



•研究报告•

南亚热带常绿阔叶林树木多样性与生物量和生产力的关联及其影响因素

朱杰^{1,2,3,4,5}, 吴安驰^{1,2}, 邹顺⁶, 熊鑫¹, 刘世忠¹, 褚国伟¹, 张倩媚¹, 刘菊秀¹, 唐旭利¹, 闫俊华¹, 张德强¹, 周国逸^{7*}

1. 中国科学院华南植物园, 广州 510650; 2. 中国科学院大学资源与环境学院, 北京 100049; 3. 广东省国土资源测绘院, 广州 510663; 4. 自然资源部华南热带亚热带自然资源重点实验室, 广州 510663; 5. 广东省自然资源科技协同创新中心, 广州 510663; 6. 贵州工程应用技术学院, 贵阳 551700; 7. 南京信息工程大学应用气象学院, 南京 210044

摘要: 生物多样性和生态系统功能的关系直接或间接地影响着生产力, 是生态学研究的关键问题。本研究旨在定量探讨亚热带自然林演替后期森林生态系统树木多样性与生物量或生产力的关系。本研究基于中国南亚热带长期永久性样地的群落调查数据以及地形和土壤养分数据, 分析了南亚热带常绿阔叶林树木多样性与生物量和生产力的关联及其影响因素。相关性分析结果表明, 物种多样性与生物量呈显著负相关, 与生产力呈显著正相关; 结构多样性与生物量呈显著正相关, 与生产力呈显著负相关。此外, 不同环境因子对多样性、生物量和生产力的影响具有显著差异, 其中土壤含水量对生产力有显著影响, 物种多样性指标与部分地形和土壤因子均有相关性, 而群落结构多样性指标与土壤因子的相关性更强。方差分解结果表明, 结构多样性对生物量和生产力的单独效应的解释率最大, 分别为35.39%和5.21%; 其次是结构多样性和物种多样性的共同效应, 对生物量和生产力的解释率分别为13.66%和3.53%; 地形和土壤因子的解释率较小。同时, 结构方程结果也表明, 结构多样性对生物量有较强的直接正影响; 生物量对生产力有强烈的直接负影响, 结构多样性通过增加生物量明显地减少了生产力; 土壤和地形因子主要是通过物种和结构多样性间接影响生物量和生产力。综上, 本研究认为在南亚热带森林演替顶极群落中, 群落结构复杂性和物种多样性的提高对促进群落生产力和生物量具有重要作用。

关键词: 生物量; 生产力; 土壤养分; 物种多样性; 结构多样性; 地形

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Relationships between tree diversity and biomass/productivity and their influence factors in a lower subtropical evergreen broad-leaved forest

Jie Zhu^{1,2,3,4,5}, Anchi Wu^{1,2}, Shun Zou⁶, Xin Xiong¹, Shizhong Liu¹, Guowei Chu¹, Qianmei Zhang¹, Juxiu Liu¹, Xuli Tang¹, Junhua Yan¹, Deqiang Zhang¹, Guoyi Zhou^{7*}

1 South China Botanical Garden, Chinese Academy of Sciences, Guangzhou 510650

2 College of Resources and Environment, University of Chinese Academy of Sciences Beijing, 100049

3 Surveying and Mapping Institute Lands and Resource Department of Guangdong Province, Guangzhou 510663

4 Key Laboratory of Natural Resources Monitoring in Tropical and Subtropical Area of South China, Ministry of Natural Resources, Guangzhou 510663

5 Guangdong Science and Technology Collaborative Innovation Center for Natural Resources, Guangzhou 510663

6 Guizhou University of Engineering Science, Guiyang, 551700

7 School of Applied Meteorology, Nanjing University of Information Science & Technology, Nanjing 210044

ABSTRACT

Aim: The relationship between biodiversity and ecosystem function contribute to productivity, both directly and

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* 通讯作者 Author for correspondence. E-mail: gyzhou@scib.ac.cn

indirectly. Therefore, it is a critical issue of ecology. The aim of this study is to quantitatively explore the relationship between tree diversity and biomass or productivity of subtropical natural forest ecosystems in late successional stages.

Methods: Based on long-term community surveys of topographies and soil nutrients from permanent forest ecosystems in the subtropical evergreen broad-leaved forest, we analyzed the relationship between tree diversity and productivity/biomass and their influencing factors. In this analysis, the correlations between tree diversity and each factor were evaluated using a Pearson correlation analysis. The single and shared effects of each factor were quantified by variance partitioning analysis (VPA). In addition, the relationships between soil nutrients and topographies and their effects on productivity and biomass were further evaluated, either directly or indirectly, through species and structural diversity by using a structural equation model (SEM).

Result: Species diversity displayed a negative correlation with biomass and a positive correlation with productivity. Contrarily, structural diversity was positively correlated with biomass and negatively correlated with productivity. The effects of environment factors on tree diversity and biomass/productivity were varied. Specifically, soil moisture had a significant effect on productivity, species diversity was correlated with soil nutrients and topographies, and structural diversity was strongly related to soil nutrients. The variance partitioning analysis results indicated that the single effect of structural diversity explained the largest portion of variance in biomass (35.39%) and productivity (5.21%), followed by the shared effect of structural and species diversity on biomass (13.66%) and productivity (3.53%). Soil nutrients and topographies explained less variation in productivity and biomass. The structural equation results analysis indicated that structural diversity had a direct positive effect on biomass, and biomass had a strong direct negative effect on productivity. Structural diversity indirectly reduced productivity by increasing biomass. Soil nutrients and topographies were mainly affected by biomass, while productivity indirectly affected tree species and structural diversity.

