



•研究报告•

浙江古田山次生与老龄常绿阔叶林群落特征的比较

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摘要: 常绿阔叶林为东亚亚热带地区的地带性植被, 对该地区的生物多样性维持和社会发展具有重要的意义。由于长期人类活动的影响, 目前我国分布的常绿阔叶林绝大部分为次生常绿阔叶林。探究次生与老龄常绿阔叶林群落特征的差异, 有利于了解人类干扰对亚热带常绿阔叶林的影响, 为其保护和恢复提供依据。本研究在古田山老龄与次生常绿阔叶林内共设置了29个0.04 ha样地, 比较两者在优势种组成、物种和功能多样性以及生物量等方面的差异。结果表明: (1)次生林与老龄林优势种组成相似, 二者均以甜槠(*Castanopsis eyrei*)、木荷(*Schima superba*)等典型常绿阔叶林优势种为主, 但这些树种在次生和老龄常绿阔叶林中的优势度次序不同。(2)整体而言, 次生林的Shannon-Wiener指数和功能离散度高于老龄林; 次生林与老龄林的物种Bray-Curtis指数和功能Sørensen指数均无显著差别。(3)就垂直层次而言, 次生林与老龄林在Shannon-Wiener指数和Bray-Curtis指数的差异主要体现在乔木层和灌木层。(4)就群落结构而言, 次生林的植株密度高于老龄林, 但群落水平和个体水平的生物量均显著小于老龄林。上述结果表明, 人类干扰改变了古田山常绿阔叶林群落的多个重要特征, 不同群落特征的恢复过程并不同步。因此, 对常绿阔叶林生物多样性和生态系统功能的保护和恢复需要从多个角度着手。

关键词: 老龄林; 次生林; 物种组成; α 多样性; β 多样性; 功能性状; 生物量; 植株密度

A comparative study on the community characteristics of secondary and old-growth evergreen broad-leaved forests in Gutianshan, Zhejiang Province

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Abstract: Evergreen broad-leaved forests (EBLFs), which are the primary zonal vegetation of subtropical East Asia, shelter high biodiversity and contribute significantly to human welfare. Today, most EBLFs are secondary growth due to long-term human activity. The few remaining old-growth EBLFs are small, scattered patches. Understanding how secondary and old-growth EBLFs differ in their community characteristics would provide guidance for their conservation and restoration. Here, we compare the dominant species composition, species and functional diversity, and aboveground biomass between old-growth (fifteen 20 m \times 20 m plots) and secondary (fourteen 20 m \times 20 m plots) EBLFs in Gutianshan National Nature Reserve (GNNR). We found that: (1) Both old-growth and secondary EBLFs were dominated by the same set of

收稿日期: 2019-02-28; 接受日期: 2019-09-01

基金项目: 科技部基础性工作专项(2015FY210200-17)和浙江省科技计划(2015C02016; 2017C02028)

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evergreen broad-leaved species, such as *Castanopsis eyrei* and *Schima superba*, but the species dominance order was inconsistent in the two forest types. (2) Secondary EBLFs had a higher Shannon-Wiener index value and greater functional dispersion than old-growth EBLFs, but neither the Bray-Curtis dissimilarity index values nor the functional Sørensen index values differed greatly between secondary and old-growth EBLFs. (3) When considering three vertical forest layers separately, the differences in the Shannon-Wiener and Bray-Curtis indices between secondary and old-growth EBLFs were mainly reflected in the tree and shrub layers. (4) Looking at the community structure overall, the stem density was greater in secondary EBLFs than old-growth EBLFs. Additionally, the community level and the individual level biomass were both lower in secondary EBLFs than old-growth EBLFs. These findings suggest that human disturbance has changed multiple characteristics of the EBLFs in GNNR, and their recovery process has been asymmetrical. Accordingly, any conservation plans to restore the biodiversity and ecosystem functioning in EBLFs should adopt a multi-faceted strategy.

Key words: old-growth forest; secondary forest; species composition; α diversity; β diversity; functional trait; biomass; stem density

亚热带常绿阔叶林是世界主要森林植被类型之一, 主要分布在中国, 以中亚热带的常绿阔叶林最为典型(吴征镒, 1980; 王希华, 2006; 宋永昌, 2013; Jin et al, 2018)。亚热带常绿阔叶林区域约占中国国土面积的1/4, 其结构复杂, 生物多样性丰富, 生态系统服务功能强, 对中国社会经济的可持续发展及生态安全有着重要作用。由于长期的人类干扰, 中国亚热带常绿阔叶林绝大部分退化为次生林或被改造为人工林, 老龄林几乎丧失殆尽(吴征镒, 1980; 宋永昌等, 2005; Wang et al, 2007; Shang et al, 2014)。比较亚热带次生和老龄常绿阔叶林群落特征的差异, 对次生常绿阔叶林植被恢复和生物多样性保护有重要意义。

人类干扰可影响森林生物多样性和群落结构, 森林在受到干扰后的恢复过程受到关注(Bruehlheide et al, 2011; Feng et al, 2014; Liu et al, 2016)。一方面, 在干扰后的演替过程中, 森林物种组成和多样性(Aiba et al, 2001)均可发生巨大变化, 进而引起群落功能多样性(Biswas & Mallik, 2010; Hu et al, 2014)和生态系统功能(Huang et al, 2018)的改变; 另一方面, 干扰后, 森林群落的生物量等特征会随演替进展发生变化(Pregitzer & Euskirchen, 2004; Ali et al, 2016)。已有研究表明, 次生林的恢复过程受到干扰历史、地形等环境因素及生物因素的共同影响(Chazdon et al, 2007; Bruehlheide et al, 2011), 不同群落常表现出不同的恢复速度, 并且对于不同功能性状的物种, 其组成和多样性的恢复速度也存在差异(Aiba et al, 2001; Martin et al, 2004; 冯广等, 2016)。处于不同演替阶段的次生林之间在物种组成、群落

结构等诸多方面存在差异, 且因地区和次生林的恢复时间而异(包维楷和刘照光, 2002; 史景宁等, 2015)。但迄今关于次生与老龄常绿阔叶林群落的比较研究极少, 以往在古田山进行的干扰历史和干扰强度对森林群落及其动态的影响研究均未涉及这一方面(Feng et al, 2014; 徐远杰等, 2014)。

古田山国家级自然保护区地处我国中亚热带东部, 其地带性植被老龄常绿阔叶林在核心区低海拔地区广泛分布, 周围的缓冲区和实验区分布有更大面积的次生常绿阔叶林(于明坚等, 2001, 2019), 为比较研究亚热带次生和老龄常绿阔叶林群落特征提供了良好的材料。本文拟通过比较古田山次生和老龄常绿阔叶林群落的优势种组成、物种和功能多样性、植株密度和生物量的差异, 探究两者物种组成和群落结构的差异, 为亚热带常绿阔叶林的生物多样性保护和恢复提供依据。

1 材料与方法

1.1 研究区概况

古田山国家级自然保护区(29°10'–29°17' N, 118°03'–118°11' E)地处黄山、怀玉、白际山脉交汇处, 面积8,107 ha。该区属中亚热带湿润季风气候, 年均温15.3℃, 最热月均温28.9℃, 最冷月均温4.1℃, 年均降水量1,963.7 mm, 年均降雨天数约140 d, 无霜期约250 d(于明坚等, 2001)。土壤类型有红壤、红黄壤、黄红壤及高山草甸土, 由于地形复杂, 形成了多种小气候和植被类型(楼炉煊和金水虎, 2000; 胡正华等, 2003), 分布有中亚热带地区少见的大面积低海拔老龄常绿阔叶林(于明坚等, 2001)。通过查

阅资料和实地走访调查, 我们从未受到明显人类干扰、保存完好的森林群落认定为老龄林, 将受到砍伐等人类干扰后经次生演替自然恢复的森林群落认定为次生林。次生林主要为1958年建立伐木场后, 因用材需求皆伐后恢复的天然次生林。1975年古田山成立省级自然保护区后, 人为砍伐现象得到控制(开化林业志编写组, 1988), 2001年成立国家级自然保护区并扩区后完全禁止。确定了老龄林大概分布范围后, 经估算发现保护区内老龄常绿阔叶林约占常绿阔叶林总面积的10%, 面积达到549 ha。

