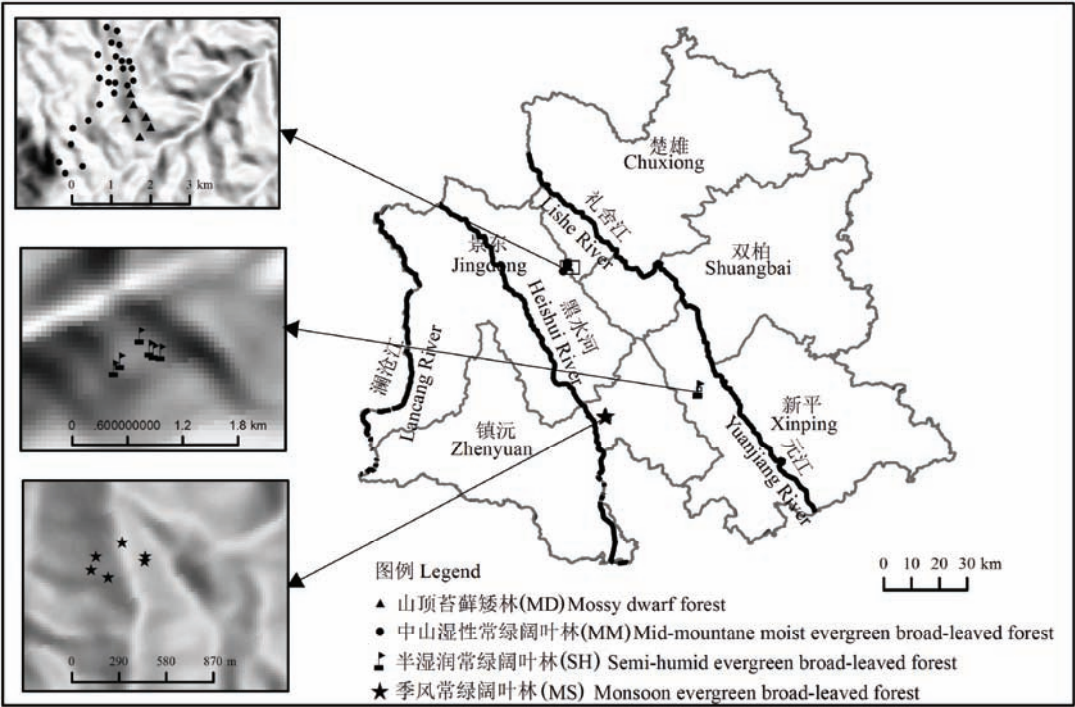


图1 哀牢山和研究区的地理位置
Fig. 1 Location of the Ailao Mountains and overview of the study area

乙酸铵浸提-火焰光度计法,有效硼用甲亚胺H分光光度法(鲍士旦, 2005)。

1.4 数据分析

相对优势度为样地内某树种的胸径截面积之和占全部树种的胸径截面积总和的比例。用相似性百分比(similarity percentage, SIMPER)检测对4种常绿阔叶林植被亚型的群落组成差异贡献最大的优势种,用非度量多维尺度分析(non-metric multidimensional scaling, NMDS)揭示森林群落在环境梯度上的分布格局及其关键影响因子。选用Margalef指数刻画样地的树种丰富度(Magurran, 2004),采用Kruskal-Wallis test及Dunn's test检验4种植被亚型的树种丰富度是否存在显著性差异。Dunn's test是一种非参数多重比较方法,适用于数据不满足方差齐性要求时组间数据的两两比较,往往在Kruskal-Wallis test检测到显著组间差异后使用(Dinno, 2015)。

为了探究树种丰富度对关键环境因子的响应以及各个预测变量的解释能力,我们采取以下分析过程:(1)以树种丰富度为响应变量,以全部环境因子为预测变量,构建广义可加模型(generalized additive model, GAM)。(2)环境因子任意组合,计算由此产生的所有模型的AICc (the second-order Akaike information criterion)值。AICc为修正后的赤池信息准则,适用于样本量较小($n/K < 40$, n 为样本量, K 为参数个数)时最佳模型的选择(Peruggia, 2003)。各个模型将按照AICc值的大小排列,AICc值最小者为最优模型,并根据AICc的权重值计算相关环境因子的相对重要性。(3)以树种丰富度为响应变量,以入选最优模型的环境因子为预测变量,重新构建广义可加模型,检验模型的解释能力以及入选环境因子的显著性。(4)最后拟合树种丰富度对入选环境因子的响应曲线。

