

古田山不同干扰程度森林的群落恢复动态

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摘要: 森林采伐后次生林的恢复过程对于生物多样性的保护和生态系统功能的重建具有重要意义。作者以古田山不同干扰程度的12个1 ha 森林样地为研究对象, 运用群落多元统计方法, 探讨了自然恢复过程中森林群落组成及物种多样性的动态变化及趋势。结果表明: 不同恢复阶段森林样地的群落组成存在显著性差异, 而同一恢复阶段的样地具有高度的相似性。物种丰富度随恢复进程有增加的趋势, 但各阶段差异并不显著; 物种均匀度除人工林较低以外, 其他恢复阶段之间无显著性差异。不同恢复阶段研究样地的群落组成及物种多样性的差异主要存在于林冠层。灌木及更新层具有各自的指示种, 人工林的指示种为落叶灌木或阳性乔木, 幼龄次生林的指示种为常绿灌木或小乔木, 老次生林的指示种为亚乔木层常绿树种, 老龄林的指示种为林冠层树种。上述结果表明古田山不同人为干扰程度森林群落的物种多样性具有较强的自我恢复能力。尽管物种组成难以预测, 但处于同一恢复阶段的森林, 其幼树的生活型组成呈现出一致的变化趋势。

关键词: 次生林恢复, 常绿阔叶林, 群落组成, 物种多样性, 人为干扰, 古田山自然保护区

Recovery dynamics of secondary forests with different disturbance intensity in the Gutianshan National Nature Reserve

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Abstract: Understanding the underlying processes of secondary forest recovery after disturbances such as logging is essential for biodiversity conservation and ecosystem rehabilitation. We surveyed 12 forest plots (1 ha in size) with different extents of anthropogenic disturbances in the Gutianshan National Nature Reserve and explored the community dynamics of secondary forest recovery by applying multivariate statistical analysis. We found significant differences in community composition among various recovery phases, whereas high similarities of community composition were observed within the same recovery phase. No significant difference in species richness was observed among recovery stages, but species richness tended to increase during the recovery process. Species evenness in Chinese fir forests was relatively low whereas no significant difference occurred in other forests. The main differences in community composition and species diversity were found in the canopy layer. Respective indicator species were found in shrubs and regeneration layers during different recovery phases. The most representative indicator species were deciduous shrubs or heliophilous trees for plantation forests of Chinese fir, evergreen shrubs or small trees for young secondary forests, sub-canopy evergreen trees for old secondary forests, and canopy species for old-growth forests, respectively. Overall, species diversity recovered rigorously. Also the life-form composition of saplings in the same recovery phase presented consistent trends in spite of complex and unpredictable changes in species composition during the recovery process.

Key words: secondary forest recovery, evergreen broad-leaved forests, community composition, species diversity, anthropogenic disturbances, Gutianshan National Nature Reserve

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常绿阔叶林作为亚热带地区的地带性植被和陆地生态系统的主体, 自然资源及生物多样性丰富, 一直受到极大的关注。但由于人类活动的长期影响, 原生林几乎丧失殆尽, 现存的植被基本上处于次生演替过程之中(丁圣彦和宋永昌, 1998; 祝燕等, 2008)。次生林的恢复动态和物种维持机制是生态恢复和生物多样性保护领域的热点问题之一(Guariguata & Ostertag, 2001; Kubota *et al.*, 2005; Wang *et al.*, 2007)。

包括森林采伐在内的各种人为干扰活动是次生林恢复过程中的决定性因素(Kubota *et al.*, 2005), 其产生的效应贯穿次生林的整个恢复过程(Guariguata & Ostertag, 2001; Kassi & Decocq, 2008)。森林采伐不仅造成森林植被碳储量的锐减(Klanderud *et al.*, 2010), 还会对群落的关键组分和过程产生不同程度的影响(Cannon *et al.*, 1994; Fornwalt *et al.*, 2009)。一方面, 采伐干扰可以促进群落内幼苗定居和林分更新(Mishra *et al.*, 2004; McDonald *et al.*, 2008), 另一方面又会造成生物多样性大量丧失而必然改变植物群落属性, 如种类成分、物种密度和种群结构等(Verburg & van Eijk-Bos, 2003; Villela *et al.*, 2006), 并导致森林生态系统功能急剧下降, 甚至丧失(Bengtsson *et al.*, 2000; von Oheimb & Härdtle, 2009)。

