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鄂西南两个自然保护区亚热带常绿落叶阔叶混交林类型及其常绿和落叶物种组成结构分析

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摘 要 为深入研究亚热带常绿落叶阔叶混交林的生物多样性维持机制，合理保护与利用此类森林植被，以鄂西南两个自然保护区——星斗山和木林子典型的亚热带常绿落叶阔叶混交林为研究对象，在野外样方调查的基础上进行了群落数量分类和排序，分析了常绿和落叶物种比例随群落类型及环境因子变化的规律。研究结果表明: (1)将鄂西南两个自然保护区的亚热带常绿落叶阔叶混交林划分为5个群落类型：即青冈-翅柃+尖连蕊茶(*Cyclobalanopsis glauca-Eurya alata + Camellia cuspidata*)群落(I)、川陕鹅耳枥+青冈-翅柃(*Carpinus fargesiana + Cyclobalanopsis glauca-Eurya alata*)群落(II)、川陕鹅耳枥+青冈-水马桑(*Carpinus fargesiana + Cyclobalanopsis glauca-Weigela japonica*)群落(III)、光叶水青冈+多脉青冈-翅柃(*Fagus lucida + Cyclobalanopsis multinervis-Eurya alata*)群落(IV)和川陕鹅耳枥+交让木+包果柯-翅柃(*Carpinus fargesiana + Daphniphyllum macropodum + Lithocarpus cleistocarpus-Eurya alata*)群落(V); (2)常绿和落叶物种的丰富度、多度、胸高断面积及重要值等指标随群落类型而变化。在群落II、III和V中落叶物种占优势，而在群落I和IV中二者无显著差异; (3)各类型群落在小径级(1–5 cm)内落叶物种的丰富度大于常绿物种，但多度、胸高断面积和重要值大都小于常绿物种。在中径级(5–10 cm)内，群落I和群落IV的各项指标都表现为常绿物种大于落叶物种，而群落II、群落III和群落V的则相反。在大径级(≥ 10 cm)内，各群落类型的落叶物种都占显著优势，其各项指标大于常绿物种; (4)海拔、坡度、坡向、土壤氮含量和土壤磷含量是影响各群落类型内常绿和落叶物种比例变化的主导因子。

关键词 群落类型，常绿落叶阔叶混交林，环境因子，常绿落叶物种比例，数量分类

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Quantitative classification of the subtropical evergreen-deciduous broadleaved mixed forest and the deciduous and evergreen species composition structure across two national nature reserves in the southwest of Hubei, China

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Abstract

Aims The subtropical evergreen-deciduous broadleaved mixed forest is the largest extant natural vegetation type in southwest Hubei. However, little knowledge exists on the types and compositions (especially the relative ratios of evergreen versus deciduous species) of this forest vegetation. Here, we quantitatively classify the less studied forest vegetation into different community types, compare their size and composition structure, and analyze species-environment relationships which is the basis for further understanding the biodiversity maintenance mechanism and reasonable protection and utilization of this forest.

Methods We established 92 20 m × 20 m plots of subtropical evergreen-deciduous broadleaved mixed forest in two national nature reserves in Enshi, Hubei Province, China. All species with stems ≥1 cm diameter at breast height (*DBH*) in each plot were identified and mapped. These plots were classified by using two-way indicator species analysis (TWINSPAN) and detrended correspondence analysis (DCA). The species richness, abundance, basal area and importance value were chosen to compare structure, species composition and evergreen and

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deciduous ratio. Permutation-based multiple regression on distance matrices and multiple stepwise regression analysis were used to examine the relationship between species distribution and environmental factors.