Conclusions: These results indicate that (1) species diversity had the greatest direct effect on productivity, and structural diversity had the greatest direct effect on biomass in southern subtropical evergreen broad-leaved forests; (2) species diversity explained productivity better than structural diversity, while structural diversity explained biomass accumulation better than species diversity; and (3) both species diversity and structural diversity can be affected by soil nutrients and topographies.

Key words: biomass; productivity; soil nutrients; species diversity; structural diversity; topographies

生物多样性和生产力是生态系统的核心指标,是实现生态系统服务与功能的根本所在(Tilman et al, 2014)。在全球气候变化的大环境下,生物多样性锐减,生态系统保护面临空前困境(Chapin et al, 2000)。因此,保护生物多样性,提高和恢复生态系统功能具有重要意义(Wilsey & Potvin, 2000)。在生物多样性和生态系统功能的关系中,多样性和生产力之间的关系及其维持机制是全球科学家所关注的核心问题之一(Loreau et al, 2001; 贺金生等, 2003)。大量研究表明物种多样性与生产力呈正相关(Wilson et al, 1990; Tilman & Downing, 1994; Ouyang et al, 2016; 吴初平等, 2018),但负相关(Liang et al, 2007)、驼峰关系(Loreau et al, 2001)和不相关(Grace et al, 2016)也有报道。森林生态系统中生物量和生产力之间既有联系又有区别,有研究表明,在森林生态系统中生产力高的物种其碳储存能力通常要低于生产力低的物种(吴初平等, 2018),且生物量和生产力对物种丰富度的响应也有差异(Cardinale et al, 2006)。综上,关于天然林中物种多样性对生产力和生物量的影响及其维持机制仍存

在较大争议(Zhang & Chen, 2015; Fotis et al, 2017)。为了加深对复杂自然生态系统中多样性与生产力关系和机制的理解,亟需进一步加强多样性与生产力和生物量关系的研究。

同时,群落结构多样性对森林生产力的影响也非常重要(Liang et al, 2007; Lei et al, 2009; Long & Shaw, 2010)。结构多样性通常被定义为空间分布、物种多样性和树木尺寸变化(如树木高度和直径)的一种或多种组合(Lei et al, 2009)。复杂的结构可以提高树木对光的捕获和利用效率,并提高树木利用水和土壤养分的效率,还可以促进森林生态系统中生物量的积累(Hardiman et al, 2011; Wang et al, 2011)。结构多样性除了能表征群落的空间分布,也可以反映群落总体的生物多样性,不同物种间的固有差异以及同种或异种个体间的不对称竞争有助于树木在空间中形成多元配置,提高资源利用效率和生产力(Yachi & Loreau, 2007; Lei et al, 2009)。研究表明,个体之间的差异、立地密度、林龄、最大径级和大树密度等林分结构属性都会改变森林生物量和生产力格局的多个方面(Paoli et al, 2008;

Slik et al, 2013; Zhang & Chen, 2015; Yuan et al, 2018)。物种多样性和林分结构属性的变化也直接关系到林分的生长和管理实践(Kant, 2002; Liang et al, 2005; Lei et al, 2009)。综上所述, 群落结构多样性对生产力和生物量的影响机制亟待进一步阐明。

植物群落的分布格局是不同尺度上气候、土壤、地形等环境因子综合作用的结果(Ricklefs et al, 1999)。植被的生产力也受到物种组成和地理环境等因素的影响(Doherty et al, 2011; Zhang et al, 2012)。土壤肥力和地形的差异都是影响植物群落结构和生产力的关键因素(Perroni-Ventura et al, 2006; Long et al, 2012)。研究表明高的土壤养分利用率可以促进植物快速生长, 进而对树木的生产力具有积极效应(Quesada et al, 2012; Prado-Junior et al, 2016)。相比于土壤贫瘠的森林, 土壤肥沃的森林中生物多样性对生产力的影响更大(Paquette & Messier, 2011)。此外, 海拔、坡度和坡向等地形特征造成的环境差异也会影响树种的分布、生物量的积累和生产力的变化(Valencia et al, 2009; Murphy et al, 2015)。由于环境条件、时空尺度和群落类型等因素的差异, 物种多样性和生产力之间的关系尚未得到一致的结论(Willig, 2011)。因此, 复杂的天然林生态系统中生物多样性与生产力的关联及其与环境因素的关系有待进一步阐明(谭凌照等, 2017)。

鼎湖山地处中国南亚热带典型季风气候区, 其地带性植被常绿阔叶林具有400多年的保护历史(方运霆等, 2003; 张亚茹等, 2014)。近年来该区域受气候变化等多重因素的影响出现了氮沉降增加和磷限制加剧等问题, 亟需加强对该生态系统生物多样性与生物量和生产力关系的研究(方运霆等, 2005; 黄文娟等, 2009; Lie et al, 2019)。分析南亚热带常绿阔叶林树木多样性与生产力和生物量的关联及其影响因素, 对于南亚热带常绿阔叶林生产力的提高和生物多样性的保护尤为重要。本研究以鼎湖山南亚热带常绿阔叶林群落为研究对象, 结合多种统计方法分析和评估树木多样性与生物量和生产力之间的关联及其影响因素。主要探讨以下问题: (1) 生产力是否受物种多样性和林分结构多样性的影响? (2) 生物量是否受物种多样性和林分结构多样性的影响? 是否与物种多样性和林分结构多样性对生产力的影响一致? (3) 环境因子如何影响物种多样性和林分结构多样性?