木本植物的种类组成和多样性被认为是次生林恢复过程中变动最大的群落属性(Capers *et al.*, 2005)。在恢复早期的森林群落中占优势的物种到成熟林阶段时, 其多度会大幅下降; 而那些在成熟林中数量极多的树种在早期阶段通常并不出现或者多度较小(Saldarriaga *et al.*, 1988; Guariguata & Ostertag, 2001; DeWalt *et al.*, 2003)。次生林群落组成阶段性变动的净效应是物种多样性在恢复过程中呈现出动态变化(Saldarriaga *et al.*, 1988; Peña-Claros, 2003; Capers *et al.*, 2005)。次生林某一特定恢复阶段的物种丰富度实质上是群落对人为干扰响应的累积结果(Sagar *et al.*, 2003), 其物种组成不仅受随机因素的影响(如物种生物学特性以及种间相互作用), 还受到生物和非生物因素相互作用的制约(如植被历史和气候特征等)(Guariguata & Ostertag, 2001)。次生林物种组成是否沿着可预测的轨迹而变化, 是森林恢复生态学中的核心议题(Finegan, 1996; Chazdon *et al.*, 2007; Norden *et al.*, 2009)。

按年龄序列设置从幼林到老龄林样地是研究次生林群落恢复和树种更新过程的有效手段(Kubota *et al.*, 2005)。古田山国家级自然保护区保存有典型的中亚热带常绿阔叶林, 但核心区外的林地大多经受过不同方式和强度的人为干扰。我们选择保护区内4种不同恢复阶段的森林类型, 拟探讨以下问题: (1)随着森林群落恢复的进行, 物种组成是否越来越接近老龄林, 或存在显著性差异; (2)物种多样性水平随群落恢复进程呈现出何种趋势; (3)灌木及更新层的响应如何。

1 材料与方法

1.1 研究区概况

研究区位于浙江省开化县的古田山国家级自然保护区(118°03'49.7"–118°11'12.2" E, 29°10' 19.4"–29°17'41.4" N), 属亚热带季风气候区, 山势高峻, 山体呈东北至西南走向, 气候冬暖夏凉、雨量充沛。年平均气温15.3℃, 年平均降雨量1,963.7 mm。土壤类型主要有红壤、黄红壤、红黄壤和沼泽土, 土壤pH值在5.5–6.5之间(胡正华等, 2003)。该区森林植被发育良好, 属中亚热带常绿阔叶林, 保存有以甜槠(*Castanopsis eyrei*)、木荷(*Schima superba*)和青冈(*Cyclobalanopsis glauca*)等为主要优势种的天然常绿阔叶林。

1.2 样地设置

按照人为干扰水平和恢复时间的不同, 古田山国家级自然保护区内的森林群落可分为4种类型: (1)老龄林(old-growth forests, 以下简称OGF), 位于保护区核心区内, 林龄有100年以上, 属典型的亚热带常绿阔叶林, 包括样地02、04、10; (2)老次生林(old secondary forests, 以下简称OSF), 位于保护区缓冲区内, 皆伐后自然更新恢复, 林龄50年, 包括样地05、06、12; (3)幼龄次生林(young secondary forests, 以下简称YSF), 位于保护区缓冲区内, 50年前皆伐, 自然更新至30年左右时进行了择伐抚育, 后自然恢复至今, 包括样地03、08、09; (4)人工林(Chinese fir forests, 以下简称CFF), 位于保护区边界区域, 是砍伐后人工种植的杉木(*Cunninghamia lanceolata*)林, 林龄约20年, 包括样地01、07、11。我们于2009年参照CTFS (Centre for Tropical Forest Science)样地的设置方法, 每种森林类型取3个重复, 共建立12个1 ha(100 m × 100 m)监测样地, 各

个样地间的地形地貌基本一致(附图1), 水平距离大于200 m。对样地内的木本植物进行群落学调查, 起测胸径为1 cm, 但调查过程中同时也记录了少量略小于1 cm的个体。调查内容包括每株植物的种类、胸径、坐标、倾斜度、存活状况等, 并挂牌标记, 以便进行长期监测。

1.3 数据分析

依据所调查的树木个体的胸径将森林群落划分为3个林层: 灌木及更新层(灌木及幼树, $DBH < 5\text{ cm}$)、亚乔木层(青年树, $5\text{ cm} \leq DBH < 10\text{ cm}$)和林冠层(成年树, $DBH \geq 10\text{ cm}$)。采用下面公式计算物种的重要值(IV): $IV = (\text{相对多度} + \text{相对优势度} + \text{相对频度})/3$ 。应用聚类分析(cluster analysis)来比较样地间的物种相似性及分组情况, 应用多响应置换过程(multi-response permutation procedure, MRPP)来检验组间分离状况及组内的一致性, 采用相似性百分比(similarity percentage, SIMPER)分析对组内相似性贡献最大的优势种, 采用无度量多维标定(non-metric multidimensional scaling, NMS)来检验森林群落在恢复阶段和林层两个梯度上物种分布的变化, 用多样性指数和 k -优势度图(k -dominance plot)分别揭示森林群落整体及各林层在不同恢复阶段物种多样性(丰富度和均匀度)的变化; 用指示种分析(indicator species analysis, ISA)检测灌木及更新层中适应了各个恢复阶段的指示性树种。其中, 聚类分析、相似性百分比、无度量多维标定和 k -优势度图在PRIMER 5.0中进行, 多样性指数计算、多响应置换过程和指示种分析由PC-ORD 6.0完成。