相似性百分比分析和多样性指数的计算在PRIMER 5.0中进行,其余分析均在R 3.2.5软件(www.cran.r-project.org)中完成。筛选GAM最佳模型和评估相关环境因子相对重要性时调用了“dredge”和“importance”函数。非度量多维尺度分析、Kruskal-Wallis秩和检验以及Dunn's多重比较、“dredge”和“importance”分别在“vegan”、“dunn.test”、“MuMIn”软件包中完成(Bartoń, 2015; Oksanen et al, 2016; Dinno, 2016)。用“mgcv”软件包(Wood, 2016)

构建广义可加模型、绘制树种丰富度对环境因子的响应曲线。在进行非度量多维尺度分析时,对树种的相对优势度和环境因子分别进行了平方根和标准化处理。

2 结果

2.1 森林群落的树种组成及分布

42个森林样地共记录乔木和灌木(胸径 ≥ 1 cm)105种,隶属34科63属。其中较大的科依次为樟科(7属16种)、壳斗科(4属16种)、山茶科(6属11种)、蔷薇科(7属7种)、杜鹃花科(4属7种)、冬青科(1属7种)、山矾科(1属6种)和五加科(2属3种)。相似性百分比分析显示,苔藓矮林样地特有的优势树种为倒卵叶石栎(*Lithocarpus crassifolius*)、云南桫欏树(*Clethra delavayi*)、露珠杜鹃(*Rhododendron irroratum*)、珍珠花(*Lyonia ovalifolia*)、珊瑚冬青(*Ilex corallina*)和云南越桔(*Vaccinium duclouxii*)的优势很明显,但也是中山湿性常绿阔叶林的优势树种。中山湿性常绿阔叶林特有的优势树种为木果石栎(*Lithocarpus xylocarpus*)、腾冲栲(*Castanopsis wattii*)、硬斗柯(*Lithocarpus hancei*)、薄叶马银花(*Rhododendron leptothrium*)、舟柄茶(*Stewartia pteropetiolata*)、滇木荷(*Schima noronhae*)和四川冬青(*Ilex szechwanensis*)。季风常绿阔叶林的优势树种有9种,主要是旱冬瓜(*Alnus nepalensis*)、高山栲(*Castanopsis delavayi*)、母猪果(*Helicia nilagirica*)、茶梨(*Anneslea fragrans*)、截头石栎(*Lithocarpus truncatus*)、小果栲(*Castanopsis fleuryi*)、滇南木姜子(*Litsea garrettii*)、西南木荷(*Schima wallichii*)、红梗润楠(*Machilus rufipes*)。半湿润常绿阔叶林的树种较为单一,其中滇青冈(*Cyclobalanopsis glaucoides*)、白穗石栎(*Lithocarpus craibianus*)、多穗石栎(*L. polystachyus*)、旱冬瓜占绝对优势(表1)。

NMDS排序的stress值为0.091,小于0.1,表明排序效果良好(图2)。海拔、土壤含水率、pH值、有效硼、有效磷的箭头连线较长,表明这些预测变量有着较强的解释能力。其中土壤含水率和pH值的箭头连线与NMDS第一轴的夹角较小,表明与其相关性较高,NMDS第一轴主要展示了土壤含水率和pH值两个梯度;此外,海拔、土壤有机质、有效磷与第一轴呈现出极显著的负相关关系($P < 0.01$)。有效硼和有效钾与第二轴正相关,坡度和全钾与第二轴

表1 4种常绿阔叶林样地树种相对优势度(%)及其对组内相似性的贡献率(括号内的数值, %)
Table 1 Relative dominance (%) of tree species and their contributions (%) to within-group similarities. The contributions of different tree species are shown in brackets.