Important findings Our results showed that the subtropical evergreen-deciduous broadleaved mixed forest in the southwest of Hubei could be classified into five community types based on quantitative methods: i.e. *Cyclobalanopsis glauca-Eurya alata + Camellia cuspidate* (community type I), *Carpinus fargesiana + Cyclobalanopsis glauca-Eurya alata* (community type II), *Carpinus fargesiana + Cyclobalanopsis glauca-Weigela japonica* (community type III), *Fagus lucida + Cyclobalanopsis multinervis-Eurya alata* (community type IV) and *Carpinus fargesiana + Daphniphyllum macropodum + Lithocarpus cleistocarpus-Eurya alata* (community type V). Species richness, abundance, basal area and importance value of evergreen and deciduous species in each community types were different. Deciduous species in community II, community III and community V were significantly higher than evergreen species in terms of species richness, stem abundance, basal area and importance value, but they had no significant differences in community I and community IV. The richness of deciduous species in most community types were higher than those of evergreen species, meanwhile the abundance, basal area and importance value of deciduous species in the small size classes (1 cm ≤ *DBH* < 5 cm) in each community types were lower than those of evergreen species. In middle size classes (5 cm ≤ *DBH* < 10 cm), the richness, abundance, basal area and importance value of deciduous species were higher than those of evergreen species in community II, community III and community V. However, in community I and community IV, the evergreen species were larger than deciduous species in the four indexes. The richness of deciduous species in majority of the community types were higher than those of evergreen species in large size classes (*DBH* ≥ 10 cm). The elevation, slope and aspect, soil total nitrogen content, soil total phosphorus content, soil available nitrogen content and soil available phosphorus content were the major factors affecting evergreen and deciduous species distribution across the five community types.

Key words community type, the evergreen-deciduous broadleaved mixed forest, environmental factors, ratio of deciduous and evergreen species, quantitative classification

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常绿落叶阔叶混交林是一种介于落叶阔叶林与常绿阔叶林之间的森林植被类型, 通常被认为是与常绿阔叶林和落叶阔叶林并列的一种植被类型(吴中伦, 2000), 并可进一步划分为不同的植被亚型(吴征镒, 1980)。目前对常绿落叶阔叶混交林自然分布的划定和分类存在不同观点(吴征镒, 1980; 安树青等, 1998; 宋永昌, 1999; 方精云, 2001)。长期以来, 我国对常绿落叶阔叶混交林的基本概念(班继德和漆根深, 1995; 周光裕, 1996)、空间分布(沈泽昊和方精云, 2001; 张谧等, 2004)、物种组成(曹铁如等, 1997; 汪正祥等, 2006; 赵丽娟等, 2013)、群落更新(熊小刚等, 2002; 汤景明等, 2010; 刘海波等, 2014)、种间关系(韩文衡等, 2009)、外来种入侵(卢少飞等, 2005)和珍稀物种分布(沈泽昊等, 1999)等方面有了一定的研究。然而, 相对于典型的常绿阔叶林和落叶阔叶林生态研究来说, 亚热带常绿落叶阔叶混交林及其生态特征的研究还非常薄弱。

湖北西南部地区是湖北重要的天然林分布区, 亚热带常绿阔叶林为该地区的地带性植被。随着海拔的升高, 含有落叶成分的亚热带常绿落叶阔叶混交林逐步成为优势植被。亚热带常绿落叶阔叶混交林植物区系成分复杂, 生物多样性丰富, 不仅为我国的经济建设提供了大量的优质木材和林副产品, 而且对我国特有的古老孑遗物种保护、维护区域生态平衡发挥着重要的作用(汤景明等, 2010)。由于气候、地质和区域物种库等方面的差异, 不同区域的常绿落叶阔叶混交林具有不同的变化特征, 针对不同区域的森林植被开展相关的生态学研究显得尤为必要。对亚热带常绿落叶阔叶混交林的群落类型进行科学划分, 不仅有助于我们对现存森林植被基本特征的认识, 而且是我们进一步深入开展生态系统功能与生态过程研究的基础。了解常绿和落叶物种比例随群落类型的变化规律, 能够揭示不同群落中环境条件对物种分布的影响, 从而为我们阐明生物多样性维持与调控机制奠定基础。亚热带常绿落叶阔叶混交林的群落类型及组成结构的研究是对其进

行有效地保育、可持续经营与合理利用的科学基础。

本研究以鄂西南星斗山和木林子自然保护区亚热带常绿落叶阔叶混交林为研究对象，在建立系列森林动态固定样地的基础上，对该地区的植物群落进行了数量分类与排序，探讨植被与环境之间的关系，并分析常绿和落叶物种随不同群落类型及环境条件的变化，以期为深入研究亚热带常绿落叶阔叶混交林的生物多样性与生态功能维持机制，合理保护与利用此类森林植被提供科学依据。