1 材料与方法

1.1 研究地概况

鼎湖山国家级自然保护区位于广东省肇庆市鼎湖区(23.16°–23.19° N, 112.51°–112.56° E), 总面积1,155 ha, 主要地形为丘陵和低山, 最高峰鸡笼山海拔1,000.3 m, 属中国南亚热带季风湿润型气候(熊鑫等, 2016)。年平均气温22.5℃, 最冷月(1月)和最热月(7月)平均气温分别为13.8℃和28.8℃。降水量1,714 mm, 4–9月为湿季, 10月至翌年3月为旱季, 干湿季分明。年平均蒸发量1,115 mm, 年平均相对湿度82%, 灾害性天气为寒潮和台风。土壤母质主要为泥盆纪砂岩、砂页岩、页岩和石英砂岩, 主要土壤类型为赤红壤和红壤。该地区主要的植被是南亚热带常绿阔叶林, 乔木层优势种主要为木荷(*Schima superba*)、锥(*Castanopsis chinensis*)、鼎湖血桐(*Macaranga sampsonii*)、香楠(*Aidia canthioides*)等。灌木层优势种主要为柏拉木(*Blastus cochinchinensis*)、九节(*Psychotria rubra*)、罗伞树(*Ardisia quinqueгона*)等。草本层优势种主要是淡竹叶(*Lophatherum gracile*)、芒萁(*Dicranopteris dichotoma*)、沙皮蕨(*Hemigramma decurrins*)等。

1.2 样地设置与群落调查

本研究选取鼎湖山南亚热带常绿阔叶林为研究对象, 该森林样地位于低山中坡, 具有400多年的保护历史, 处于演替顶极群落阶段, 郁闭度约95%。样地面积为1 ha (100 m × 100 m), 群落调查时先将样地划分为100个10 m × 10 m的II级样方, 每个II级样方再划分为4个5 m × 5 m的III级样方(共400个)。对样地内所有胸径(DBH) ≥ 1 cm的木本植物进行调查, 记录其种名、胸径、树高、生长状态和空间坐标, 每个植株给定一个唯一的编号以便后续进行追踪测定。2010年和2015年我们在样地内共调查了8,084棵木本植物, 隶属37科60属。

1.3 土壤取样和地形指标测定

在每个III级样方内0–30 cm深的土壤中利用土钻采集5个样品(对角线上), 去掉上层浮土, 混合均匀。取一部分迅速装于密封袋内, 剩余部分装在土壤袋中带回实验室测定土壤含水量(WC)、有机碳(C)、pH值(pH)、全氮(N)、铵态氮(NH₄⁺)、速效磷(AP)和速效钾(AK) 7个指标(刘光菘等, 1996)。用标尺、重锤和激光笔配合测定各III级样方边缘的相对高

差,以整个样地海拔最低的一边为基线,推算每个样地的相对海拔。以样地最低点作为零点,推算出每个Ⅲ级样方的顶角在样地中的相对海拔。每个Ⅲ级样方的相对海拔值由四个顶角坐标的平均值表示。每个样地的地形变量包括相对海拔(RA)、东西坡度(S_{EW})、南北坡度(S_{NS})、东西相对高差(RD_{EW})和南北相对高差(RD_{NS}) (表1)。

1.4 多样性测度

1.4.1 物种多样性

本研究选用物种丰富度(R)、Shannon-Wiener多样性指数(H')、Simpson多样性指数(D)和Pielou均匀度指数(E) 4个常用指数测度群落物种多样性。计算公式如下(Whittaker, 1972; Pielou, 1975):

$$R = S \quad (1)$$

$$H' = -\sum P_i \ln P_i \quad (2)$$

$$D = 1 / \sum P_i^2 \quad (3)$$

$$E = H' / \ln S \quad (4)$$

式中, S 为样方中物种数量,选取2015年和2010年同一样方的平均物种数; P_i 为群落中第 i 个物种的重要值。利用重要值(importance value, IV)来反映每个物种在群落中的相对重要性,计算公式为: $IV = (\text{相对多度} + \text{相对优势度})/2$ 。

1.4.2 结构多样性

本研究选用胸径和树高的标准偏差(standard deviation, SD)、变异系数(coefficient of variation, CV)和基尼系数(Gini coefficient, GC) 3个常用指数测度群落结构多样性。其中,胸径变异系数是描述林分分布频率的常用指标,系数值越大表示林木大小分化程度越高;基尼系数是描述个体胸径或树高偏离绝对均匀程度的指标,当个体间没有差异时取值为0,当差异最大化时取值无限接近于1 (Lexerød & Eid, 2006)。计算公式如下(谭凌照等, 2017; Schnabel et al, 2019):

表1 南亚热带常绿阔叶林样地基础变量信息统计表

Table 1 The statistical information of basic variables in the sampling plot in a lower subtropical evergreen broad-leaved forest