1.2 样地设置及调查方法

在保护区内选择有代表性的地点, 共设置29个20 m × 20 m样地, 其中老龄常绿阔叶林(以下简称老龄林)样地15个; 次生常绿阔叶林(以下简称次生林)样地14个, 样地间隔大于140 m。次生林位于保护区的实验区和缓冲区, 距离村庄、道路等较近; 老龄林主要位于核心区, 人迹罕至, 其中常保留有胸径较大、树高较高的植株(比如马尾松(*Pinus massoniana*)、甜槠(*Castanopsis eyrei*)和木荷(*Schima superba*))。为了解次生林恢复时间长度, 利用Bruehlheide等(2011)的公式, 通过样地内胸径排名前五的乔木层个体的平均年龄推算出次生林林龄。每个样地被划分为16个5 m × 5 m小样方, 以1 cm为起测胸径(离地1.3 m的主干直径), 对样地内木本植物进行每木调查, 测定坐标、胸径, 并鉴定物种, 部分样地还测定了植株高度。在每个样地中央位置记录经纬度和地形因子。地形因子包括海拔、坡度和坡向。此外, 基于人类干扰程度的不同, 将几乎未受人类干扰的样地划入老龄林, 干扰强(如皆伐)的样地划分为次生林。

1.3 功能性状

群落内的生境因子会随演替过程发生变化, 导致物种在光合效率、植株高度和传播方式等方面均发生显著改变(李庆康和马克平, 2002; 宋光满等, 2018)。因此, 我们选择了叶生活型、生长型和传播方式3个物种水平上的功能性状(李庆康和马克平, 2002; R̃ Ehounková& Prach, 2010)。其中, 叶生活型包括常绿阔叶、落叶阔叶和针叶; 生长型包括灌木和乔木; 传播方式包括动物传播(zoochory)、风力传播(anemochory)和自身传播(autochory)。

1.4 群落结构

部分样地缺少树高数据, 我们利用Lin等(2012)

提供的方程通过胸径估算树高, 未列出的其他物种利用近缘种公式来计算, 若无近缘种, 利用“其他树种”方程来估算。参考冀艳利^①对古田山常绿阔叶林垂直层次的划分标准, 根据树高将群落划分为三个层次: 灌木层(< 5 m)、亚乔木层[5 m, 15 m)和乔木层(≥ 15 m)。

计算每个样地的植株密度(株/ha)。利用主要树种的生物量方程(附录1)估算每株植物的地上部分生物量, 未列出的物种采用其近缘种的生物量方程估算; 无近缘种的物种利用“其他树种”方程估算, 这类物种约占总个体数的10%。

1.5 统计与分析方法

1.5.1 优势种组成

采用重要值(importance value, *IV*)衡量物种的优势度(宋永昌, 2016)。以样地群落数据为基础, 分别计算老龄林和次生林的物种重要值。公式为 $IV = (Dr + Pr + Fr)/3$ 。其中, *Dr*为相对多度(某个种的株数/全部种的总株数), *Pr*为相对显著度(某个种的胸高断面积/全部种的胸高断面积), *Fr*为相对频度(某个种在5 m × 5 m小样方的频度/全部种的总频度)。

1.5.2 物种和功能多样性指标

以Shannon-Wiener指数(H') ($H' = -\sum p_i \ln p_i$, p_i 为物种相对多度)衡量物种 α 多样性。以Bray-Curtis指数衡量物种 β 多样性(物种组成差异)。对老龄林和次生林进行稀疏化(rarefaction)分析, 稀疏曲线能较为客观地反映个体数与物种丰富度的关系(黄冰, 2012)。

用功能离散度(functional dispersion, *Fdis*)衡量群落的功能 α 多样性(Lalibert & Legendre, 2010)。功能离散度反映了群落内功能性状的异质性, 是指每个物种离所有物种功能性状多维空间质心的平均距离, 并经物种相对多度加权, 不受物种丰富度的影响(Laliberté & Legendre, 2010)。用Sørensen指数衡量功能 β 多样性(功能组成差异)(Baselga, 2012), 它通过逐对比较样地间的功能性状相异性, 反映两个群落之间的总体 β 多样性。物种间功能性状距离采用Gower距离计算(Gower, 1971)。

1.5.3 统计方法

采用Wilcoxon秩和检验(Wilcoxon rank-sum test)比较次生林与老龄林在Shannon-Wiener指数和

^① 冀艳利 (2016) 古田山 24 ha 样地木本植物物种多样性及优势种群更新动态研究. 硕士学位论文, 浙江师范大学, 浙江金华。

功能离散度两个方面的差异。进一步,分别在乔木层、亚乔木层和灌木层比较次生林与老龄林间 Shannon-Wiener 指数的差异。采用卡方检验分析次生林和老龄林群落在各个功能群所占相对丰富度及相对多度的差异。利用线性回归模型控制地形因子作用,了解人类干扰对 Shannon-Wiener 指数和功能离散度的影响。地形因子中,坡向为环状变量,被分解为南北向(坡向的余弦值)和东西向(坡向的正弦值)分量。然后,选出 AICc 值最小的模型作为最优模型(附录 2, 3)。采用 Wilcoxon 秩和检验评估老龄林与次生林内部及二者之间物种 Bray-Curtis 指数和功能 Sørensen 指数的差异(Borcard et al, 2011)。进一步利用偏 Mantel 检验的多元回归方法,在控制地形和地理距离影响的基础上,了解人类干扰对物种 Bray-Curtis 指数和功能 Sørensen 指数的影响。

通过 Wilcoxon 秩和检验比较次生林和老龄林间植株密度的差异,并分别比较次生林和老龄林在群落和个体水平的生物量差异。用 Levene 检验分析次生林和老龄林内个体水平生物量变异程度的差异。通过模型选择和线性回归模型,在考虑地形因素影响的同时,了解人类干扰对森林群落水平上生物量和植株密度的影响。进一步,用卡方检验分析次生林与老龄林生物量在三种功能性状组成上的差异。

为进一步了解林龄对群落结构特征的影响,利用一元线性回归模型,探究次生常绿阔叶林 Shannon-Wiener 指数、功能离散度、植株密度和地上部分生物量与林龄的线性关系。

所有数据分析均通过 R 3.2.4 软件(R Core Team,

2016)进行。其中稀疏曲线和 nMDS 分析采用 vegan 软件包(Oksanen et al, 2016),地理距离计算采用 fossil 软件包(Matthew, 2012),功能离散度计算采用 FD 软件包(Laliberté et al, 2014),偏 mantel 检验采用 phytools 软件包(Revell, 2012),线性回归模型的模型选择使用 MuMIn 软件包(Bartoń, 2017)。

2 结果

2.1 物种组成

29 个 0.04 ha 样地共调查到木本植物 50 科 95 属 164 种,其中常绿阔叶植物 85 种,落叶阔叶植物 77 种,针叶植物 2 种。15 个老龄林样地含木本植物 42 科 77 属 123 种,其中常绿阔叶植物 71 种,落叶阔叶植物 50 种,针叶植物 2 种,0.04 ha 样地平均物种数为 30.9 ± 8.5 ; 14 个次生林样地含 40 科 78 属 133 种,0.04 ha 样地平均物种数为 38.8 ± 8.6 ,其中常绿阔叶植物 72 种,落叶阔叶植物 59 种,针叶植物 2 种,次生林样地内物种数显著高于老龄林($P < 0.05$, Wilcoxon 秩和检验)。

次生林和老龄林均具有明显优势种,且物种组成较为相似(表 1)。二者的差异主要体现在优势种的次序,老龄林重要值前三位的乔木为甜槠、木荷和马尾松,灌木为马银花(*Rhododendron ovatum*)、格药桉(*Eurya muricata*)和鹿角杜鹃(*Rhododendron latoucheae*);次生林重要值前三位的乔木为木荷、甜槠和青冈(*Cyclobalanopsis glauca*),灌木为欏木(*Loropetalum chinense*)、格药桉和鹿角杜鹃。值得注意的是,杉木(*Cunninghamia lanceolata*)在次生林

表 1 古田山国家级自然保护区老龄和次生常绿阔叶林重要值排名前十的木本植物

Table 1 Importance value (IV) of the top 10 dominant species in old-growth and secondary evergreen broad-leaved forests in Gutianshan National Nature Reserve