1 研究区概况

研究地点位于湖北恩施的星斗山国家级自然保护区和木林子国家级自然保护区。以上2个保护区是鄂西南天然森林植被保存最为完好的区域，是鄂西南现存天然森林植被的典型代表。

星斗山国家级自然保护区位于鄂西南恩施、利川与咸丰三县(市、州)交界处，地理坐标29.95°–30.17° N, 108.95°–109.45° E。是齐岳山向东北的延伸部分，因有大巴山系巫山余脉作屏障，成为第三纪植物的“避难所”。海拔672–1 751 m。雨量充沛，气候温和，年平均气温12.8℃，年降水量1 200–1 400 mm，无霜期234天，相对湿度85%左右。土壤以山地黄壤、黄棕壤、棕壤为主(艾训儒和谭建锡, 1999; 方元平和刘胜祥, 2006)。

湖北木林子国家级自然保护区位于湖北省恩施土家族苗族自治州鹤峰县境内，地理坐标29.21°–30.17° N, 109.98°–110.81° E，海拔1 100.0–2 095.6 m，属武陵山脉北支余脉，地势由西北和东南向中间逐渐倾斜。该区属于亚热带季风性湿润气候，雨热同期，时空分布不均，年降水量1 733 mm，春秋多阴雨，夏季雨量较多，冬季雨少雾多，蒸发小，湿度大，年平均相对湿度为82%，无霜期270–279天。年平均气温为15.5 ℃，最冷月(1月)平均气温为4.6 ℃，最热月(7月)平均气温为26 ℃。土壤以黄棕壤、棕壤、黄壤为主(葛继稳等, 2009)。

2 研究方法

2.1 固定样地的建立与调查

2013年9月–2014年6月，在湖北星斗山自然保护区和湖北木林子自然保护区的典型天然森林植被中，分别随机设置永久性森林动态样地45个和47个，每个样地面积均为20 m × 20 m。这些样地分布于海拔1 248–1 800 m之间。样地建设采用CTFS森林动态样地监测标准(Condit, 1998)。在每个样地中利用网格法将其分割成16个5 m × 5 m的小样方，在小样方内对所有胸径≥1 cm的乔木、灌木和藤本进行编号、测量点刷漆标记并开展每木检尺，记录内容包括物种名称、胸径、坐标、萌生与死亡状况，同时记录样地所在坡度、海拔、凋落物厚度。

2.2 常绿和落叶物种的确定

常绿和落叶物种的划分主要通过查阅《湖北植物志》(傅书遐, 2002)及咨询植物分类专家来确定，对于那些不明确的物种，由作者在冬季进行实地观测和采访当地林业工作者获得。

2.3 数据处理

坡向以正北为起点(0°)，采用顺时针旋转的角度表示，数字等级划分为：1表示阴坡(0°–45°和315°–360°), 2表示半阴坡(45°–90°和270°–315°), 3表示半阳坡(90°–135°和225°–270°)，4表示阳坡(135°–225°)，数值越大，表示光照越多。土壤因子的测定方法为：土壤pH值用电位法、土壤有机质用重铬酸钾容量法、土壤碱解N用碱解扩散法、速效P用双酸法浸提-钼锑抗比色法、全N用半微量凯氏定氮法、全P用硫酸-高氯酸消解法。

以样地为单位分别计算物种的重要值，计算公式为：重要值(*IV*) = (相对多度+相对显著度+相对频度)/3。采用VEAPAN软件包中的TWINSPAN进行群落分类；通过CANOCO 4.5软件(张金屯, 1995)对样地和物种的重要值矩阵进行DCA排序。根据个体胸径(*DBH*)将物种划分为3个等级：小径级(1 cm ≤ *DBH* < 5 cm)、中径级(5 cm ≤ *DBH* < 10 cm)和大径级(*DBH* ≥ 10 cm)。基于Bray-Curtis相似距离，采用基于矩阵的多元回归分析(Permutation-based multiple regression on distance matrices, MRM)确定显著影响群落物种组成变化的环境因子(Lichstein, 2007)。运用多元逐步回归分析(multiple regression analysis)来分析常绿和落叶物种与环境因子之间的关系。