变量 Variables	范围 Range	平均值 Mean	标准偏差 SD
物种丰富度 Species richness (R)	6.00–21.50	12.86	3.69
Shannon-Wiener多样性指数 Shannon-Wiener diversity index (H')	1.23–2.68	2.07	0.31
Simpson多样性指数 Simpson diversity index (D)	0.62–0.91	0.82	0.06
Pielou均匀度指数 Pielou evenness index (E)	0.59–0.98	0.82	0.08
胸高断面标准偏差 Basal area standard deviation (SD_{ba})	14.83–4,696.75	333.41	678.16
胸高断面变异系数 Basal area coefficient of variation (CV_{ba})	86.49–2,069.74	486.98	371.29
胸高断面基尼系数 Basal area Gini coefficient (GC_{ba})	0.55–1.00	0.82	0.10
树高标准偏差 Height standard deviation (SD_h)	1.49–8.40	4.14	1.77
树高变异系数 Height coefficient of variation (CV_h)	28.73–147.37	79.32	30.73
树高基尼系数 Height Gini coefficient (GC_h)	0.18–0.54	0.35	0.08
坡度(南北) Slope degree (Northsouth) (S_{NS}) (°)	0.00–89.61	10.52	11.86
坡度(东西) Slope degree (Eastwest) (S_{EW}) (°)	4.72–39.00	26.79	5.78
相对高差(南北) Relative dispersion (Northsouth) (RD_{NS}) (m)	0.00–3.07	0.95	0.83
相对高差(东西) Relative dispersion (Eastwest) (RD_{EW}) (m)	0.39–4.09	2.58	0.62
相对海拔 Relative altitude (RA) (m)	4.50–66.20	33.42	15.47
土壤含水量 Water content (WC)	0.20–0.30	0.24	0.02
pH值 pH value	3.74–4.05	3.85	0.06
有机碳 Organic carbon (C) (mg/g)	18.79–42.75	26.18	4.37
全氮 Total nitrogen (TN) (mg/g)	1.61–3.62	2.14	0.33
铵态氮 Ammonium nitrogen (NH_4^+) (mg/g)	0.00–0.01	0.01	0.00
速效磷 Available phosphorus (AP) (mg/g)	0.00–0.01	0.00	0.00
速效钾 Available potassium (AK) (mg/g)	0.08–0.23	0.12	0.03

$$CV_{ba} = 100 \times \frac{SD_{ba}}{\bar{x}_{ba}}; CV_h = 100 \times \frac{SD_h}{\bar{x}_h} \quad (5)$$

$$GC_{ba} = \frac{\sum_{j=1}^n (2 \times j - n - 1) \times ba_j}{\sum_{j=1}^n (n - 1) \times ba_j}; \quad (6)$$

$$GC_h = \frac{\sum_{j=1}^n (2 \times j - n - 1) \times h_j}{\sum_{j=1}^n (n - 1) \times h_j} \quad (7)$$

式中, ba_j 是样方内按大小升序第 j 棵树的胸高断面积, h_j 是样方内按大小升序第 j 棵树的树高(m), \bar{x}_{ba} 指样方中所有个体胸高断面积的平均值, \bar{x}_h 指样方中所有树高的平均值, j 是树的等级, 从1升到 n 。其中胸径和树高选取2015年和2010年同一个体的平均胸径和平均树高。

1.5 生物量和生产力的计算

生物量(温达志等, 1997)和生产力(Lasky et al, 2014; 吴初平等, 2018)的计算如下:

$$\text{生物量}(B): B = a \times DBH^b \quad (8)$$

$$\text{生产力}(P): P = (Biomass_{2015}/Biomass_{2010})/t \quad (9)$$

式中, DBH 为胸径(cm), a 和 b 是回归系数。考虑到地形和土壤数据是两年份之间的调查数据, 本研究的生物量采用2015年和2010年的平均生物量。考虑到样方内起始的生物量可能会反过来影响样方内生物量的变化值, 本研究用生物量的相对变化量表示群落的初级生产力(文中统称为“生产力”)。为了保证数据的正态性, 对生物量和生产力的数据进行对数转换。 $Biomass_{2015}$ 为2015年调查时样方内所有个体生物量之和, $Biomass_{2010}$ 为2010年调查时样方内所有个体生物量之和, t 为从2010年到2015年的时间间隔。

1.6 数据统计和分析

首先, 分别对物种多样性、结构多样性、土壤养分和地形因子进行主成分分析(principal component analysis, PCA), 再运用一元回归模型检验树木多样性与生物量和生产力之间的关系。其次, 利用Pearson相关性分析解释物种多样性、结构多样性、生产力、生物量、土壤养分和地形因子变化之间的相关关系, 统计显著性水平设为 $P < 0.05$ 。最后, 运用方差分解(variation partitioning analysis, VPA)解释每组因子的单独效应和共同效应, 利用韦恩图表示各因子对生物量和生产力变化的相对贡献。同

时, 利用结构方程模型(structural equation modeling, SEM)检验土壤养分和地形因子通过物种多样性和结构多样性对生产力和生物量的直接和间接效应。采用最大似然法对结构方程模型进行拟合, 利用比较拟合指数(CFI)、渐进残差均方和平方根(RMSEA)、显著性概率值(P)评价模型优度, 拟合优度的临界值为 $CFI > 0.9$, $RMSEA < 0.08$, $P > 0.05$, AIC 越小越好(温纯和金光泽, 2019)。数据整理与计算使用Excel 2016, 结构方程模型构建采用AMOS 21.0, 统计分析及作图在R 3.3.3软件中完成。