树种名 Species name	苔藓矮林 MD	中山湿性阔叶林 MM	季风常绿阔叶林 MS	半湿润常绿阔叶林 SH
倒卵叶石栎 <i>Lithocarpus crassifolius</i>	25.54(23.40)			
云南桫欏树 <i>Clethra delavayi</i>	12.81(17.81)			
露珠杜鹃 <i>Rhododendron irroratum</i>	19.47(17.51)			
云南越桔 <i>Vaccinium duclouxii</i>	8.37(13.47)	8.68(21.18)		
珍珠花 <i>Lyonia ovalifolia</i>	10.45(12.52)	9.99(10.38)		
珊瑚冬青 <i>Ilex corallina</i>	5.94(6.35)	8.50(13.34)		
木果石栎 <i>Lithocarpus xylocarpus</i>		16.88 (20.10)		
腾冲栲 <i>Castanopsis wattii</i>		7.50(7.53)		
硬斗柯 <i>Lithocarpus hancei</i>		8.96(6.42)		
薄叶马银花 <i>Rhododendron leptothrium</i>		3.30(4.70)		
舟柄茶 <i>Stewartia pteropetiolata</i>		3.94(3.51)		
滇木荷 <i>Schima noronhae</i>		5.13(2.59)		
四川冬青 <i>Ilex szechwanensis</i>		2.72(2.01)		
旱冬瓜 <i>Alnus nepalensis</i>			19.39(21.73)	9.71(18.22)
高山栲 <i>Castanopsis delavayi</i>			9.56(21.37)	
母猪果 <i>Helicia nilagirica</i>			4.29(10.23)	
茶梨 <i>Anneslea fragrans</i>			2.51(8.21)	
截头石栎 <i>Lithocarpus truncatus</i>			10.20 (7.47)	
小果栲 <i>Castanopsis fleuryi</i>			8.93(7.35)	
滇南木姜子 <i>Litsea garrettii</i>			4.37(6.19)	
西南木荷 <i>Schima wallichii</i>			6.13(4.77)	
红梗润楠 <i>Machilus rufipes</i>			4.96(2.97)	
滇青冈 <i>Cyclobalanopsis glaucoides</i>				35.04(27.95)
白穗石栎 <i>Lithocarpus craibianus</i>				28.38(27.93)
多穗石栎 <i>Lithocarpus polystachyus</i>				20.47(24.96)

MD, Mossy dwarf forest; MM, Mid-mountane moist evergreen broad-leaved forest; MS, Monsoon evergreen broad-leaved forest; SH, Semi-humid evergreen broad-leaved forest.

表2 NMDS排序轴与环境因子的相关性系数
Table 2 Correlation coefficients of the NMDS ordination axes and the environmental factors

环境因子 Environmental factors	NMDS第一轴 NMDS1	NMDS第二轴 NMDS2	r^2	P
海拔 Elevation	-0.779	-0.627	0.897	0.001
凹凸度 Convexity	0.992	-0.128	0.098	0.134
坡向 Aspect	-0.025	-1.000	0.035	0.490
坡度 Slope	-0.352	-0.936	0.241	0.007
土壤含水率 Soil water content (SW)	-0.994	-0.107	0.635	0.001
土壤有机质 Soil organic matter (SOM)	-0.825	-0.566	0.293	0.003
土壤pH值 pH	0.998	0.067	0.597	0.001
全氮 Total nitrogen (TN)	-0.367	-0.930	0.060	0.312
全磷 Total phosphorus (TP)	-0.543	0.840	0.108	0.121
全钾 Total potassium (TK)	0.150	-0.989	0.374	0.002
有效氮 Available nitrogen (AN)	-0.582	0.813	0.079	0.210
有效磷 Available phosphorus (AP)	-0.918	0.396	0.432	0.001
有效钾 Available potassium (AK)	0.112	0.994	0.316	0.001
有效硼 Available boron (AB)	-0.272	0.962	0.503	0.001

P 值表示环境因子与NMDS第一轴或第二轴相关系数的显著性。 P refers to significant correlation between the environmental variables and either NMDS axis 1, or NMDS axis 2.