使用R 3.1.1和Origin 8.5进行统计分析和作图。

3 结果和分析

3.1 群落数量分类与排序

应用TWINSPAN分类可将所调查的92个样地分为5个群落类型(图1)。在DCA排序图(图2)中，DCA前两轴的贡献率分别为56.7%和29.8%，累计

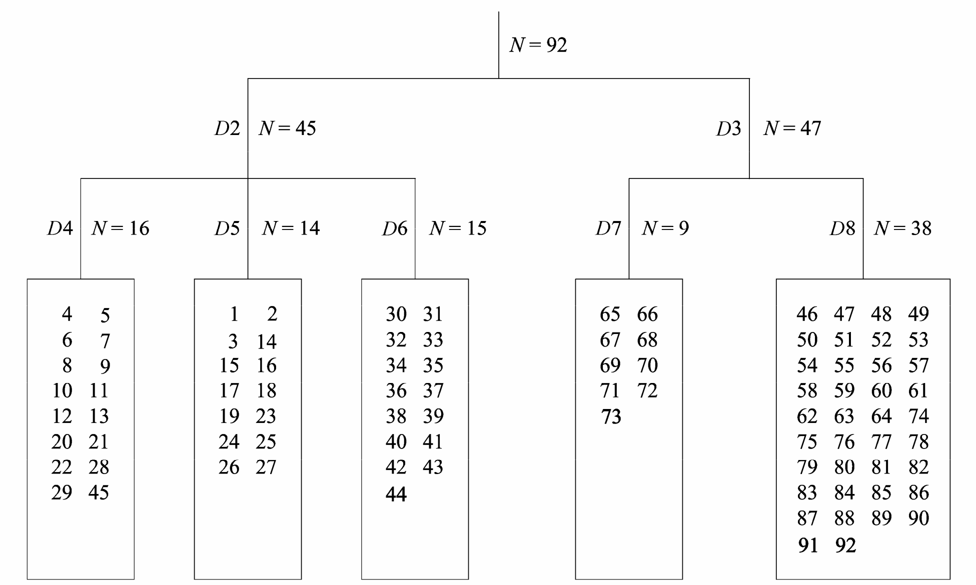

图1　鄂西南两个保护区亚热带常绿落叶阔叶混交林92个样地的TWINSPAN分类树状图。*D*, 分类次数; *N*, 样方数。
Fig. 1　Dendrogram of TWINSPAN classification for 92 plots in the subtropical evergreen-deciduous broadleaved mixed forest across two nature reserves in Southwest Hubei, China. *D*, division number; *N*, number of plot.

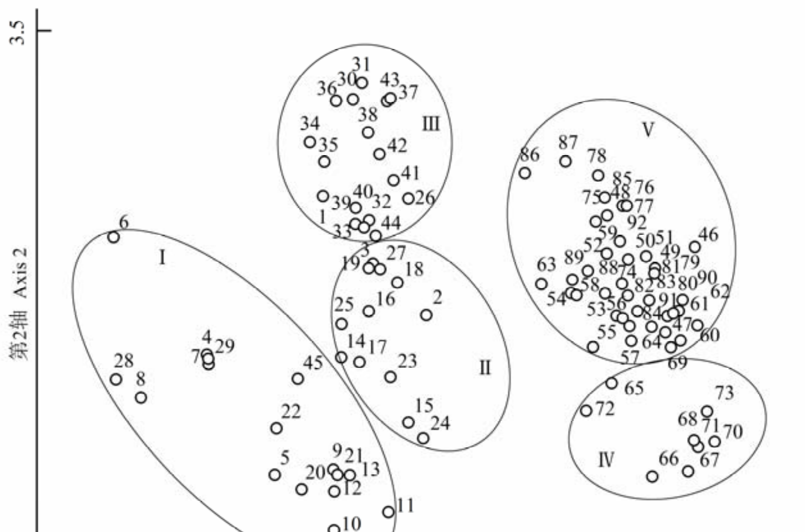

图2　鄂西南两个保护区亚热带常绿落叶阔叶混交林92个样地的DCA二维排序图。罗马数字(I, II, III, IV, V)代表不同的群落类型。
Fig. 2　Two-dimensional DCA ordination diagram for 92 plots in the subtropical evergreen-deciduous broadleaved mixed forest across two nature reserves in Southwest Hubei, China. Roman numerals (I, II, III, IV, V) indicate different community types.