排名 Rank	老龄林 Old-growth forest	重要值 IV	排名 Rank	次生林 Secondary forest	重要值 IV
1	甜槠 <i>Castanopsis eyrei</i>	17.22	1	木荷 <i>Schima superba</i>	16.86
2	木荷 <i>Schima superba</i>	9.09	2	甜槠 <i>Castanopsis eyrei</i>	11.34
3	马银花 <i>Rhododendron ovatum</i>	5.00	3	格药桉 <i>Eurya muricata</i>	4.25
4	格药桉 <i>Eurya muricata</i>	3.63	4	欏木 <i>Loropetalum chinense</i>	3.80
5	马尾松 <i>Pinus massoniana</i>	3.09	5	青冈 <i>Cyclobalanopsis glauca</i>	3.42
6	虎皮楠 <i>Daphniphyllum oldhami</i>	3.07	6	石栎 <i>Lithocarpus glaber</i>	3.26
7	红楠 <i>Machilus thunbergii</i>	2.54	7	马尾松 <i>Pinus massoniana</i>	2.46
8	青冈 <i>Cyclobalanopsis glauca</i>	2.45	8	鹿角杜鹃 <i>Rhododendron latoucheae</i>	2.23
9	毛花连蕊茶 <i>Camellia trichoclada</i>	2.41	9	杉木 <i>Cunninghamia lanceolata</i>	2.22
10	鹿角杜鹃 <i>Rhododendron latoucheae</i>	2.12	10	马银花 <i>Rhododendron ovatum</i>	2.21

中的重要值排在前十位。

2.2 物种多样性和功能多样性

Wilcoxon秩和检验显示, 整体上次生林的Shannon-Wiener指数显著高于老龄林(图1A)。就垂直层次而言, 次生林灌木层的Shannon-Wiener指数显著高于老龄林, 而乔木层则显著低于老龄林, 但亚乔木层差异不显著(图2)。考虑地形影响后所选出的最优线性回归模型结果显示, 人类干扰和坡向对Shannon-Wiener指数有显著影响(表2, 附录2), 但次生林林龄与Shannon-Wiener指数并没有显著的线性相关关系(图3)。稀疏曲线显示取样个体数较少时,

次生林内单位个体包含的物种数大于老龄林, 次生林物种丰富度随个体数的增加而快速上升, 比老龄林更早达到平缓(图4)。另一方面, 次生林的功能离散度也显著高于老龄林(图1B); 但针对功能离散度的最优线性回归模型显示人类干扰的影响并不显著(表2, 附录3)。次生林所含常绿阔叶植物的相对丰富度和相对多度均低于老龄林, 落叶阔叶植物的相对丰富度高于老龄林, 而生长型和传播方式的不同功能群在次生林和老龄林所占的相对丰富度和相对多度均没有显著差异(附录4)。

Wilcoxon秩和检验发现次生林与老龄林的

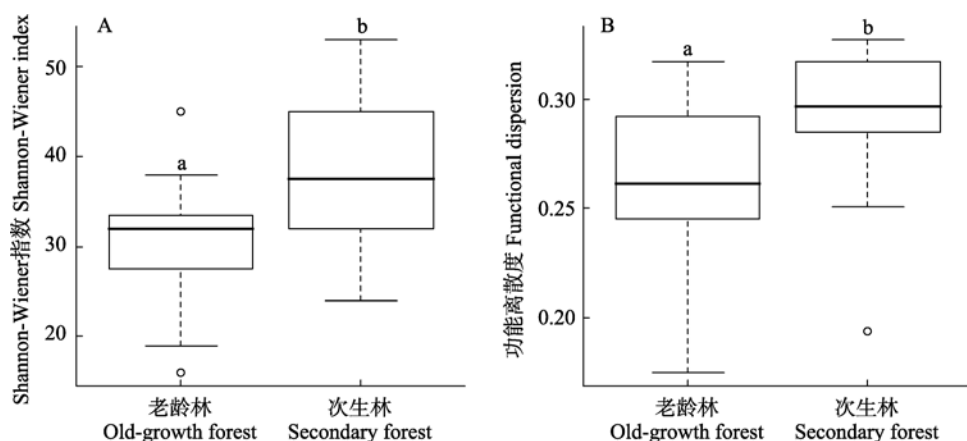


图1 古田山国家级自然保护区老龄和次生常绿阔叶林Shannon-Wiener指数(A)和功能离散度(B)的比较。若两个箱线图上方的字母不同, 则表明存在显著性差异($P_{\text{adj}} < 0.05$, Wilcoxon秩和检验, P 值通过Holm方法校正)。

Fig. 1 Comparisons of Shannon-Wiener index and functional dispersion between old-growth and secondary evergreen broad-leaved forests in Gutianshan National Nature Reserve. Different lower-case letters above the boxes indicate significant pairwise difference ($P_{\text{adj}} < 0.05$, Wilcoxon rank-sum test, P value was adjusted using the Holm method).

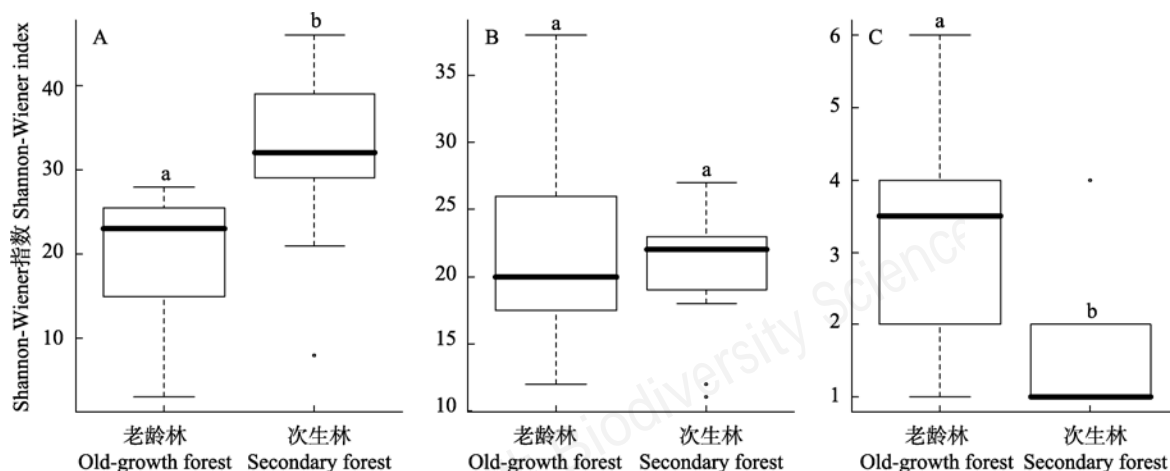


图2 古田山国家级自然保护区老龄和次生常绿阔叶林灌木层(A)、亚乔木层(B)和乔木层(C)的Shannon-Wiener指数比较。若两个箱线图上方的字母不同, 则表明存在显著性差异($P_{\text{adj}} < 0.05$, Wilcoxon秩和检验, P 值通过Holm方法校正)。

Fig. 2 Comparisons of Shannon-Wiener index of shrub layer (A), sub-tree layer (B) and tree layer (C) between old-growth and secondary evergreen broad-leaved forests in Gutianshan National Nature Reserve. Different lower-case letters above the boxes indicate significant pairwise difference ($P_{\text{adj}} < 0.05$, Wilcoxon rank-sum test, P value was adjusted using the Holm method).