分析前对数据进行了标准化和平方根处理, 本研究采用Bray-Curtis距离系数, 并用蒙特卡罗(Monte Carlo)方法检验多响应置换过程和指示种分析结果的统计显著性。

2 结果

2.1 群落恢复中的物种组成

样地内共记录木本植物80,644株, 隶属于53科122属192种。在51.7%相似度水平上, 12个样地可划分为人工林(CFF)、老龄林(OGF)、次生林样地3组(图1)。人工林(CFF)与其他3种森林类型差异较大, 在41.6%相似度水平上首先区分出来。老次生林(OSF)和幼龄次生林(YSF)具有较高的相似性, 但在66.1%水平上可分为两组。多响应置换过程结果表

明, 不同恢复阶段组间的物种差异显著($T = -5.4296$, $P < 0.0002$), 组内的物种组成具有高度的一致性($A = 0.6261$, $P < 0.0002$)。其中, T 是描述组间分离的检验统计量, T 为负值时的绝对值越大, 表示组间分离越强; A 是与随机预测值相比较时描述组内同质性的一致性统计量。

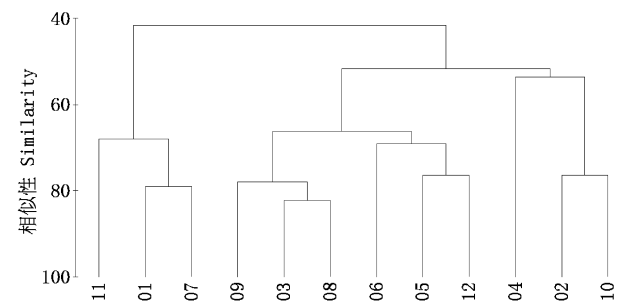


图1 古田山不同恢复阶段森林样地聚类分析图。人工林样地包括01, 07, 11; 幼龄次生林样地包括03, 08, 09; 老次生林样地包括05, 06, 12; 老龄林样地包括02, 04, 10。

Fig. 1 Hierarchical clustering of 12 forest plots during four recovery phases in the Gutianshan National Nature Reserve. Chinese fir forest plots include 01, 07, 11; Young secondary forest plots include 03, 08, 09; Old secondary forest plots include 05, 06, 12; Old-growth forest plots include 02, 04, 10.

表1列出了各阶段重要值的平均值和对组内相似性贡献率最大的前10个优势种, 其中, 杉木、山合欢(*Albizia kalkora*)、黄瑞木(*Adinandra millettii*)、柳叶蜡梅(*Chimonanthus salicifolius*)、黄檀(*Dalbergia hupeana*)和拟赤杨(*Alniphyllum fortunei*)是人工林(CFF)样地特有的优势种; 浙江红山茶(*Camellia chekiangoleosa*)、浙江新木姜子(*Neolitsea aurata* var. *chekiangensis*)、红楠(*Machilus thunbergii*)和窄基红褐柃(*Eurya rubiginosa* var. *attenuata*)等优势种仅为老龄林所有; 短尾越橘(*Vaccinium carlesii*)为幼龄次生林(YSF), 栲(*Castanopsis fargesii*)、杨梅(*Myrica rubra*)为老次生林(OSF)独有的优势种; 其余10个优势种出现在两个以上的恢复阶段, 但不同阶段的重要值及贡献率均不同。

无度量多维标定结果揭示了物种组成在恢复阶段和林层(径级)两个梯度上的变化, $Stress$ 值为0.11, 表明排序结果良好(图2)。图2中, 沿横轴, 人工林(CFF)、老次生林(OSF)、幼龄次生林(YSF)、老龄林(OGF)从左至右依次排列且界限明显; 沿纵

表1 古田山不同恢复阶段森林样地优势种重要值的平均值(%)及其对组内相似性的贡献率(%)
Table 1 Average importance values (%) of dominant species and their contributions (%) to within-group similarity