贡献率达86.5%。结合TWINSPAN分类与DCA排序的结果, 可将鄂西南星斗山和木林子自然保护区亚热带常绿落叶阔叶混交林的森林群落划分为5类, 其中木林子包括I (青冈-翅柃+尖连蕊茶群落(*Cyclobalanopsis glauca*-*Eurya alata* + *Camellia cuspidata*))、II (川陕鹅耳枥+青冈-翅柃群落(*Carpinus fargesiana* + *Cyclobalanopsis glauca*-*Eurya alata*))和III (川陕鹅耳枥+青冈-水马桑群落(*Carpinus fargesiana* + *Cyclobalanopsis glauca*-*Weigela japonica*)) 3个群落, 星斗山包括IV (光叶水青冈+多脉青冈-翅柃群落(*Fagus lucida* + *Cyclobalanopsis multinervis*-*Eurya alata*))和V (川陕鹅耳枥+交让木+包果柯-翅柃群落(*Carpinus fargesiana*+*Daphniphyllum macropodum* + *Lithocarpus cleistocarpus*-*Euryaalata*)) 2个群落。各群落的主要物种组成见表1。各样地的物种状况见附录1。

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表1 鄂西南两个保护区亚热带常绿落叶阔叶混交林5种群落类型内重要值排名前10位的物种

Table 1 Importance value (*IV*) of the top 10 species in the five community types in the subtropical evergreen-deciduous broadleaved mixed forest across two nature reserves in Southwest Hubei, China