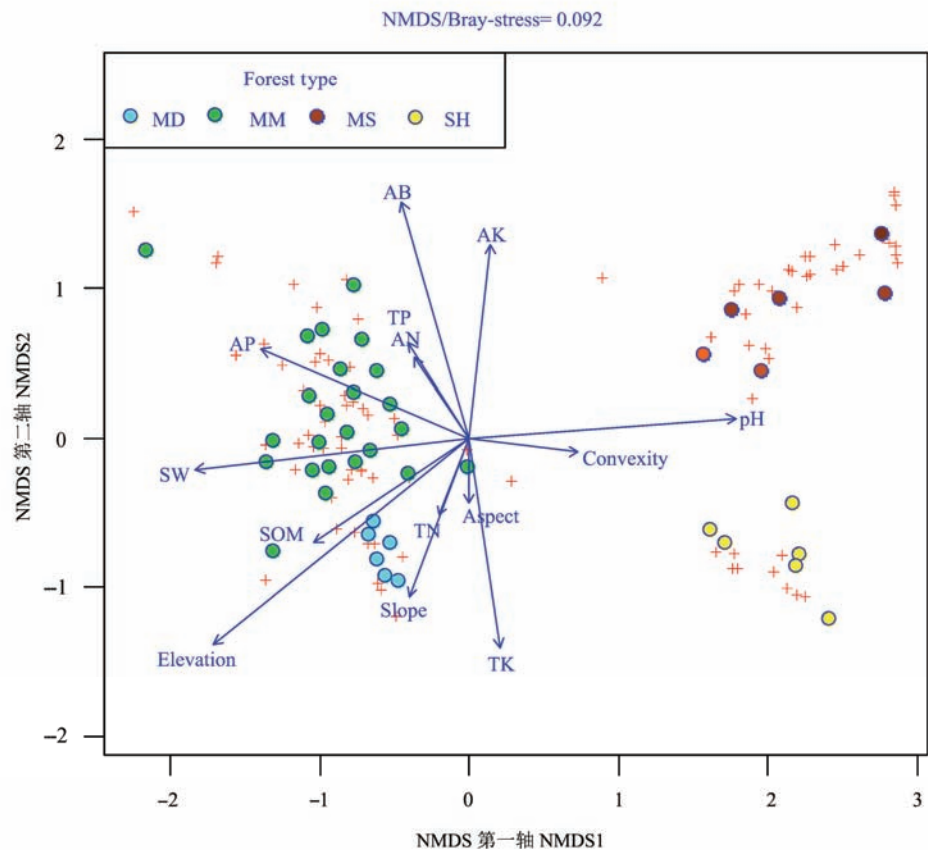


图2 哀牢山4种植被亚型森林样地非度量多维尺度分析。圆圈、+、箭头分别代表样地、树种及环境因子(图注同图1及表2)
Fig. 2 Non-metric multidimensional scaling ordination of forest plots (4 vegetation sub-types) in the Ailao Mountains. Colored circles, symbols “+” and arrows indicate plots, tree species and environmental factors respectively. Notes see Fig. 1 and Table 2.

负相关, 均达到极显著水平(表2)。苔藓矮林样地之间的距离最近, 表明其树种组成有较大的相似性; 而组成季风常绿阔叶林样地的树种差异相对较大。季风常绿阔叶林和半湿润常绿阔叶林的生境都具有土壤含水率较低、pH值较高的特征, 不同之处在于季风常绿阔叶林的海拔和土壤有机质含量较低, 而半湿润常绿阔叶林的土壤有效磷和有效硼含量较低。苔藓矮林位于海拔高、坡度大的地段, 土壤有机质和全钾含量均较高。中山湿性常绿阔叶林具有较高的土壤含水率、有效磷含量以及较低的pH值(图2)。

2.2 树种丰富度格局及其关键影响因子
Kruskal-Wallis秩和检验结果表明至少有一种常绿阔叶林的树种丰富度与其他植被亚型存在极显著差异($\chi^2 = 22.845, P = 0.000$), Dunn's多重比较进一步显示, 季风常绿阔叶林的树种丰富度极显著地高于中山湿性常绿阔叶林($z = 2.463, P = 0.007$)、

山顶苔藓矮林($z = 3.177, P = 0.001$)及半湿润常绿阔叶林($z = 4.518, P = 0.000$); 中山湿性常绿阔叶林极显著地高于半湿润常绿阔叶林($z = 3.252, P = 0.001$); 中山湿性常绿阔叶林与山顶苔藓矮林($z = 1.555, P = 0.060$)以及山顶苔藓矮林与半湿润常绿阔叶林($z = 1.341, P = 0.090$)之间的差异没有达到显著性水平(图3)。