物种名 Species name	人工林 Chinese fir forests (CFF)	幼龄次生林 Young secondary forests (YSF)	老次生林 Old secondary forests (OSF)	老龄林 Old-growth forests (OGF)
杉木 <i>Cunninghamia lanceolata</i>	71.27 (25.85)			
槲木 <i>Loropetalum chinensis</i>	3.06 (4.69)	2.70 (2.89)	6.17 (4.74)	
隔药柃 <i>Eurya muricata</i>	3.02 (4.68)		2.78 (3.04)	2.80 (3.77)
马尾松 <i>Pinus massoniana</i>	1.71 (3.79)	7.37 (4.92)	14.33 (7.55)	
石栎 <i>Lithocarpus glaber</i>	1.90 (3.54)	5.32 (3.89)	7.98 (5.36)	
山合欢 <i>Albizia kalkora</i>	0.81 (2.82)			
黄瑞木 <i>Adinandra millettii</i>	0.77 (2.34)			
柳叶蜡梅 <i>Chimonanthus salicifolius</i>	3.05 (2.08)			
黄檀 <i>Dalbergia hupeana</i>	0.64 (1.98)			
拟赤杨 <i>Alniphyllum fortunei</i>	0.59 (1.95)			
甜槠 <i>Castanopsis eyrei</i>		23.76 (9.03)	5.89 (4.31)	15.69 (8.73)
米槠 <i>C. carlesii</i>		9.04 (5.27)	8.32 (3.43)	
木荷 <i>Schima superba</i>		4.56 (3.51)	11.30 (6.61)	10.95 (6.25)
马银花 <i>Rhododendron ovatum</i>		3.11 (3.26)		5.44 (4.86)
鹿角杜鹃 <i>R. latoucheae</i>		2.95 (3.18)		5.36 (5.26)
短尾越橘 <i>Vaccinium carlesii</i>		3.30 (3.04)		
青冈 <i>Cyclobalanopsis glauca</i>		2.52 (2.80)	5.39 (4.02)	5.12 (2.53)
栲 <i>Castanopsis fargesii</i>			2.18 (2.94)	
杨梅 <i>Myrica rubra</i>			2.04 (2.82)	
浙江红山茶 <i>Camellia chekiangoleosa</i>				2.43 (2.94)
浙江新木姜子 <i>Neolitsea aurata</i> var. <i>chekiangensis</i>				1.47 (2.81)
红楠 <i>Machilus thunbergii</i>				2.74 (2.46)
窄基红褐柃 <i>Eurya rubiginosa</i> var. <i>attenuata</i>				2.38 (2.49)

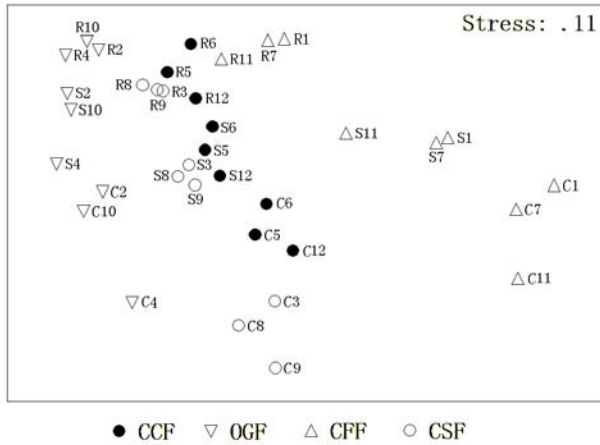


图2 古田山不同恢复阶段森林样地主林层、亚乔木层、灌木及更新层无度量多维标定图。C: 林冠层; S: 亚乔木层; R: 灌木及更新层。不同林层后面的数字为样方号。OGF, OSF, YSF, CFF同表1。

Fig. 2 Non-metric multidimensional scale (NMS) ordination of canopy, sub-canopy, and shrub and regeneration layers of 12 forest plots during four recovery phases in the Gutianshan National Nature Reserve. C, S, R represent canopy layer, sub-canopy layer, shrub and regeneration layer, respectively. Numbers are plot codes. CFF, OGF, OSF, YSF, see Table 1.

轴, 灌木及更新层、亚乔木层、林冠层从上至下依次分布。各恢复阶段的林冠层之间距离较远, 而灌木及更新层则较为聚集, 表明各恢复阶段的物种组成差异主要存在于林冠层, 而灌木及更新层物种之间的差异较小。老次生林(OSF)的3个林层之间距离最小, 老龄林(OGF)次之, 幼龄次生林(YSF)和人工林(CFF)的3个林层之间距离较大且界限明显。老次生林(OSF)和幼龄次生林(YSF)的样地相距较近, 表明经过采伐干扰后的森林样地在物种组成上具有相似性。人工林的林冠层和亚乔木层位于排序图的右侧, 与其他样地的林层相距甚远, 表现出较大的差异。

2.2 群落恢复中的物种多样性

由于各多样性指数之间的相关性, 只选取 Margalef和Pielou指数来说明恢复进程中森林群落整体物种丰富度和均匀度的变化。结果显示, 虽然物种丰富度随群落恢复进程有增加的趋势, 但差异并不显著; 就均匀度来说, 除人工林(CFF)较低且

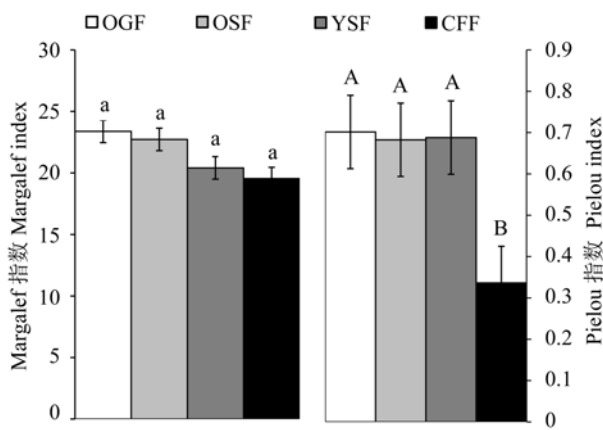


图3 古田山不同恢复阶段森林样地物种多样性指数。CFF, OGF, OSF, YSF同表1。

Fig. 3 Species diversity indices of 12 forest plots during four recovery phases in the Gutianshan National Nature Reserve. CFF, OGF, OSF, YSF, see Table 1.