2 结果

2.1 树木多样性与生产力和生物量之间的关系

利用主成分分析对物种多样性指标和结构多样性指标进行聚类分析(表2)。结果表明物种多样性第一主轴的解释率为73.4%, 第二主轴的解释率为25.5% (图1a)。结构多样性第一主轴的解释率为70.4%, 第二主轴的解释率为15.5% (图1b)。其第一主轴载荷量均大于0.7, 说明第一个主轴能代表物种多样性和结构多样性的变化。树木多样性与生物量和生产力的一元线性回归结果显示, 在南亚热带常绿阔叶林中生产力随着物种多样性的增加而极显著增加($R^2 = 0.12$, $P < 0.01$, 图1c), 而生物量随着物种多样性的增加极显著减少($R^2 = 0.10$, $P < 0.01$, 图1c)。相反, 生产力随着结构多样性的增加而减少($R^2 = 0.20$, $P < 0.001$, 图1d), 生物量随着结构多样性的增加而极显著增加($R^2 = 0.52$, $P < 0.01$, 图1d)。

2.2 环境因子与树木多样性、生产力和生物量的相关性

Person相关性分析结果显示, 生产力与土壤含水量显著负相关($P < 0.05$), 而生物量与地形和土壤养分均没有显著的相关关系(图2)。物种丰富度与有机碳、速效磷和速效钾呈显著负相关($P < 0.05$), 与坡度(南北)和相对高差(南北)极显著负相关($P < 0.01$), 与全氮呈负相关($P < 0.001$)。Shannon-Wiener多样性指数与坡度(南北)显著负相关($P < 0.05$), 与全氮极显著负相关($P < 0.01$), 与铵态氮极显著正相关($P < 0.01$)。Simpson多样性指数与相对高差(南北)显著负相关($P < 0.05$), 与铵态氮显著正相关, 与坡度(南北)和全氮极显著负相关($P < 0.01$)。Pielou均匀度指数与土壤含水量和铵态氮显著正相关($P < 0.05$)。胸高断面积变异系数与土壤含水量和铵态氮

显著负相关($P < 0.05$)。胸高断面面积基尼系数与速效磷呈显著负相关($P < 0.05$)。树高标准偏差与相对海拔、土壤含水量和速效磷呈显著负相关($P < 0.05$)；树高变异系数与有机碳、铵态氮、速效磷和速效钾呈显著负相关($P < 0.05$)，与土壤含水量极显著负相关($P < 0.01$)。树高基尼系数与相对海拔、土壤含水量、有机碳和速效磷呈显著负相关($P < 0.05$) (图2)。

2.3 环境因子对生产力和生物量的直接和间接影响

方差分解分析结果表明，结构多样性对生产力的单独效应的解释率最大，为5.21%；结构多样性和物种多样性共同效应的解释率次之，为3.53%；地形与结构多样性共同效应和土壤养分与结构多样性共同效应的解释率较小，分别为1.09%和0.19%

(图3a)。结构多样性对生物量单独效应的解释率最大，为35.39%；结构多样性和物种多样性共同效应的解释率次之，为13.66%；地形与结构多样性共同效应和土壤养分与结构多样性共同效应的解释率较小，分别为3.52%和3.49% (图3b)。进一步利用结构方程模型进行分析，结果表明各变量分别解释生产力和生物量的变化的34%和52% (图3c)。物种多样性对生产力有显著的直接影响($P < 0.05$)，反映作用大小的路径系数为0.18。结构多样性对生物量具有直接影响($P < 0.001$ ，路径系数为0.72)。各变量分别解释了物种多样性和结构多样性变化的29%和5%。地形和土壤养分对物种多样性具有显著的直接影响，路径系数分别为-0.23和-0.26；土壤养分对