广义可加模型的筛选结果显示土壤有效硼、海拔、全钾、凹凸度等4个环境因子为树种丰富度格局的最佳解释变量。“importance”函数的评估结果表明除以上环境因子外, 土壤有效钾和pH值对树种丰富度也有较大影响(表3)。最佳模型累积解释了树种丰富度格局63.2%的变异, 4个环境因子对树种丰富度的影响力依次是有效硼($F = 19.288, P = 0.000$)、海拔($F = 11.973, P = 0.001$)、全钾($F = 5.096, P = 0.030$)和凹凸度($F = 2.859, P = 0.099$)。其中, 有效硼和海拔达到极显著水平, 全钾达到显著水平,

表3 “dredge”模型筛选表
Table 3 Model selection with the “dredge” function

	有效硼 AB	有效钾 AK	凹凸度 Convexity	海拔 Elevation	pH	全钾 TK	自由度 df	AICc	ΔAICc	权重值 Weight
1	1.796		-0.128	-0.001		-0.345	5	90.0	0.00	0.261
2	2.082			-0.001		-0.250	4	90.4	0.39	0.214
3	2.374			-0.001			4	91.0	0.95	0.162
4	2.001	-0.005	-0.124	-0.002		-0.409	6	91.3	1.26	0.139
5	2.290	-0.005		-0.002		-0.320	6	91.5	1.44	0.127
6	2.544				0.676	-0.302	5	92.0	2.00	0.096
相对重要性 Importance	1.00	0.27	0.40	0.90	0.10	0.84				

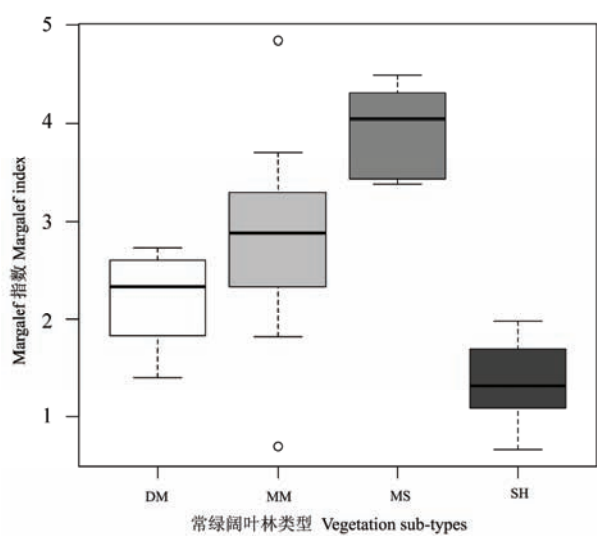


图3 哀牢山4种植被亚型森林的树种丰富度。林型代号同图1。
Fig. 3 Tree species richness of four vegetation sub-types in the Ailao Mountains. Forest types see Fig. 1.

凹凸度对模型的影响不显著。具体而言, 树种丰富度随土壤有效硼含量的增加而直线上升; 与海拔的关系是非线性的, 在1,800–2,200 m范围内呈下降趋势, 并在2,188 m处达到极值, 在2,200–2,500 m范围内呈上升趋势, 之后又随海拔的升高而下降。树种丰富度与土壤有效钾之间整体上呈负相关关系, 拟合曲线波动下降。树种丰富度对凹凸度的变异响应虽未到达显著水平, 但呈现出随之近线性平缓下降的关系(图4)。

3 讨论

哀牢山4种常绿阔叶林群落在树种组成和丰富度格局上均有显著的差异, 非度量多维尺度分析表明关键环境因子的梯度变化是控制森林群落和树

种分布的主要原因。入选预测树种丰富度格局的最佳模型的环境因子也是非度量尺度分析揭示的重要环境梯度, 即土壤有效硼、海拔、全钾和凹凸度。尽管凹凸度与NMDS第一轴相关系数高达0.992, 但没有达到显著水平($P = 0.134$)(表2); 同样在GAM最佳模型中也未达到显著水平($F = 2.859, P = 0.099$); 其余3个环境因子的影响都达到了极显著或显著的水平。影响树种分布和丰富度格局的是同一组环境因子, 这可能是因为树种对地形和土壤属性的空间变异产生响应而常常表现出非随机分布的状态(Clark et al, 1999; Palmiotto et al, 2004; Baldeck et al, 2013), 而树种对特定生境的偏好又是形成树种丰富度空间变异格局的主要原因(Yasuhiro et al, 2004)。对应于优势树种组成和树种丰富度格局的异质性, 4种常绿阔叶林的生境也呈现出空间分异特征, 说明生境的分化对局地尺度上的群落构建和多样性维持具有极其重要的作用(Itoh et al, 2003; Russo et al, 2005; Lundholm, 2009; Chuyong et al, 2011)。