差异达到极显著水平外,其他恢复阶段无显著性差异(图3)。

在林冠层,物种多样性呈现出明显的差异,其中老龄林(OGF)的累积优势度曲线位于最下方,曲线最长,表明物种丰富度和优势度均远高于其他恢复阶段。老次生林(OSF)的物种多样性低于老龄林(OGF),幼龄次生林(YSF)更低;人工林(CFF)的物种丰富度远低于其他恢复阶段,均匀度由于受到建群种杉木的影响也极低。在亚乔木层,各恢复阶段之间的物种多样性水平差距有缩小的趋势,其中老次生林(OSF)的物种丰富度和均匀度已恢复至老龄林(OGF)水平,幼龄次生林(YSF)略低,人工林(CFF)的物种丰富度也已有较大的恢复,但均匀度仍远低于其他恢复阶段。在灌木及更新层,老次生林(OSF)和幼龄次生林(YSF)的物种丰富度和均匀度都已恢复至老龄林(OGF)水平,人工林(CFF)也已具备与之相当的物种丰富度,但均匀度仍明显低于其他恢复阶段(图4)。

2.3 灌木及更新层物种对不同恢复阶段的响应

指示种分析检测出灌木及更新层中对各恢复阶段具有指示意义的物种共计37个($P < 0.05$)。其中人工林(CFF)为14种,除杉木外,主要为落叶灌木或小乔木,如椴木(*Aralia chinensis*)、紫珠(*Calli-carpa bodinieri*)、大青(*Clerodendrum cyrtophyllum*)、豆腐柴(*Premna microphylla*)及水马桑(*Weigela*

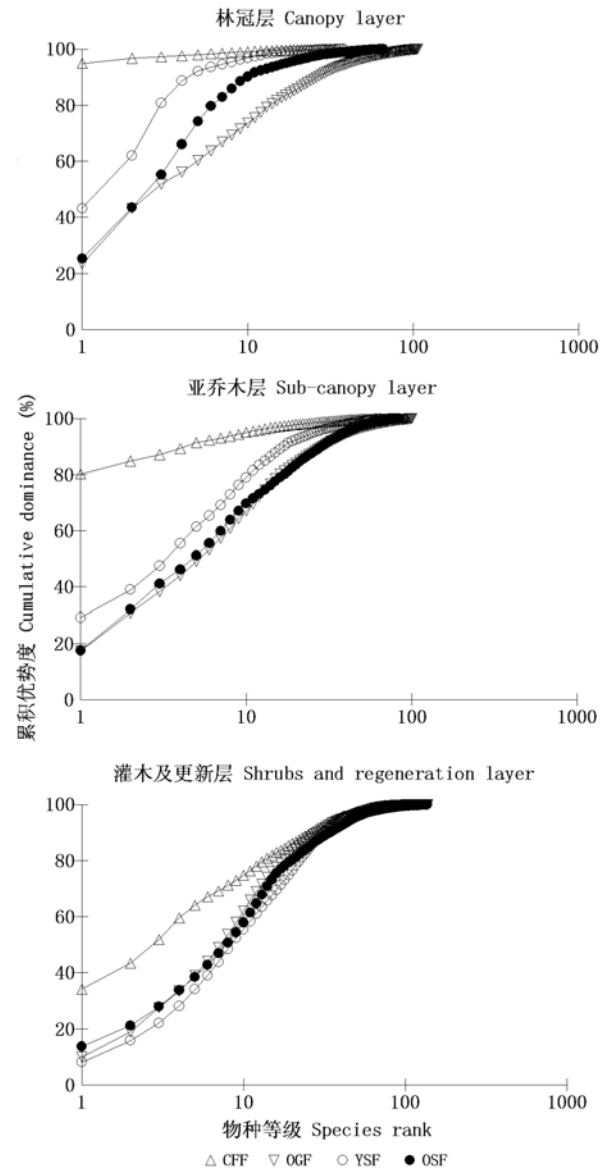


图4 古田山不同恢复阶段森林样地林冠层、亚乔木层、灌木及更新层k-优势度图。CFF, OGF, OSF, YSF同表1。

Fig. 4 K-dominance plot of canopy, sub-canopy, shrubs and regeneration layers of 12 forest plots during four recovery phases in the Gutianshan National Nature Reserve. CFF, OGF, OSF, YSF, see Table 1.