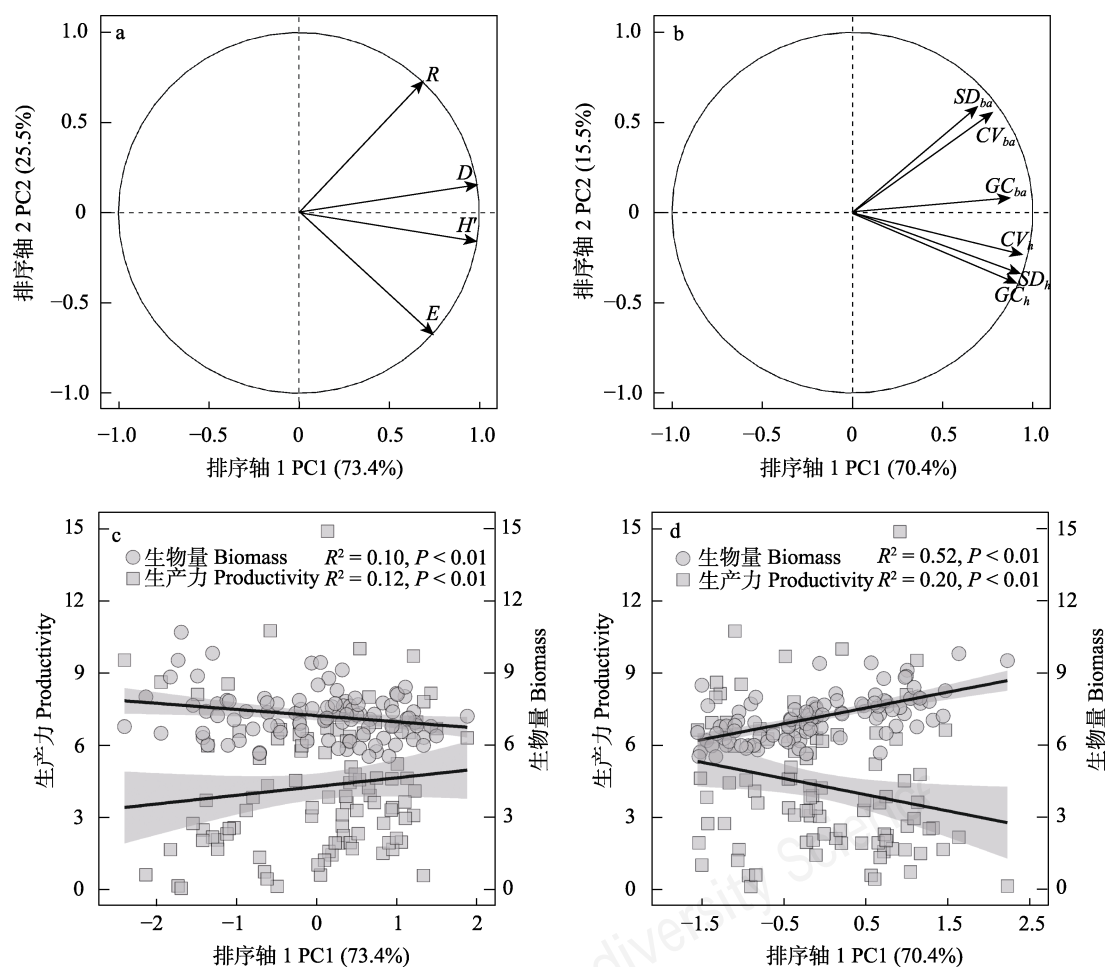


图1 物种多样性和结构多样性与生物量和生产力之间的相关关系。(a) 4个物种多样性指标的第一轴和第二轴载荷量；(b) 6个结构多样性指标的第一轴和第二轴载荷量；(c)物种多样性第一主轴载荷量与生物量和生产力之间的关系；(d)结构多样性第一主轴载荷量与生物量和生产力之间的关系。缩写代表含义同表1。

Fig. 1 Relationship between species diversity and structural diversity with plant biomass and productivity. (a) Loadings on the first and second axes of four species diversity indexes; (b) Loadings on the first and second axes of six structural diversity indexes; (c) Relationship between loadings on the first axis of species diversity and plant biomass and productivity; (d) Relationship between loadings on the first axis of structural diversity and plant biomass and productivity. Abbreviations have the same as in Table 1.

表2 物种多样性、结构多样性、地形和土壤养分主成分的特征值和贡献率

Table 2 Eigenvalues and contribution rate of species diversity factors, structural diversity factors, topography factors and soil nutrients factors.

类型 Class	成分 Component	特征值 Eigenvalue	方差贡献率 Contribution rate of variance (%)	方差累积贡献率 Cumulative contribution rate of variance (%)
物种多样性 Species diversity	1	2.93	73.45	73.45
	2	1.02	25.52	98.97
	3	0.03	0.76	99.73
	4	0.01	0.27	100
结构多样性 Structural diversity	1	4.22	70.37	70.37
	2	0.93	15.54	85.91
	3	0.47	7.78	93.69
	4	0.25	4.19	97.88
	5	0.07	1.11	98.99
	6	0.06	1.01	100
地形 Topography	1	2.77	55.35	55.35
	2	1.49	29.77	85.12
	3	0.61	12.13	97.25
	4	0.13	2.66	99.91
	5	0.00	0.09	100
土壤养分 Soil nutrients	1	3.51	50.17	50.17
	2	1.37	19.62	69.79
	3	0.84	11.98	81.77
	4	0.65	9.22	90.99
	5	0.42	6.05	97.04
	6	0.13	1.89	98.93
	7	0.07	1.07	100

结构多样性具有显著的直接影响，路径系数为-0.22。结构多样性对物种多样性具有极显著影响，路径系数为-0.48；生物量对生产力具有极显著影响，路径系数为-0.50 (图3c)。

3 讨论

3.1 物种多样性与生产力和生物量的关系

本研究结果表明物种多样性与生产力呈显著正相关关系，这与早期生产力与物种多样性关系的研究结果相似(黄小荣等, 2018; Liu et al, 2019)。这可能由于鼎湖山南亚热带常绿阔叶林群落郁闭度较高，林龄超过200年，生态位分化合理，使得空间资源能够被充分利用，进而增加了植被的生产力(Loreau et al, 2001; Chen et al, 2016)。并且以往研究

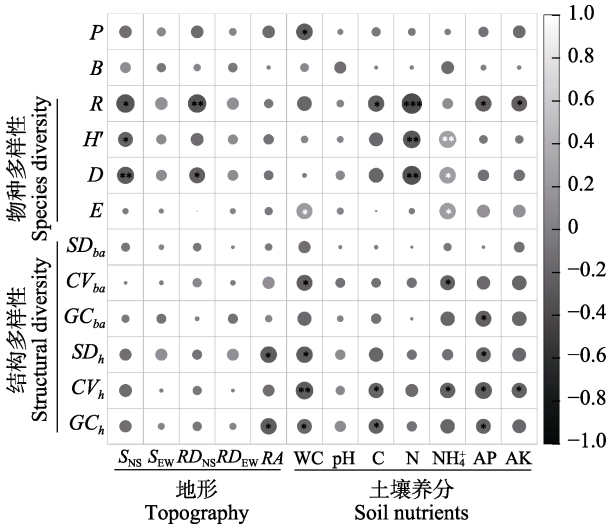


图2 南亚热带常绿阔叶林树木多样性、生物量和生产力与土壤养分和地形因子之间的 Pearson 相关关系。P: Productivity; B: Biomass; 其余缩写代表含义同表1, *, $P < 0.05$, **, $P < 0.01$, ***, $P < 0.001$, 白色*为正相关, 黑色*为负相关。

Fig. 2 Pearson correlation between tree species diversity, plant biomass, plant productivity and soil nutrients, topographic factors in subtropical evergreen broadleaved forest. The letter B and P mean biomass and productivity, and other abbreviations have the same as in Table 1, *, $P < 0.05$, **, $P < 0.01$, ***, $P < 0.001$, white sign (*) is positive correlation, black sign (*) is negative correlation.