表2 古田山国家级自然保护区常绿阔叶林Shannon-Wiener指数和功能离散度与环境因子的关系。*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$ 。

Table 2 Relationship between environmental factors and Shannon-Wiener index and functional dispersion of evergreen broad-leaved forests in Gutianshan National Nature Reserve. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

	Shannon-Wiener指数 Shannon-Wiener index	功能离散度 Functional dispersion
截距 Intercept	19.933***	0.1944***
人类干扰 Human disturbance	10.271**	0.0259
sin(坡向) sin(Aspect)		
cos(坡向) cos(Aspect)	-4.658*	
海拔 Elevation		0.0001
坡度 Slope		

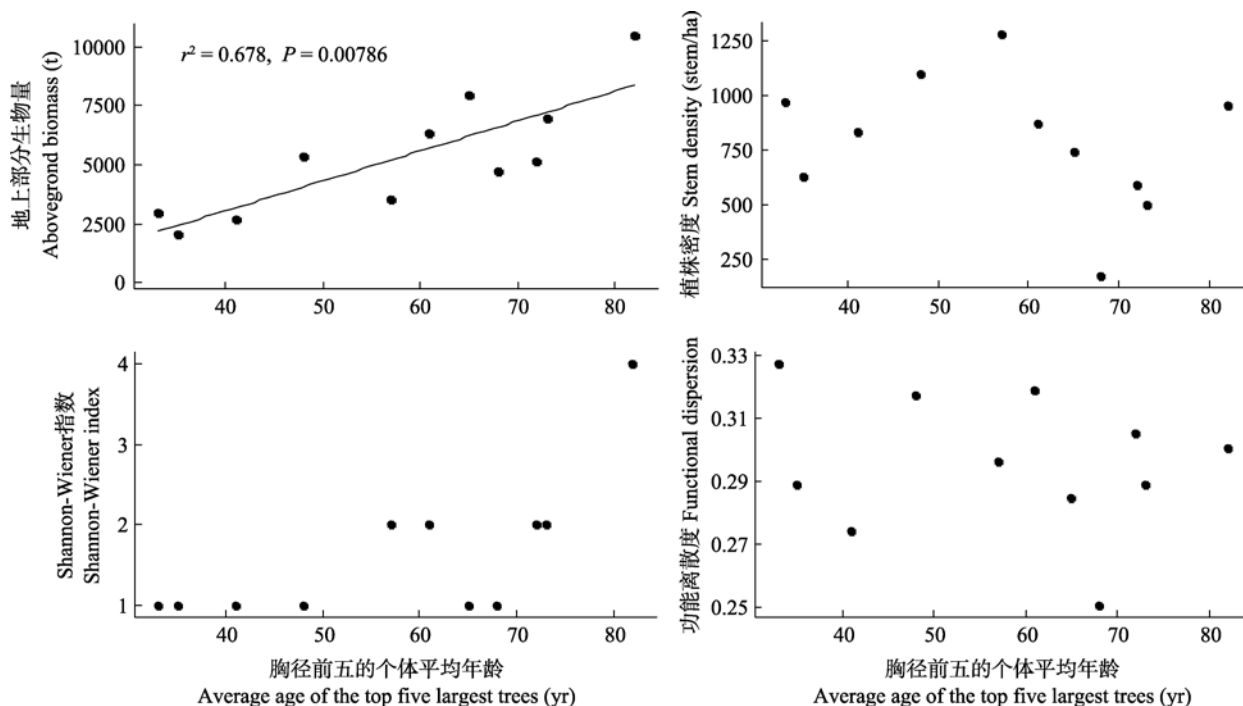


图3 古田山国家级自然保护区次生常绿阔叶林群落特征与林龄的线性回归模型结果

Fig. 3 Linear regression model results of age effects on community structure of secondary evergreen broad-leaved forests in Gutianshan National Nature Reserve

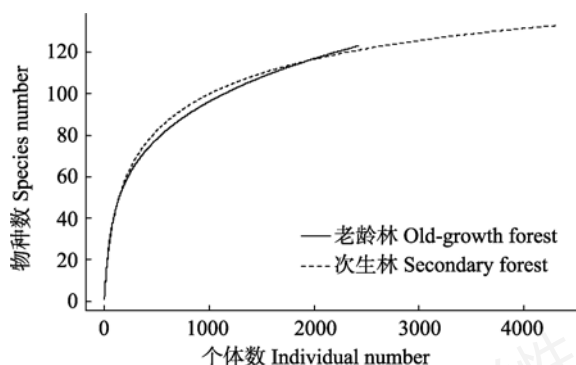


图4 古田山国家级自然保护区老龄林和次生林的物种稀疏曲线

Fig. 4 Species rarefaction curves of old-growth forest and secondary forest in Gutianshan National Nature Reserve

Bray-Curtis指数略有差异(图5A)。次生林间的Bray-Curtis指数显著低于次生林与老龄林间的Bray-Curtis指数,而老龄林间和次生林与老龄林间没有显著差异。针对功能 β 多样性的Wilcoxon秩和检验显示,次生林与老龄林间的功能Sørensen指数显著小于老龄林,但次生林与老龄林内没有显著差异(图5B)。进一步,用偏Mantel检验的多元回归方法控制地形和地理距离的影响后,发现人类干扰对物种Bray-Curtis指数和功能Sørensen指数的影响均不显著(附录5)。就垂直层次而言,次生林内灌木层的Bray-Curtis指数显著低于老龄林,乔木层则显著高于老龄林,但亚乔木层没有显著差异(图6)。

2.3 群落结构

次生林的植株密度(773.9 ± 277.9 株/ha)显著高于老龄林(404 ± 163.9 株/ha) ($P < 0.001$, Wilcoxon秩和检验)。线性回归结果显示, 控制地形影响后, 人类干扰对植株密度有显著影响(附录6, 表3)。但次生林的林龄与植株密度没有显著的线性相关性(图3)。

次生林0.04 ha样地的地上部分生物量($5.25 \pm$

2.31 t)显著低于老龄林(8.09 ± 3.04 t) ($P < 0.01$, Wilcoxon秩和检验)。次生林地上部分生物量随林龄的增加有显著增加的趋势(图3)。控制地形影响后, 人类干扰对地上生物量有显著影响(附录7, 表3)。次生林和老龄林在叶生活型、生长型和传播方式等不同功能群的生物量所占比例上均无显著差别(附录8)。另一方面, 次生林植株个体的生物量显著小于老龄林($P < 0.001$, Wilcoxon秩和检验), 但次生林个

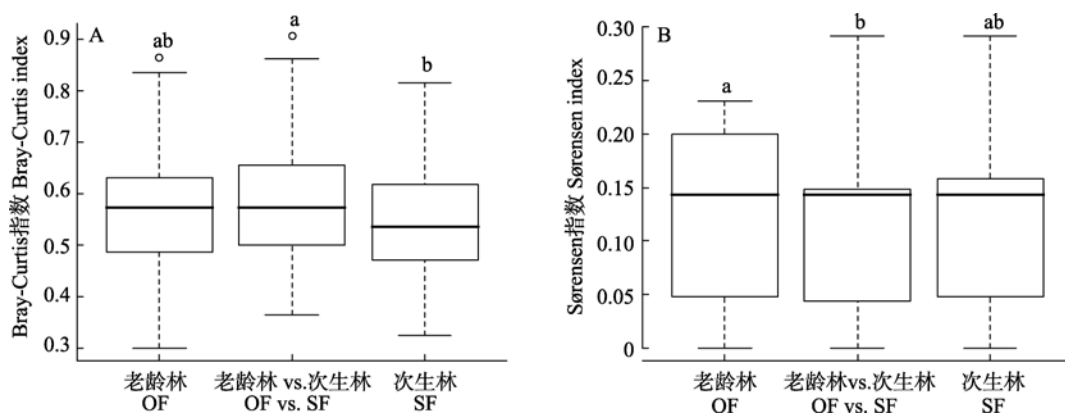


图5 古田山国家级自然保护区老龄和次生常绿阔叶林间物种Bray-Curtis指数(A)和功能Sørensen指数(B)比较。若两个箱线图上方的字母不同, 则表明存在显著性差异($P_{\text{adj}} < 0.05$, Wilcoxon秩和检验, P 值通过Holm方法校正)。

Fig. 5 Comparisons of species Bray-Curtis index (A) and functional Sørensen index (B) between old-growth and secondary evergreen broad-leaved forests in Gutianshan National Nature Reserve. Different lower-case letters above the boxes indicate significant pairwise difference ($P_{\text{adj}} < 0.05$, Wilcoxon rank-sum test, P value was adjusted using the Holm method). OF, Old-growth Forest; SF, Secondary Forest.