尽管地形变异被认为是控制植被格局和树种多样性的关键因子(Poulos & Camp, 2010), 但受地形因子调节的资源梯度(如土壤养分和太阳辐射)才是树种分布和森林更新的直接决定因素(Tateno & Takeda, 2003)。山谷是适宜树木生长的地形, 土层深厚、水分充足, 因而支持了较高水平的树种多样性(Homeier et al, 2010)。与之相适应的是, 分布在山谷的树种在获取光资源方面有较强的竞争力, 而山顶树种则更能有效获取土壤氮素(Tateno & Takeda, 2003)。坡度与森林群落的分布有很强的关系(Bohlman et al, 2008), 生长在陡坡上的森林群落具有较高的树种多样性(Guo et al, 2016)。凹凸度是影

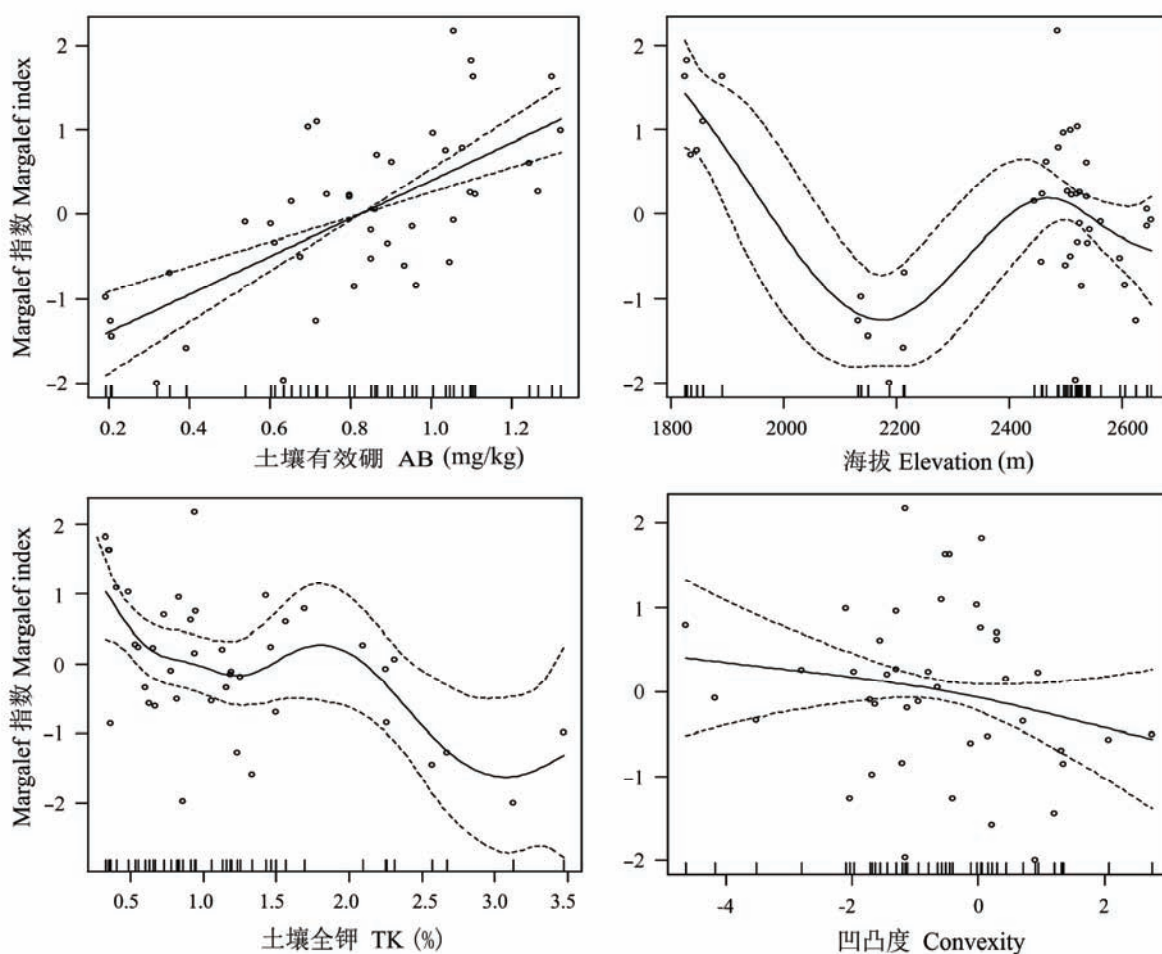


图4 树种丰富度对环境因子的响应。图中实线表示树种丰富度的期望值, 虚线表示95%置信区间。

Fig. 4 Responds of tree species richness to environmental factors. The solid line shows the estimations of tree richness, and the dashed lines indicate 95% confidence interval.

响土壤水分含量的重要因子, 越小越有利于水分存留(郭屹立等, 2016), 在本研究中, 凹凸度与树种丰富度之间呈现出负相关关系, 说明了水分因素的影响不可忽视。本研究中海拔因子对群落分布、树种组成及其丰富度格局都有极显著的影响, 但海拔与丰富度之间并未呈现出确定的关系, 这可能是因为植物群落物种多样性的海拔格局很大程度上取决于环境变量之间的协变与互作(Lomolino, 2001)。

树种沿土壤养分资源梯度的生态位分化被认为是物种极其丰富的森林群落中树种共存的潜在机制之一(Steidinger, 2015)。稀有种的多样性在土壤氮磷含量最高时达到峰值, 而常见种的丰富度与土壤变量无显著相关关系(Laurance et al, 2010)。树种丰富度是在土壤肥力水平中等或较低时最大(Potts et al, 2002); 本研究中树种丰富度随土壤全钾含量