表明物种丰富度高的群落更偏向于增加高产物种进入群落的机会，而本研究鼎湖山南亚热带常绿阔叶林已经处于群落演替后期，高产物种已经形成了稳定的种间关系，因此高物种多样性也是植被生产力增加的原因之一(Vile et al, 2006; Cadotte, 2017)。此外，鼎湖山南亚热带常绿阔叶林中群落物种多样性与生物量呈负相关，该结果与在浙江定海次生林生物量与物种多样性的结果并不一致(吴初平等, 2018)。这可能由于本研究群落处于近演替顶极阶段(邹顺等, 2018)，在演替后期南亚热带常绿阔叶林群落结构较为稳定，群落的总生物量主要取决于群落中的高碳储量的物种，高碳储量的物种竞争性导致更多的生物量积累(Potter & Woodall 2014; Ouyang et al, 2016)。而鼎湖山常绿阔叶林以往研究显示，过去30年间群落中大径级个体和不抗旱植物个体数减少，小径级个体和抗旱或速生植物个体数增加，使得群落中总生物量呈现下降的趋势，这可以用来解释本研究中物种多样性与生物量的负相关关系(邹顺等, 2018)。相关研究也表明当生物量超过一定

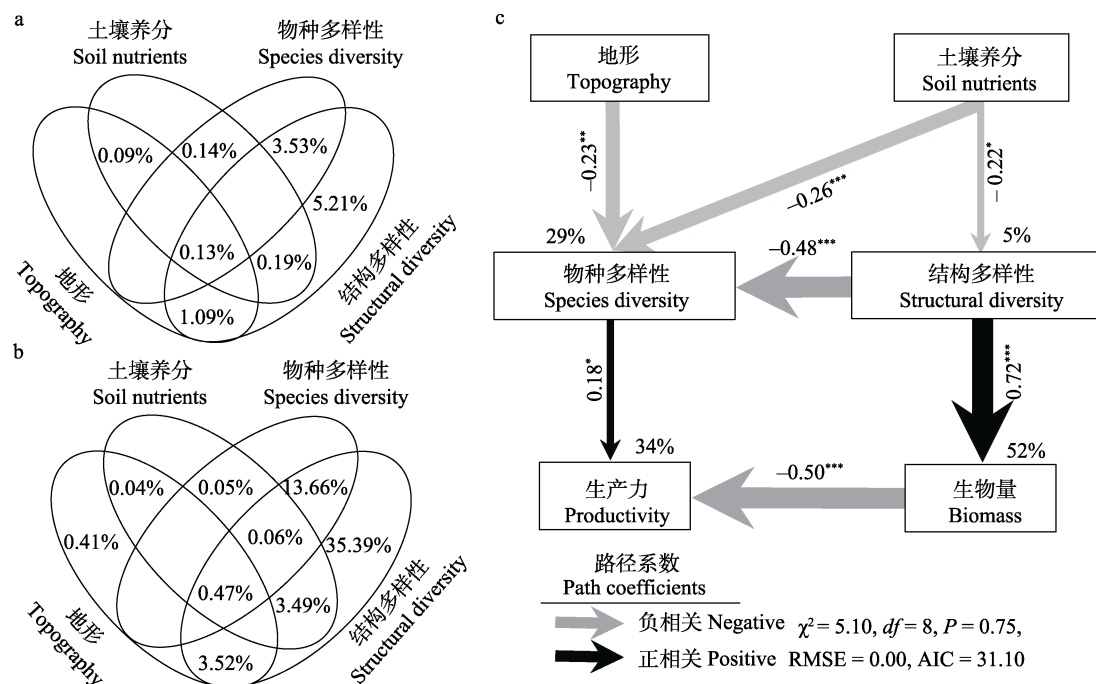


图3 物种多样性、结构多样性、地形和土壤养分对生产力和生物量的影响。(a)方差分解解释各因子对生产力的单独效应和共同效应；(b)方差分解解释各因子对生物量的单独效应和共同效应；(c)结构方程模型(SEM)解释地形和土壤养分通过物种多样性和结构多样性对生产力的直接和间接影响($N = 100$)。SEM考虑了所有可能的路径， R^2 表示所解释的方差比例。箭头上的数字表示标准化的路径系数。箭头宽度表示路径系数的强度。*, $P < 0.05$, **, $P < 0.01$, ***, $P < 0.001$ 。

Fig. 3 The impact of species diversity, structural diversity, topography and soil nutrients on plant productivity and biomass. (a) Variation partitioning analysis explains the pure and shared effect of factors on plant productivity. (b) Variation partitioning analysis explains the pure and shared effect of factors on plant biomass. (c) Structural equation model (SEM) reveals the direct and indirect effects of species diversity, structural diversity, topography and soil nutrients on plant productivity and biomass ($N = 100$). The SEM considered all plausible pathways, to increase the degrees of freedom, R^2 indicates the proportion of variance explained. The numbers on the arrows indicate standardized path coefficients. The arrow width is proportional to the strength of the path coefficients. *, $P < 0.05$, **, $P < 0.01$, ***, $P < 0.001$.