japonica var. *sinica*)等;其余还有一些阳性乔木树种,如马尾松、拟赤杨等。幼龄次生林(YSF)共有7个指示种,其中,栀子(*Gardenia jasminoides*)、短尾越桔、赤楠(*Syzygium buxifolium*)及石斑木(*Rhaphiolepis indica*)为常绿灌木,厚叶冬青(*Ilex elmerriliana*)和宁波木犀(*Osmanthus cooperi*)为常绿小乔木。老次生林(OSF)仅具5个指示种,其中欆木(*Loropetalum chinensis*)为常绿灌木,冬青(*I. chinensis*)

sis)、乳源木莲(*Manglietia yuyuanensis*)、刨花楠(*Machilus pauhoi*)为常绿乔木, 浙闽樱(*Prunus schneideriana*)为落叶小乔木。老龄林(OGF)有11个指示种, 除浙江红山茶、浙江樟(*Cinnamomum japonicum*)等亚乔木层常绿树种外, 还具备了常绿阔叶林的林冠层树种, 如钩栲(*Castanopsis tibetana*)、小叶青冈(*Cyclobalanopsis gracilis*)及细叶青冈(*C. myrsinaefolia*)(表2)。

3 讨论

人为干扰引起森林环境中光照、温度、养分和水分条件发生变化, 使主要树种的生理生态过程受到不同程度的影响, 从而在恢复过程中对森林群落的物种组成起决定性的作用。对于那些物种极其丰富的森林群落, 人为干扰还通过为某些树种提供适宜的生境而对物种多样性的维持机制产生影响(Baker *et al.*, 2005)。聚类分析和多响应置换过程的结果均表明古田山常绿阔叶林在遭受不同程度的采伐干扰后, 虽已经过不同年限的自然恢复, 但其物种组成仍具有显著差异。之前的研究大多关注不同恢复阶段中占主导地位的树种(Guariguata & Ostertag, 2001; Peña-Claros, 2003), 而本研究中的相似性百分比显示, 除了一些特定的优势种与某一恢复阶段相对应外, 还有相当数量的优势种为两个以上的恢复阶段所共有, 但在各阶段中所占比例不同。Sagar等(2003)指出, 在经过5种不同水平的人为干扰后, 各森林类型的物种组成表现为不同比例的优势种和共优种在群落中的组合, 本研究的结论与此相一致。

无度量多维标定的结果表明, 各恢复阶段物种组成的差异主要存在于林冠层, 而灌木及更新层差异较小。已有研究发现, 在物种相似性方面, 次生林与老龄林的幼苗、幼树比成年树具有更快的恢复速度(Peña-Claros, 2003; Norden *et al.*, 2009)。Guariguata和Ostertag (2001)指出次生林物种组成的差异主要存在于林冠层, 这是土壤中种子可用性和寿命的差异以及扩散限制等因素综合作用的结果。另一方面, 有研究指出次生林的群落构建过程深受土地利用历史、人为干扰强度和周围环境状况等因素的影响和制约(Chazdon, 2003; Dent *et al.*, 2012)。就本研究而言, 在幼龄次生林恢复至30年时对大径级的树种进行了择伐抚育, 这一措施主要对优势种

表2 古田山不同恢复阶段森林样地灌木及更新层指示种
Table 2 Indicator species of shrubs and regeneration layer of 12 forest plots during four recovery phases in the Gutianshan National Nature Reserve