呈波动下降趋势, 与前人的研究结论一致。土壤钾素含量对森林的生产力和维持具有重要的作用(Tripler et al, 2006), 已有研究表明, 过量的土壤钾素会降低群落水平的细根生物量(Wright et al, 2011)。由于其普遍的稀缺性, 土壤有效硼是引起树种生态位分化的一个重要的土壤养分资源轴(John et al, 2007), 树种丰富度与有效硼之间存在正相关关系(Christensen & Heilmann-Clausen, 2009), 这一结论在本研究中得到了验证。值得注意的是, 有效硼与树种丰富度之间呈现出线性关系, 而入选最佳模型的其他3个环境因子与树种丰富度之间的关系为非线性。Steidinger (2015)对Barro Colorado Island上的193个树种生态位宽度的研究提供了可能的解释, 即树种对土壤磷和钙的专化利用主要集中在资源轴的前半段, 也就是说树种针对土壤磷和钙的生

态位分化只发生在磷和钙含量较低的情况下; 树种对土壤锰和铝的专化利用主要集中在资源轴的后半段, 而发生生态位分化的树种在土壤硼的整个资源轴上都有分布, 这可能是土壤硼比其他化学元素更能对森林群落的组成和结构产生影响的原因。

理解树种沿环境梯度的分布格局是制定森林保护方案的基础(John et al, 2005), 土壤资源梯度和地形因素对群落树种组成的变异具有相当的解释能力(Baldeck et al, 2013)。但目前对于这些格局产生的机制尚不清楚, 研究具体树种对相关环境变异梯度的反应是一个重要的途径(Engelbrecht et al, 2007)。由于所处地理位置的海拔较低, 位于保护区之外, 哀牢山的季风常绿阔叶林和半湿润常绿阔叶林普遍遭受到了长期的人为干扰, 如砍伐栎木作为薪柴、林下放牧等, 从而森林呈现出残存的岛屿状星散分布。根据本文结果, 季风常绿阔叶林蕴藏着更为丰富多样的树种; 半湿润常绿阔叶林虽然树种较为单一, 但是非常独特, 除优势种外, 部分伴生树种也仅在这一类型中分布, 如金叶子(*Craibiodendron stellatum*)、云南柃木(*Docynia delavayi*)、毛杨梅(*Myrica esculenta*)等。因此, 季风常绿阔叶林和半湿润常绿阔叶林的保护工作亟需加强, 这对于保护哀牢山常绿阔叶林和维持生物多样性具有重要的意义。

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