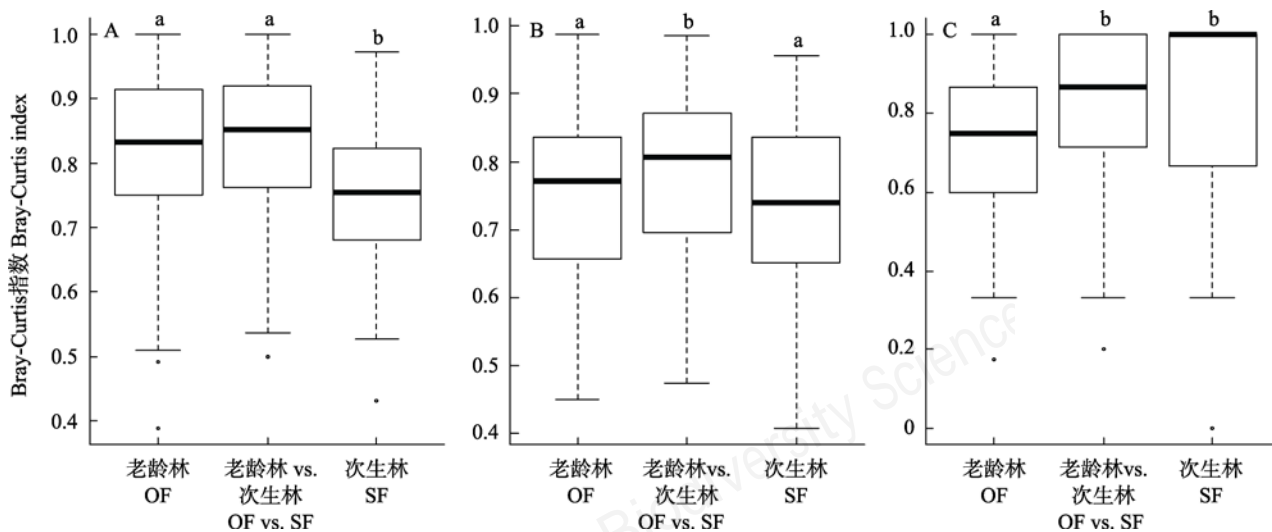


图6 古田山国家级自然保护区老龄和次生常绿阔叶林灌木层(A)、亚乔木层(B)和乔木层(C)的物种Bray-Curtis指数比较。若两个箱线图上方的字母不同, 则表明存在显著性差异($P_{\text{adj}} < 0.05$, Wilcoxon秩和检验, P 值通过Holm方法校正)。

Fig. 6 Comparisons of species Bray-Curtis index of shrub layer (A), sub-tree layer (B) and tree layer (C) between old-growth and secondary evergreen broad-leaved forests in Gutianshan National Nature Reserve. Different lower-case letters above the boxes indicate significant pairwise difference ($P_{\text{adj}} < 0.05$, Wilcoxon rank-sum test, P value was adjusted using the Holm method).

表3 环境因子对样地植株密度和地上部分生物量影响的线性回归结果。*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$ 。

Table 3 Linear regression model of environmental factors effects on aboveground biomass of each plot. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

	植株密度 Stem density	地上部分生物量 Aboveground biomass
截距 Intercept	-1.4915**	7231.301*
人类干扰 Human disturbance	1.0059***	-2881.881*
海拔 Elevation		6.135
sin (坡向) sin (Aspect)		
cos (坡向) cos (Aspect)		
坡度 Slope	-0.4319**	

体水平生物量的变异程度与老龄林无显著差异。

3 讨论

以往很多研究探讨了人类干扰对常绿阔叶林演替过程中物种多样性(例如, Aiba et al, 2001; Bruelheide et al, 2011; 徐远杰等, 2014)或谱系多样性(例如, 宋凯等, 2011; Feng et al, 2014)的影响, 但仍缺乏对同地区人类干扰对常绿阔叶林群落特征影响的综合研究(Ding et al, 2012)。本文综合比较了古田山次生和老龄常绿阔叶林的群落特征, 发现人类干扰对于常绿阔叶林产生的影响是多元的。

3.1 物种组成

次生林与老龄林的主要优势种虽然组成相似, 但各优势种重要值存在一些差异。例如, 木荷和甜槠虽然都是古田山常绿阔叶林的主要优势种(胡正华等, 2003), 但甜槠在老龄林中的重要值为木荷的近2倍, 而在次生林中则低于木荷。这可能是由于甜槠耐阴性较强, 在成熟林中更新能力强于木荷, 常在老龄林中占优势(徐学红等, 2005); 而木荷习性偏阳性且生长速度快, 在常绿阔叶林恢复过程中常作为先锋树种(宋永昌, 2013), 因此在次生林内的重要值更大。优势种组成的相似性说明次生林有向老龄林演替的潜力, 而其差异性则可能更多地指明了次生林演替的方向, 长期的群落监测有助于证实这个猜测。杉木是亚热带地区很好的用材树种, 在古田山保护区成立前, 当地村民大面积营造杉木人工林, 保护区建立后人工经营逐渐消失, 有一部分演替为常绿阔叶林, 但部分杉木个体尚存, 故在古田山的次生常绿阔叶林中尚有一定优势度(钱海源等,

2018; 于明坚等, 2019)。虎皮楠(*Daphniphyllum oldhami*)和红楠(*Machilus thunbergii*)也属于耐阴种, 它们在老龄林中的重要值分别占第六和第七位, 也显示了老龄林与次生林不同的干扰历史。

3.2 物种多样性和功能多样性

次生林的Shannon-Wiener指数高于老龄林, 这与Aiba等(2001)发现日本南部常绿阔叶次生林物种 α 多样性大于老龄林吻合, 也与Wang等(2007)、农友等(2018)发现常绿阔叶林物种丰富度在演替中期达到峰值后下降的结果一致。垂直层次上, 次生林与老龄林的差异主要体现在灌木层和乔木层, 在亚乔木层则差异不显著。次生林灌木层的Shannon-Wiener指数较高, 而乔木层显著低于老龄林, 表明亚热带常绿阔叶林在演替后期会丢失一些灌木物种, 比如本研究中满山红(*Rhododendron mariesii*)、白背麸杨(*Rhus hypoleuca*)等植物在次生林中存在, 但在老龄林中未见; 而一些乔木层的演替后期优势种, 如钩栲(*Castanopsis tibetana*)、米槠(*Castanopsis carlesii*)等物种只出现在老龄林, 而未见于次生林。进一步, 次生林的功能离散度显著高于老龄林, 反映了在演替后期常绿阔叶林中具有某些功能性状特征的物种可能会减少。物种稀疏曲线表明, 老龄林和次生林均受到生境异质性的较大影响(Stein et al, 2014)。次生林与老龄林物种丰富度的差异与取样尺度有关, 大面积的老龄林可能比次生林蕴含着更高的物种丰富度, 体现了森林群落物种多样性的空间异质性(芦伟等, 2018)。因此本研究中次生林 α 多样性显著高于老龄林可能是取样面积(0.04 ha)较小所致。

另一方面, 物种Bray-Curtis指数的比较结果显示次生林与老龄林间的物种组成差异显著高于次生林内。在不同垂直层次, 次生林与老龄林的物种Bray-Curtis指数也表现出显著差异。老龄林间的灌木层物种组成差异较大, 表明在常绿阔叶林演替进程的后期, 异质性生境条件对常绿阔叶林群落灌木层的物种组成有较大影响; 同时, 次生林间乔木层的物种Bray-Curtis指数显著高于老龄林, 说明随着林龄增长, 次生林间乔木层物种组成差异趋于减小(Ding et al, 2012; Purschke et al, 2013)。但控制地形和地理距离的影响后, 人类干扰对物种Bray-Curtis指数和功能Sørensen指数的影响均不显著, 说明次生林与老龄林物种和功能 β 多样性的差异主要受到环境而非干扰历史的影响。

3.3 群落结构

生物量是重要的生态系统功能(Cardinale et al, 2011), 次生林在群落水平和个体水平的生物量均显著低于老龄林, 说明次生林的生态系统功能低于老龄林。次生林比老龄林具有更高的植株密度, 表明老龄林的生物量更多来源于大植株个体的贡献。另一方面, 随着林龄的增加, 次生林地上部分生物量呈增长趋势, 表明人类干扰对地上部分生物量有显著影响。本研究结果验证了Ali等(2016)认为林龄是中国东部亚热带次生林地上部分生物量的主要影响因素的观点, 我们由此推测, 在次生林向老龄林的演替进程中, 生物量在个体水平和群落水平都将有显著增长。

综上, 本研究显示人类干扰对古田山的常绿阔叶林产生了多角度的影响: 亚热带常绿阔叶林在受到干扰后, 次生林整体的物种组成和功能组成恢复较快, 但就不同垂直层次而言, 其灌木层和乔木层的物种组成特征仍与老龄林有差异; 并且次生林植株密度和地上部分生物量等群落结构特征与老龄林也有显著差异。因此, 次生林在演替后期可能会减少部分物种和功能 α 多样性, 将补充更典型的常绿阔叶林优势种, 形成更低的植株密度, 并提高地上部分生物量。

致谢: 浙江大学王月霞、骆杨青等同学参与古田山野外调查、数据录入等工作, 郑朝宗教授对植物识别进行指导, 仲磊和巫东豪博士生对本文数据分析提供宝贵建议; 赖正标、赖祯熙等师傅在野外调查工作中付出辛勤劳动, 在此致谢。同时, 向附录引用的地上生物量计算公式的研究者致谢!