树种 Tree species	组别 Group	指示值 Value	P值 P<0.05
山合欢 <i>Albizia kalkora</i>	CFF	84.3	0.0188
拟赤杨 <i>Alniphyllum fortunei</i>	CFF	59.7	0.0346
槲木 <i>Aralia chinensis</i>	CFF	80.4	0.0188
紫珠 <i>Callicarpa bodinieri</i>	CFF	69.0	0.0412
大青 <i>Clerodendrum cyrtophyllum</i>	CFF	62.3	0.0346
杉木 <i>Cunninghamia lanceolata</i>	CFF	98.6	0.0188
黄檀 <i>Dalbergia hupeana</i>	CFF	79.7	0.0188
小果冬青 <i>Ilex micrococca</i>	CFF	93.5	0.0188
山胡椒 <i>Lindera glauca</i>	CFF	85.0	0.0188
山鸡椒 <i>Litsea cubeba</i>	CFF	89.2	0.0188
马尾松 <i>Pinus massoniana</i>	CFF	66.2	0.0188
化香 <i>Platycarya strobilacea</i>	CFF	86.3	0.0354
豆腐柴 <i>Premna microphylla</i>	CFF	68.4	0.0168
水马桑 <i>Weigela japonica var. sinica</i>	CFF	86.2	0.0188
梔子 <i>Gardenia jasminoides</i>	CSF	45.0	0.0486
野漆 <i>Toxicodendron succedaneum</i>	YSF	74.6	0.0496
短尾越桔 <i>Vaccinium carlesii</i>	YSF	48.8	0.0456
厚叶冬青 <i>Ilex elmerrilliana</i>	YSF	67.9	0.0128
宁波木犀 <i>Osmanthus cooperi</i>	YSF	74.7	0.0160
石斑木 <i>Raphiolepis indica</i>	YSF	65.7	0.0160
赤楠 <i>Syzygium buxifolium</i>	YSF	75.7	0.0088
冬青 <i>Ilex chinensis</i>	OSF	67.1	0.0190
浙闽樱 <i>Prunus schneideriana</i>	OSF	51.4	0.0130
槲木 <i>Loropetalum chinensis</i>	OSF	49.9	0.0166
乳源木莲 <i>Manglietia yuyuanensis</i>	OSF	91.6	0.0376
刨花楠 <i>Machilus pauhoi</i>	OSF	100.0	0.0190
浙江红山茶 <i>Camellia chekiangoleosa</i>	OGF	94.0	0.0146
窄基红褐柃 <i>Eurya rubiginosa var. attenuata</i>	OGF	64.6	0.0332
鹿角杜鹃 <i>Rhododendron latoucheae</i>	OGF	55.1	0.0162
秀丽槭 <i>Acer elegantulum</i>	OGF	100.0	0.0162
钩栲 <i>Castanopsis tibetana</i>	OGF	96.9	0.0446
浙江樟 <i>Cinnamomum japonicum</i>	OGF	97.8	0.0162
灰白蜡瓣花 <i>Corylopsis glandulifera</i>	OGF	99.3	0.0162
小叶青冈 <i>Cyclobalanopsis gracilis</i>	OGF	97.5	0.0162
细叶青冈 <i>C. myrsinaefolia</i>	OGF	100.0	0.0162
尾叶冬青 <i>Ilex wilsonii</i>	OGF	96.5	0.0066
马醉木 <i>Pieris japonica</i>	OGF	74.7	0.0334

CFF, OGF, OSF, YSF同表1。CFF, OGF, OSF, YSF, see Table 1.

产生影响(Smith *et al.*, 2005); 人工林的年龄仅为20年, 在种植杉木前, 除皆伐外林地还经过了刨根和火烧等处理。因此推断, 人为干扰的方式、强度以及恢复时间等方面的不同可能是造成林冠层物种组成差异显著的重要原因。

与群落组成不同, 次生林的物种丰富度在短时

期内能够恢复到与老龄林一样的水平(Guariguata & Ostertag, 2001)。Smith等(2005)比较了采伐后和未受干扰的亚热带雨林的树种多样性, 研究显示, 经历不同强度采伐后的森林群落在短期内都恢复到了采伐前的物种丰富度水平, 恢复时间相同而且不受采伐强度的影响。本研究中除人工林的均匀度极显著低于其他阶段外, 其他各阶段在丰富度和均匀度两方面都没有显著性差异。*k*-优势度图进一步显示物种多样性的差异主要存在于林冠层, 而灌木及更新层差异较小。这一方面说明亚热带常绿阔叶林具有很强的自我更新能力; 另一方面也表明在植被得以有效保护的古田山地区, 其周围地区及采伐迹地保存的繁殖体能够迅速填充并占领受干扰之后的森林群落空白区域而成功定居, 使得物种多样性在短时期内得到恢复。以上结果证实了邻近地区种子传播的有效性对多样性维持的作用(Guariguata & Ostertag, 2001), 而且, 由于种子库的存在, 森林群落即便受到了人为干扰, 物种丰富度也会持续增长(Bruehlheide *et al.*, 2011)。

指示种方法是评价环境干扰对生态系统影响的最为快捷有效的方式(Carignan & Villard, 2001), 被广泛应用于分析植被和潜在环境变量的变化趋势(Diekmann, 2003)。虽然Bruehlheide等(2011)的研究指出, 古田山森林群落中持续存在幼苗随机迁入的过程, 但我们的研究表明定居下来的幼树在生活型组成方面呈现出一定的规律, 即人工林、幼龄次生林、老次生林和老龄林分别以落叶灌木及阳性乔木、常绿灌木或小乔木、亚乔木层常绿树种和林冠层树种为主要指示种。这说明树种对于人为干扰的响应是不同的(Verburg & van Eijk-Bos, 2003), 因而在群落恢复过程中呈现出一些特定物种与某一阶段相适应的特点。此外, 采伐强度增大会导致乔木层的稀疏和森林小气候的改变, 促进喜光灌木定居(Mishra *et al.*, 2004; McDonald *et al.*, 2008), 这可能是本研究中人工林和幼龄次生林样地都以灌木树种为主要指示种的原因。Capers等(2005)的研究表明, 树种生活型组成的变化与森林群落恢复过程中光的可利用性持续下降相关。次生林群落的耐阴性随着林龄的增加而增强, 表现为林下层耐阴树种逐渐取代喜光树种(Dent *et al.*, 2012)。较大的林冠空隙有利于喜光的阳性树种更新, 同时会导致物种多样性的降低。而自然状态下的林冠空隙有利于提高物