水平时，物种丰富度与生物量呈显著的负相关(郭志华等, 2002)。此外，本研究显示鼎湖山亚热带常绿阔叶林生物量与生产力具有负相关关系，这与早期在该地区的研究结果一致(Prado-Junior et al, 2016)。这可能是由于环境因素对生物量和生产力关系的影响(Ma et al, 2010)，本研究群落处于演替后期阶段，林分内养分循环处于稳定甚至关闭的状态，小径级个体虽有生长，但大径级个体生物量在群落中占主导地位，而研究区域内大径级个体受到环境因素的影响个体数减少，导致群落生物量与生产力之间表现出负相关关系。

3.2 结构多样性与生产力和生物量的关系

早期研究表明，群落结构变异在一定程度上反映了物种在资源利用上的生态位互补，是促进生产

力的一个重要机制(谭凌照等, 2017)。而鼎湖山亚热带常绿阔叶林结构多样性与生物量呈显著的正相关关系，与生产力却呈显著的负相关关系。本研究中结构多样性与生产力的关系与大多数结果不一致(即结构多样性促进生产力)(谭凌照等, 2017; Lei et al, 2009)。这可能是由研究样地所处的演替阶段、环境条件和群落结构差异所导致的。亚热带常绿阔叶林受到气候条件变化和自然干扰的影响，群落整体、群落垂直层次内和垂直层次之间的正相关关系逐渐减弱，物种间的互补性不足，对资源的利用效率下降，导致群落结构多样性与生产力呈现负相关关系。这可能是由于鼎湖山常绿阔叶林群落更新率和死亡率上升，大径级个体占据主要地位，虽有小径级个体快速更新提升群落生产力，但仍然

不能够弥补大径级个体死亡对群落所造成的影响(邹顺等, 2018)。群落结构多样性与生物量的正向关系可以在一定程度上表明结构多样性是促进个体生物量积累的。一方面群落结构与资源的充分利用具有密切关系, 竞争和资源的充分利用决定了物种分布格局的多样化; 另一方面群落结构与物种组成有密切的关系, 高碳储量的物种占据着群落主要地位(Potter & Woodall 2014; Ouyang et al, 2016)。因此, 南亚热带常绿阔叶林群落结构多样性是促进群落生物量积累的。此外, 本研究显示结构多样性与生产力和生物量的关系与物种多样性与生产力和生物量的关系呈相反的趋势, 这可能是由于本研究中结构多样性对物种多样性具有反向作用, 群落属于近演替顶极, 群落结构较为稳定, 而近年来该群落受环境影响个体不断死亡造成群落巨大波动, 影响了物种组成, 使结构多样性与物种多样性呈现出负相关关系(邹顺等, 2018)。

3.3 环境因子对多样性的影响

地形和土壤养分的变化决定了物种分布、森林碳库组成和功能的多个方面。自然群落中的物种组成是在漫长的演化过程中, 物种与环境之间相互依赖、相互作用, 从而适应当地环境条件所形成的特定群落结构, 是对环境响应的综合反映(Ricklefs et al, 1999)。我们的研究结果表明地形对植被生产力和生物量无显著的直接影响, 但对物种多样性具有显著的负影响, 这与吴初平等(2018)在浙江定海次生林地的研究具有一定的差异。当然, 群落结构特性也受区域特征和群落发展阶段的影响(方精云等, 2004; Jafari et al, 2004)。本研究中地形对物种多样性的影响主要是由于样地的斑块状特征, 坡度呈西南-东北走向, 从南到北坡度逐渐增加, 而物种多样性逐渐下降, 导致地形与物种多样性呈现显著的负相关关系。

土壤和植被的养分状况常作为衡量环境对植被生长养分限制状况的指标。在热带和亚热带地区, 由于土壤高度风化以及土壤中磷的有效性低等特点, 土壤养分常常成为该地区限制植物生长的主要因素(Vitousek & Howarth, 1991)。本研究中南亚热带常绿阔叶林高土壤有机碳和土壤有效磷含量的环境条件下, 群落结构复杂; 而高土壤氮含量环境条件下, 物种多样性较低, 这与早期研究具有相似

的结果(冯健等, 2021)。这可能是由于南亚热带常绿阔叶林物种多样性和结构多样性主要受土壤有效磷和氮沉降的影响, 植物生长所需要的土壤有效磷主要来源于土壤, 植被中土壤有效磷含量越多, 结构多样性越复杂。并且南亚热带常绿阔叶林由于氮沉降导致物种多样性逐渐降低(鲁显楷等, 2008)。因此, 南亚热带常绿阔叶林土壤养分对物种多样性和结构多样性有明显的影响。

综上, 本研究以未经人为干扰的中国南亚热带地区的地带性顶极群落为研究对象, 基于森林生态系统乔木层群落调查数据, 结合样地的地形和土壤养分, 研究了南亚热带常绿阔叶林树木多样性和生产力之间的关联及其影响因素。主要结论如下: (1) 物种多样性对生产力有最大直接效应, 结构多样性对生物量有最大直接效应; (2) 在南亚热带常绿阔叶林中物种多样性在解释生产力方面要优于结构多样性, 而结构多样性在解释生物量积累方面要优于物种多样性; (3) 物种多样性和结构多样性均受地形和土壤因子的影响。因此, 在南亚热带常绿阔叶林的经营和管理过程中充分考虑物种多样性和结构多样性对生产力和生物量的影响, 将有助于更好的保持南亚热带常绿阔叶林的结构多样性, 以维持演替顶级群落的生物多样性和快速生长。

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