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附录 Supplementary Material

附录1 主要物种地上部分生物量异速生长方程

Appendix 1 Allometric equations for aboveground biomass of main species

<http://www.biodiversity-science.net/fileup/PDF/2019059-1.pdf>

附录2 环境因子对Shannon-Wiener指数影响的线性回归模型选择结果

Appendix 2 Results of comparison of linear model of environmental factors effects on Shannon-Wiener index of each plot

<http://www.biodiversity-science.net/fileup/PDF/2019059-2.pdf>

附录3 环境因子对功能离散度影响的线性回归模型选择结果

Appendix 3 Results of comparison of linear model of environmental factors effects on functional dispersion of each plot

<http://www.biodiversity-science.net/fileup/PDF/2019059-3.pdf>

附录4 次生与老龄常绿阔叶林3种功能性状的相对丰富度和相对多度比较

Appendix 4 Comparisons of relative richness and relative abundance of three functional traits between secondary and old-growth evergreen broad-leaved forests

<http://www.biodiversity-science.net/fileup/PDF/2019059-4.pdf>

附录5 古田山常绿阔叶林物种组成和功能组成与环境因子的关系

Appendix 5 Relationship between environmental factors and species composition and functional composition of evergreen broad-leaved forest in Gutianshan National Nature Reserve

<http://www.biodiversity-science.net/fileup/PDF/2019059-5.pdf>

附录6 环境因子对样地植株密度影响的线性回归模型选择结果

Appendix 6 Results of comparison of linear model of environmental factors effects on stem density of each plot

<http://www.biodiversity-science.net/fileup/PDF/2019059-6.pdf>

附录7 环境因子对样地地上部分生物量影响的线性回归模型选择结果

Appendix 7 Results of comparison of linear model of environmental factors effects on aboveground biomass of each plot

<http://www.biodiversity-science.net/fileup/PDF/2019059-7.pdf>

附录8 次生林与老龄林间3种功能性状地上部分生物量所占比例的比较

Appendix 8 Comparisons of proportion of total aboveground biomass between secondary and old-growth evergreen broad-leaved forests

<http://www.biodiversity-science.net/fileup/PDF/2019059-8.pdf>

张田田, 王璇, 任海保, 余建平, 金毅, 钱海源, 宋小友, 马克平, 于明坚. 浙江古田山次生与老龄常绿阔叶林群落特征的比较. 生物多样性, 2019, 27 (10): 1069–1080. <http://www.biodiversity-science.net/CN/10.17520/biods.2019059>

附录1 主要物种地上部分生物量异速生长方程。AGB: 地上部分生物量; D: 胸径; H: 树高。
Appendix 1 Allometric equations for aboveground biomass of main species. AGB, Aboveground biomass (kg); D, Diameter at breast height (cm); H, Tree height (m).

物种 Species	方程 Equations	R^2	参考文献 Reference
木荷 <i>Schima superba</i>	$AGB = 0.07103 \times (D^2 \times H)^{0.91}$	0.96	Lin et al, 2012
马尾松 <i>Pinus massoniana</i>	$AGB = 0.1359 \times (D^2 \times H)^{0.79}$	0.91	Lin et al, 2012
青冈 <i>Cyclobalanopsis glauca</i>	$AGB = 0.08542 \times (D^2 \times H)^{0.91}$	0.93	Lin et al, 2012
米槠 <i>Castanopsis carlesii</i>	$AGB = 0.0453 \times D^{1.716} + 0.037 \times D^{2.4599} + 0.1565 \times D^{2.2772}$	0.98	Lin et al, 2012
小叶青冈 <i>Cyclobalanopsis myrsinifolia</i>	$AGB = 0.1019 \times e^{0.1387D} + 0.0358 \times D^{2.4556} + 0.3152 \times D^{2.016}$	0.96	Lin et al, 2012
甜槠 <i>Castanopsis eyrei</i>	$AGB = 0.06491 \times (D^2 \times H)^{0.92}$	0.98	Lin et al, 2012
石栎 <i>Lithocarpus glaber</i>	$AGB = 0.04268 \times (D^2 \times H)^{0.98}$	0.99	Lin et al, 2012
栎属 <i>Quercus</i>	$AGB = 0.1199 \times (D^2 \times H)^{0.8509}$	0.99	Lin et al, 2012
拟赤杨 <i>Alniphyllum fortunei</i>	$AGB = 0.8003 \times (D^2 \times H)^{0.5276} + 0.1768 \times (D^2 \times H)^{0.5648} + 0.564 \times (D^2 \times H)^{0.3191}$	0.95	Lin et al, 2012
槲木 <i>Loropetalum chinense</i>	$AGB = 0.1599 \times D^{2.35119}$	0.99	Lin et al, 2012
马银花 <i>Rhododendron ovatum</i>	$AGB = 0.3323 \times D^{1.7874}$	0.96	Lin et al, 2012
鹿角杜鹃 <i>Rhododendron latoucheae</i>	$AGB = 0.2212 \times D^{1.9932}$	0.92	Lin et al, 2012
其他物种 Other species	$AGB = 0.09459 \times (D^2 \times H)^{0.87}$	0.91	Lin et al, 2012
杉木 <i>Cunninghamia lanceolata</i>	$AGB = 0.0508 \times D^{2.665}$	0.952	Chen et al, 2013
栲 <i>Castanopsis fargesii</i>	$AGB = 0.05115184 \times (D^2 \times H)^{0.9280}$	0.998	杨同辉等, 2007
细叶青冈 <i>Cyclobalanopsis gracilis</i>	$AGB = 0.08151426 \times (D^2 \times H)^{0.9598}$	0.998	杨同辉等, 2007
苦槠 <i>Castanopsis sclerophylla</i>	$AGB = 0.060143 \times (D^2 \times H)^{0.9274}$	0.961	刘其霞等, 2005
枫香树 <i>Liquidambar formosana</i>	$AGB = 0.034514 \times (D^2 \times H)^{1.0037}$	0.955	刘其霞等, 2005
格药枰 <i>Eurya muricata</i>	$AGB = 0.7059 \times 0.313375 \times \pi \times D^2$	0.939	Ali et al, 2014
窄基红褐枰 <i>Eurya rubiginosa</i> var. <i>attenuata</i>	$AGB = 0.7 \times 0.30405 \times \pi \times D^2$	0.964	Ali et al, 2014
毛花连蕊茶 <i>Camellia trichoclada</i>	$AGB = 0.7234 \times 0.30405 \times \pi \times D^2$	0.914	Ali et al, 2014
老鼠矢 <i>Symplocos stellaris</i>	$AGB = 0.7848 \times (-1 + 0.39728 \times \pi \times D^2)$	0.926	Ali et al, 2014
山矾 <i>Symplocos sumuntia</i>	$AGB = 0.7797 \times 0.2062 \times \pi \times D^2$	0.942	Ali et al, 2014
江南越桔 <i>Vaccinium mandarinorum</i>	$AGB = 0.7 \times 0.29192 \times \pi \times D^2$	0.978	Ali et al, 2014
杨梅 <i>Myrica rubra</i>	$AGB = 0.7 \times (-6 + 1.35732 \times \pi \times D^2)$	0.997	Ali et al, 2014
赤楠 <i>Syzygium buxifolium</i>	$AGB = 0.7 \times (0.04 + 0.28075 \times \pi \times D^2)$	0.947	Ali et al, 2014
钩栲 <i>Castanopsis tibetana</i>	$AGB = 0.094 \times (D^2 \times H)^{0.8799}$	0.97	左舒翟等, 2015
猴欢喜 <i>Sloanea sinensis</i>	$AGB = 0.1614 \times (D^2 \times H)^{0.7802}$	0.92	左舒翟等, 2015
虎皮楠 <i>Daphniphyllum oldhami</i>	$AGB = 0.0975 \times (D^2 \times H)^{0.8657}$	0.94	左舒翟等, 2015
乳源木莲 <i>Manglietia fordiana</i>	$AGB = 0.0584 \times (D^2 \times H)^{0.9003}$	0.95	左舒翟等, 2015
杨桐 <i>Adinandra millettii</i>	$AGB = e^{(-3.83 + 1.99 \times \ln(D) + 0.860 \times \ln(H))}$	0.99	Ali et al, 2015
柿 <i>Diospyros kaki</i>	$AGB = e^{(-5.57 + 1.89 \times \ln(D) + 1.16 \times \ln(H) + 2.72 \times 0.53)}$	0.99	Ali et al, 2015
红楠 <i>Machilus thunbergii</i>	$AGB = e^{(-3.51 + 2.59 \times \ln(D))}$	0.99	Ali et al, 2015
褐叶青冈 <i>Cyclobalanopsis stewardiana</i>	$AGB = e^{(-3.67 + 3.07 \times \ln(D))}$	0.98	Ali et al, 2015
樟 <i>Cinnamomum camphora</i>	$AGB = 0.175374 \times (D^2 \times H)^{0.819874} - 0.184736 \times (D^2 \times H)^{0.616421}$	0.96	姚迎九等, 2003
水杉 <i>Metasequoia glyptostroboides</i>	$AGB = 0.06291 \times D^{2.4841}$	0.972	庄红蕾等, 2012