种多样性, 促进耐阴树种定居, 并对次生林物种组成向老龄林趋同性恢复过程产生加速作用(Dupuy & Chazdon, 2008)。

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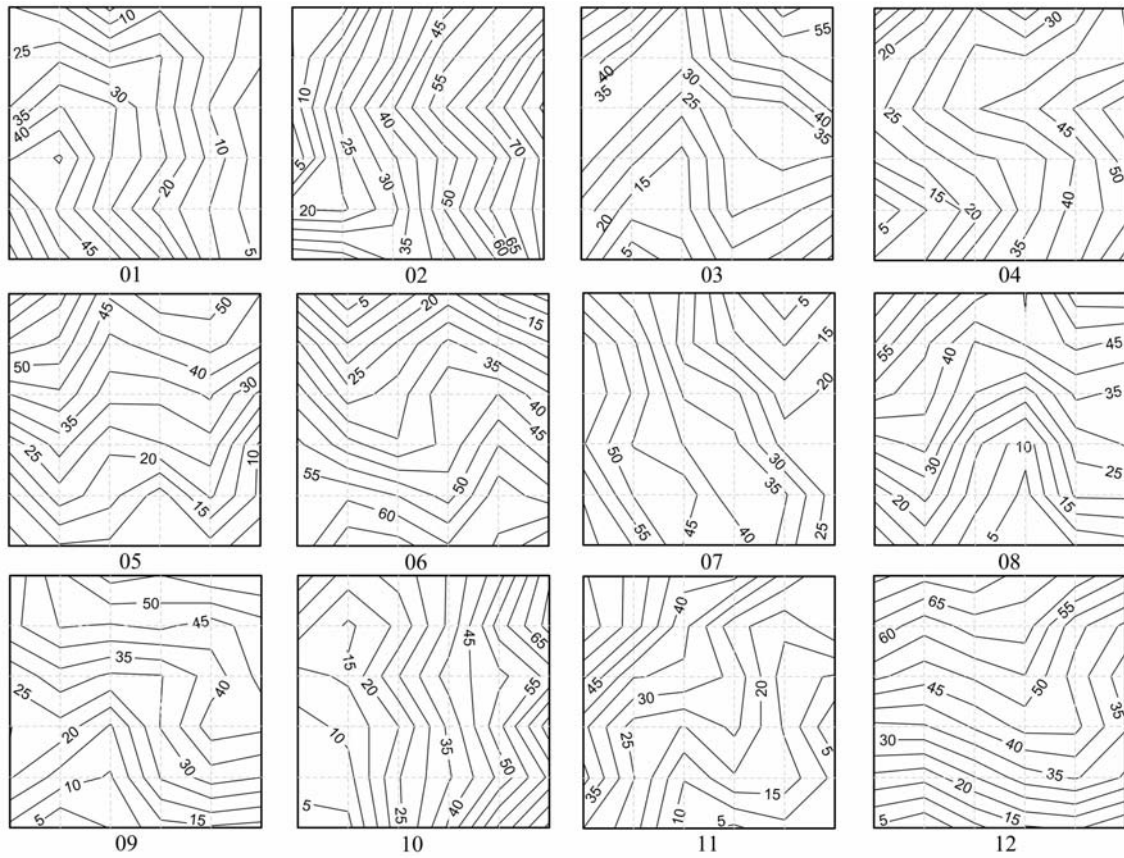
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附录 Supplementary Material

附图1 古田山不同恢复阶段森林样地(100 m × 100 m)地形图。图中数字为相对高程; 人工林样地包括01, 07, 11; 幼龄次生林样地包括03, 08, 09; 老次生林样地包括05, 06, 12; 老龄林样地包括02, 04, 10。

Fig. S1 Topographical maps of 12 forest plots during four recovery phases in the Gutianshan National Nature Reserve. The figures in the map refer to relative elevations of forest plots; Chinese fir forest plots include 01, 07, 11; Young secondary forest plots include 03, 08, 09; Old secondary forest plots include 05, 06, 12; Old-growth forest plots include 02, 04, 10.

<http://www.biodiversity-science.net/fileup/PDF/w2013-202-1.pdf>



附图1 古田山不同恢复阶段森林样地(100 m × 100 m)地形图。图中数字为相对高程; 人工林样地包括01, 07, 11; 幼龄次生林样地包括03, 08, 09; 老次生林样地包括05, 06, 12; 老龄林样地包括02, 04, 10。

Fig. S1 Topographical maps of 12 forest plots during four recovery phases in the Gutianshan National Nature Reserve. The figures in the map refer to relative elevations of forest stands; Chinese fir forest plots include 01, 07, 11; Young secondary forest plots include 03, 08, 09; Old secondary forest plots include 05, 06, 12; Old-growth forest plots include 02, 04, 10.