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附录2 环境因子对Shannon-Wiener指数影响的线性回归模型选择结果。最优模型以粗体标出。AICc, 根据样本数量修正过后的AIC值; delta, 模型与AICc最小模型间的AICc值差异; weight, 模型为最优模型的概率。
Appendix 2 Results of comparison of linear model of environmental factors effects on Shannon-Wiener index of each plot. The best supported model is in bold. AICc, AIC corrected by limited sample size; delta, difference in AICc between the model and the parsimonious model; weight, possibility of the model being the best supported model.

截距	cos(坡向)	海拔	sin(坡向)	坡度	人类干扰	自由度	AICc	delta	weight
Intercept	cos(Aspect)	Elevation	sin(Aspect)	Slope	Human disturbance	df			
20.06	-4.658				10.27	4	208.8	0	0.252
26.66	-5.208			-0.148	9.153	5	209.4	0.6	0.187
13.43	-4.994	0.0106			10.37	5	210.3	1.49	0.12
22.95					7.919	3	211.1	2.26	0.081
20.09	-4.655		0.137		10.26	5	211.7	2.94	0.058
21.51	-5.303	0.0063		-0.120	9.423	6	212.2	3.36	0.047
26.81	-5.207		0.378	-0.149	9.107	6	212.6	3.78	0.038
27.75				-0.102	6.954	4	212.8	4.02	0.034
18.39		0.0075			7.871	4	213.1	4.35	0.029
13.33	-5	0.0107	-0.179		10.39	6	213.5	4.69	0.024
23			0.218		7.9	4	213.8	4.96	0.021
40.43				-0.175		3	214.6	5.83	0.014
34.69						2	214.7	5.88	0.013
42.39	-3.495			-0.221		4	214.8	6.05	0.012
24.12		0.0044		-0.082	7.116	5	215.6	6.78	0.009
21.66	-5.301	0.0062	0.152	-0.121	9.399	7	215.7	6.87	0.008
27.9			0.392	-0.104	6.906	5	215.7	6.93	0.008
18.39		0.0075	-2.000E-04		7.871	5	216.1	7.29	0.007
34.98	-2.293					3	216.1	7.35	0.006
29.75		0.0081				3	216.6	7.81	0.005
34.75			0.625			3	217.1	8.32	0.004
40.57			0.834	-0.176		4	217.2	8.43	0.004
39.23		0.0016		-0.168		4	217.3	8.52	0.004
42.56	-3.514		0.919	-0.223		5	217.6	8.84	0.003
40.74	-3.511	0.0022		-0.211		5	217.7	8.95	0.003
29.05	-2.58	0.0097				4	218	9.2	0.003
24.36		0.0043	0.236	-0.084	7.081	6	218.8	9.98	0.002
35.05	-2.298		0.645			4	218.8	9.99	0.002
29.91		0.0079	0.396			4	219.3	10.49	0.001
39.78		0.001	0.798	-0.172		5	220.2	11.36	0.001
41.34	-3.524	0.0016	0.864	-0.216		6	220.8	12.03	0.001
29.2	-2.577	0.01	0.369			5	220.9	12.12	0.001

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附录3 环境因子对功能离散度影响的线性回归模型选择结果。最优模型以粗体标出。AICc, 根据样本数量修正过后的AIC值; delta, 模型与AICc最小模型间的AICc值差异; weight, 模型为最优模型的概率。

Appendix 3 Results of comparison of linear model of environmental factors effects on functional dispersion of each plot. The best supported model is in bold. AICc, AIC corrected by limited sample size; delta, difference in AICc between the model and the parsimonious model; weight, possibility of the model being the best supported model.

截距	cos(坡向)	海拔	sin(坡向)	坡度	人类干扰	自由度	AICc	delta	weight
Intercept	cos(Aspect)	Elevation	sin(Aspect)	Slope	Human disturbance	df			
0.194		7.22E-05			0.026	4	-107.2	0	0.135
0.238					0.026	3	-106.5	0.67	0.097
0.303				-7.889E-04		3	-105.7	1.47	0.065
0.232		7.38E-05				3	-105.5	1.62	0.06
0.265				-5.711E-04	0.021	4	-105.5	1.68	0.059
0.199		6.81E-05	0.008		0.025	5	-105	2.14	0.046
0.277						2	-105	2.19	0.045
0.24			0.01		0.025	4	-104.9	2.26	0.044
0.305			0.012	-8.167E-04		4	-104.6	2.53	0.038
0.215		6.11E-05		-2.918E-04	0.023	5	-104.6	2.54	0.038
0.264		5.19E-05		-5.715E-04		4	-104.4	2.8	0.033
0.197	0.003	7.04E-05			0.024	5	-104.3	2.83	0.033
0.241	0.005				0.024	4	-104.1	3.06	0.029
0.269			0.011	-6.102E-04	0.02	5	-104	3.19	0.028
0.276	0.011					3	-103.8	3.33	0.026
0.234	0.009	6.83E-05				4	-103.8	3.36	0.025
0.236		6.91E-05	0.009			4	-103.7	3.4	0.025
0.278			0.012			3	-103.7	3.44	0.024
0.299	0.007			-6.998E-04		4	-103.5	3.61	0.022
0.272		4.42E-05	0.011	-6.281E-04		5	-102.7	4.45	0.015
0.265	0.003			-5.440E-04	0.02	5	-102.7	4.5	0.014
0.224		5.41E-05	0.009	-3.559E-04	0.022	6	-102.4	4.74	0.013
0.277	0.011		0.011			4	-102.4	4.75	0.013
0.244	0.005		0.01		0.023	5	-102.3	4.86	0.012
0.301	0.007		0.012	-7.305E-04		5	-102.2	4.92	0.012
0.261	0.006	5.08E-05		-4.918E-04		5	-101.9	5.21	0.01
0.202	0.003	6.61E-05	0.008		0.024	6	-101.9	5.22	0.01
0.238	0.009	6.34E-05	0.01			5	-101.8	5.33	0.009
0.216	0.002	6.04E-05		-2.761E-04	0.022	6	-101.5	5.69	0.008
0.27	0.003		0.011	-5.828E-04	0.018	6	-100.9	6.27	0.006
0.269	0.006	4.32E-05	0.011	-5.498E-04		6	-100	7.13	0.004
0.225	0.002	5.33E-05	0.009	-3.396E-04	0.021	7	-99	8.19	0.002

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附录4 次生与老龄常绿阔叶林3种功能性状的相对丰富度和相对多度比较(老龄林/次生林)。*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$ 。

Appendix 4 Comparisons of relative richness and relative abundance of three functional traits between secondary and old-growth evergreen broad-leaved forests (Old-growth forests/ Secondary forests). *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

	叶生活型 Leaf life forms			生长型 Growth forms		传播方式 Dispersal vector		
	常绿阔叶	落叶阔叶	针叶	乔木	灌木	自身传播	风力传播	动物传播
	Evergreen broad-leaved plant	Deciduous broad-leaved plant	Needle plant	Tree	Shrub	Autochory	Anemochory	Zoochory
相对丰富度	75.71/66.44**	21.97/31.44**	2.08/3.57	53.42/51.32	46.58/48.68	25.49/23.28	20.59/17.81	53.92/58.91*
Relative richness (%)								
相对多度	87.33/81.70	11.28/15.75	1.70/4.62	44.49/53.84	50.51/46.16	25.69/27.39	26.94/20.53	47.37/52.08
Relative abundance (%)								

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附录5 古田山常绿阔叶林物种组成和功能组成与环境因子的关系。*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$ 。

Appendix 5 Relationship between environmental factors and species composition and functional composition of evergreen broad-leaved forest in Gutianshan National Nature Reserve. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

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变量 Variables	物种组成 Species composition	功能组成 Functional composition
截距 Intercept	0.544	0.131
地理距离 Geographical distance	−0.001	−0.004
海拔 Elevation	8.530E-05	4.000E-07
坡度 Slope	−3.483E-04	7.350E-05
cos(坡向) cos (Aspect)	−0.001	−0.002
sin(坡向) sin(Aspect)	0.01	−0.004
人类干扰 Human disturbance	0.027*	0.004

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附录6 环境因子对样地植株密度影响的线性回归模型选择结果。最优模型以粗体标出。AICc, 根据样本数量修正过后的AIC值; delta, 模型与AICc最小模型间的AICc值差异; weight, 模型为最优模型的概率。

Appendix 6 Results of comparison of linear model of environmental factors effects on stem density of each plot.

The best supported model is in bold. AICc, AIC corrected by limited sample size; delta, difference in AICc between the model and the parsimonious model; weight, possibility of the model be the best supported model.

截距	cos(坡向)	海拔	sin(坡向)	坡度	人类干扰	自由度	AICc	delta	weight
Intercept	cos(Aspect)	Elevation	sin(Aspect)	Slope	Human disturbance	df			
-1.491				-0.432	1.006	4	65.4	0	0.314
-1.437			0.201	-0.448	0.969	5	65.4	0	0.314
-1.396		-0.109	0.217	-0.497	0.942	6	67.8	2.47	0.092
-1.468		-0.069		-0.462	0.99	5	68	2.67	0.083
-1.504	-0.015			-0.435	1.014	5	68.3	2.93	0.073
-1.449	-0.014		0.201	-0.451	0.977	6	68.5	3.2	0.064
-1.476	-0.01	-0.068		-0.464	0.996	6	71.2	5.87	0.017
-1.402	-0.006	-0.108	0.217	-0.498	0.945	7	71.3	5.98	0.016
-1.885					1.271	3	72.5	7.2	0.009
-1.852			0.168		1.249	4	73.8	8.46	0.005
-1.878		0.114			1.267	4	74.6	9.25	0.003
-1.821	0.065				1.228	4	75.1	9.72	0.002
7.67E-17			0.242	-0.604		4	75.7	10.36	0.002
7.02E-17				-0.592		3	75.7	10.39	0.002
-1.849		0.095	0.157		1.247	5	76.3	10.94	0.001
-1.785	0.068		0.169		1.204	5	76.5	11.19	0.001
7.53E-17		-0.177	0.267	-0.677		5	77.4	12.02	0.001
-1.830	0.049	0.107			1.234	5	77.4	12.09	0.001
6.95E-17	0.128			-0.557		4	77.8	12.41	0.001
6.86E-17		-0.132		-0.645		4	77.8	12.44	0.001
7.60E-17	0.123		0.239	-0.571		5	78	12.61	0.001
-1.795	0.054	0.088	0.159		1.21	6	79.4	14.01	0
7.44E-17	0.128	-0.181	0.265	-0.644		6	79.8	14.44	0
6.78E-17	0.133	-0.137		-0.611		5	80	14.62	0
-3.35E-17						2	85.7	20.39	0
-2.21E-17	0.278					3	85.9	20.57	0
-2.97E-17			0.211			3	86.9	21.57	0
-1.84E-17	0.276		0.209			4	87.2	21.87	0
-2.30E-17		0.127				3	87.8	22.42	0
-1.51E-17	0.265	0.09				4	88.4	23.02	0
-2.14E-17		0.103	0.199			4	89.3	23.96	0
-1.35E-17	0.267	0.066	0.201			5	90	24.67	0

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附录7 环境因子对样地地上部分生物量影响的线性回归模型选择结果。最优模型以粗体标出。AICc, 根据样本数量修正过后的AIC值; delta, 模型与AICc最小模型间的AICc值差异; weight, 模型为最优模型的概率。

Appendix 7 Results of comparison of linear model of environmental factors effects on aboveground biomass of each plot. The best supported model is in bold. AICc, AIC corrected by limited sample size; delta, difference in AICc between the model and the parsimonious model; weight, possibility of the model be the best supported model.

截距	cos(坡向)	海拔	sin(坡向)	坡度	人类干扰	自由度	AICc	delta	weight
Intercept	cos(Aspect)	Elevation	sin(Aspect)	Slope	Human disturbance	df			
7,231		6.135			-2,882	4	545.7	0	0.282
10,930					-2,843	3	547	1.33	0.145
13,050				-45.09	-3,267	4	548	2.3	0.089
7,001		6.352	-437.3		-2,845	5	548.2	2.57	0.078
8,668		5.355		-20.62	-3,071	5	548.3	2.6	0.077
7,426	195.7	6.014			-2,980	5	548.5	2.86	0.068
11,170	385.9				-3,038	4	549.4	3.75	0.043
10,880			-253.8		-2,820	4	549.6	3.93	0.04
13,090	225.7			-43.11	-3,363	5	550.8	5.14	0.022
12,980			-179.2	-44.47	-3,246	5	550.9	5.19	0.021
8,277		5.649	-386.9	-17.93	-3,014	6	551.2	5.52	0.018
3,072		5.949				3	551.3	5.62	0.017
7,186	182.1	6.236	-430.8		-2,937	6	551.4	5.7	0.016
8,740	145.4	5.305		-19.57	-3,134	6	551.4	5.77	0.016
6,719						2	551.7	6.03	0.014
11,120	382.1		-247.1		-3,014	5	552.2	6.58	0.01
2,838		6.241	-580.5			4	553.5	7.83	0.006
2,937	-497.9	6.274				4	553.5	7.86	0.006
2,150		6.577		16.33		4	553.8	8.15	0.005
13,020	225.3		-178.6	-42.49	-3,341	6	554	8.29	0.004
6,681		-399				3	554	8.32	0.004
6,759	-313.4					3	554	8.36	0.004
7,089			-11.23			3	554.1	8.44	0.004
8,349	140.1	5.599	-384.7	-16.94	-3,075	7	554.7	9	0.003
2,699	-502.7	6.571	-585.7			5	556	10.29	0.002
1,715		7.015	-626.2	19.57		5	556.2	10.52	0.001
2,344	-450.6	6.655		10.73		5	556.4	10.73	0.001
6,721	-310.7		-396.3			4	556.5	10.85	0.001
7,315	-403.5			-16.54		4	556.5	10.88	0.001
7,023			-386.7	-10.37		4	556.6	10.95	0.001
1,910	-441.1	7.086	-617.9	14.04		6	559	13.37	0
7,247	-395.8		-377.1	-15.59		5	559.3	13.63	0

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附录8 次生林与老龄林间3种功能性状地上部分生物量所占比例的比较(%)
Appendix 8 Comparisons of proportion of total aboveground biomass between secondary and old-growth evergreen broad-leaved forests (%)

	叶生活型 Leaf life forms			生长型 Growth forms		传播方式 Dispersal vector		
	常绿阔叶 Evergreen broad-leaved plant	落叶阔叶 Deciduous broad-leaved plant	针叶 Needle plant	乔木 Tree	灌木 Shrub	动物传播 Zoochory	风力传播 Anemochory	自身传播 Autochory
老龄林 Old-growth forest	86.37	9.55	4.08	78.47	21.53	66.67	6.01	27.32
次生林 Secondary forest	83.27	11.64	6.04	87.31	12.69	64.83	6.66	28.51