群落类型 Community type	物种 Species	多度 Abundance	胸径 *DBH* (cm)	重要值 *IV*	叶习性 Leaf habit
群落I	青冈 *Cyclobalanopsis glauca*	752	6.38	2.48	常绿 Evergreen
Type I	翅柃 *Eurya alata*	599	4.02	1.12	常绿 Evergreen
	尖连蕊茶 *Camellia cuspidata*	487	3.64	1.11	常绿 Evergreen
	木荷 *Schima superba*	248	5.94	0.99	常绿 Evergreen
	山矾 *Symplocos sumuntia*	535	3.05	0.95	常绿 Evergreen
	锥栗 *Castanea henryi*	17	53.96	0.83	落叶 Deciduous
	黄丹木姜子 *Litsea elongata*	385	2.85	0.82	常绿 Evergreen
	薄叶山矾 *Symplocos anomala*	207	3.59	0.39	常绿 Evergreen
	茶条果 *Symplocos phyllocalyx*	137	3.81	0.38	常绿 Evergreen
	四照花 *Dendrobenthamia japonica*	70	7.58	0.36	落叶 Deciduous
群落II	川陕鹅耳枥 *Carpinus fargesiana*	669	4.05	1.28	落叶 Deciduous
Type II	山矾 *Symplocos sumuntia*	1 007	2.57	1.26	常绿 Evergreen
	青冈 *Cyclobalanopsis glauca*	382	4.84	1.02	常绿 Evergreen
	四照花 *Dendrobenthamia japonica*	367	3.9	0.84	落叶 Deciduous
	亮叶桦 *Betula luminifera*	92	15.45	0.78	落叶 Deciduous
	翅柃 *Eurya alata*	452	2.44	0.65	常绿 Evergreen
	水马桑 *Weigela japonica*	172	4.51	0.40	落叶 Deciduous
	灯台树 *Bothrocaryum controversum*	68	8.54	0.36	落叶 Deciduous
	黄丹木姜子 *Litsea elongata*	136	3.13	0.34	常绿 Evergreen
	枫香树 *Liquidambar formosana*	56	10.92	0.31	落叶 Deciduous
群落III	川陕鹅耳枥 *Carpinus fargesiana*	1 108	4.03	1.63	落叶 Deciduous
Type III	水马桑 *Weigela japonica*	843	3.89	1.41	落叶 Deciduous
	青冈 *Cyclobalanopsis glauca*	850	3.93	1.18	常绿 Evergreen
	四照花 *Dendrobenthamia japonica*	580	3.25	0.82	落叶 Deciduous
	灰柯 *Lithocarpus henryi*	353	4.90	0.73	常绿 Evergreen
	亮叶桦 *Betula luminifera*	144	9.80	0.72	落叶 Deciduous
	小叶青冈 *Cyclobalanopsis myrsinifolia*	432	4.76	0.68	常绿 Evergreen
	盐肤木 *Rhus chinensis*	163	7.14	0.57	落叶 Deciduous
	贵定桤叶树 *Clethra cavaleriei*	355	3.11	0.57	落叶 Deciduous
	山鸡椒 *Litsea cubeba*	344	3.08	0.57	落叶 Deciduous
群落IV	光叶水青冈 *Fagus lucida*	325	9.77	1.64	常绿 Evergreen
Type IV	多脉青冈 *Cyclobalanopsis multinervis*	414	6.87	1.23	落叶 Deciduous
	翅柃 *Eurya alata*	526	3.13	0.95	常绿 Evergreen
	川陕鹅耳枥 *Carpinus fargesiana*	140	8.16	0.62	落叶 Deciduous
	宜昌润楠 *Machilus ichangensis*	77	7.88	0.31	常绿 Evergreen
	交让木 *Daphniphyllum macropodum*	72	7.12	0.28	常绿 Evergreen
	杜鹃 *Rhododendron simsii*	196	2.11	0.20	常绿 Evergreen
	荚蒾 *Viburnum dilatatum*	119	2.04	0.20	落叶 Deciduous
	光叶山矾 *Symplocos lancifolia*	60	4.28	0.17	常绿 Evergreen
	包果柯 *Lithocarpus cleistocarpus*	48	7.69	0.17	常绿 Evergreen
群落V	川陕鹅耳枥 *Carpinus fargesiana*	1 359	7.63	4.67	落叶 Deciduous
Type V	翅柃 *Eurya alata*	1 710	2.84	2.53	常绿 Evergreen
	包果柯 *Lithocarpus cleistocarpus*	502	8.13	1.71	常绿 Evergreen
	交让木 *Daphniphyllum macropodum*	461	5.08	1.53	常绿 Evergreen
	亮叶桦 *Betula luminifera*	201	12.09	1.40	落叶 Deciduous
	齿缘吊钟花 *Enkianthus serrulatus*	1 268	3.03	1.37	落叶 Deciduous
	长蕊杜鹃 *Rhododendron stamineum*	854	3.29	1.17	常绿 Evergreen
	水马桑 *Weigela japonica*	345	5.56	1.17	落叶 Deciduous
	锥栗 *Castanea henryi*	145	16.32	1.16	落叶 Deciduous
	石灰花楸 *Sorbus folgneri*	519	4.91	1.09	落叶 Deciduous

DBH, diameter at breast height. *IV*, importance value.

3.2　不同群落类型内常绿和落叶物种丰富度、多度、胸高断面积及重要值的变化

在5个群落类型中, 群落II、群落III和群落V内落叶物种的物种丰富度显著大于常绿物种(p < 0.001) (图3A)。群落I与群落IV内常绿和落叶物种的物种丰富度差异不显著(p > 0.05)。

群落I和群落III中常绿与落叶物种的多度存在显著的差异(p < 0.001), 但群落I的落叶物种多度显著小于常绿物种, 而群落III呈现相反的趋势(图3B)。其他3个群落类型中常绿与落叶物种的多度差异不显著(p > 0.05)。

群落II、群落III和群落V中落叶物种的胸高断面积均显著(p < 0.001)大于常绿物种(图3C)。群落I与群落IV的常绿和落叶物种的胸高断面积差异不显著(p > 0.05), 但群落IV中落叶物种的胸高断面积略高于常绿树种。

群落II、群落III和群落V中落叶物种的重要值显著大于常绿物种(p < 0.01) (图3D), 群落I中的常绿物种重要值显著大于落叶物种, 群落IV的常绿物种重要值大于落叶物种, 但差异并不显著(p > 0.05)。

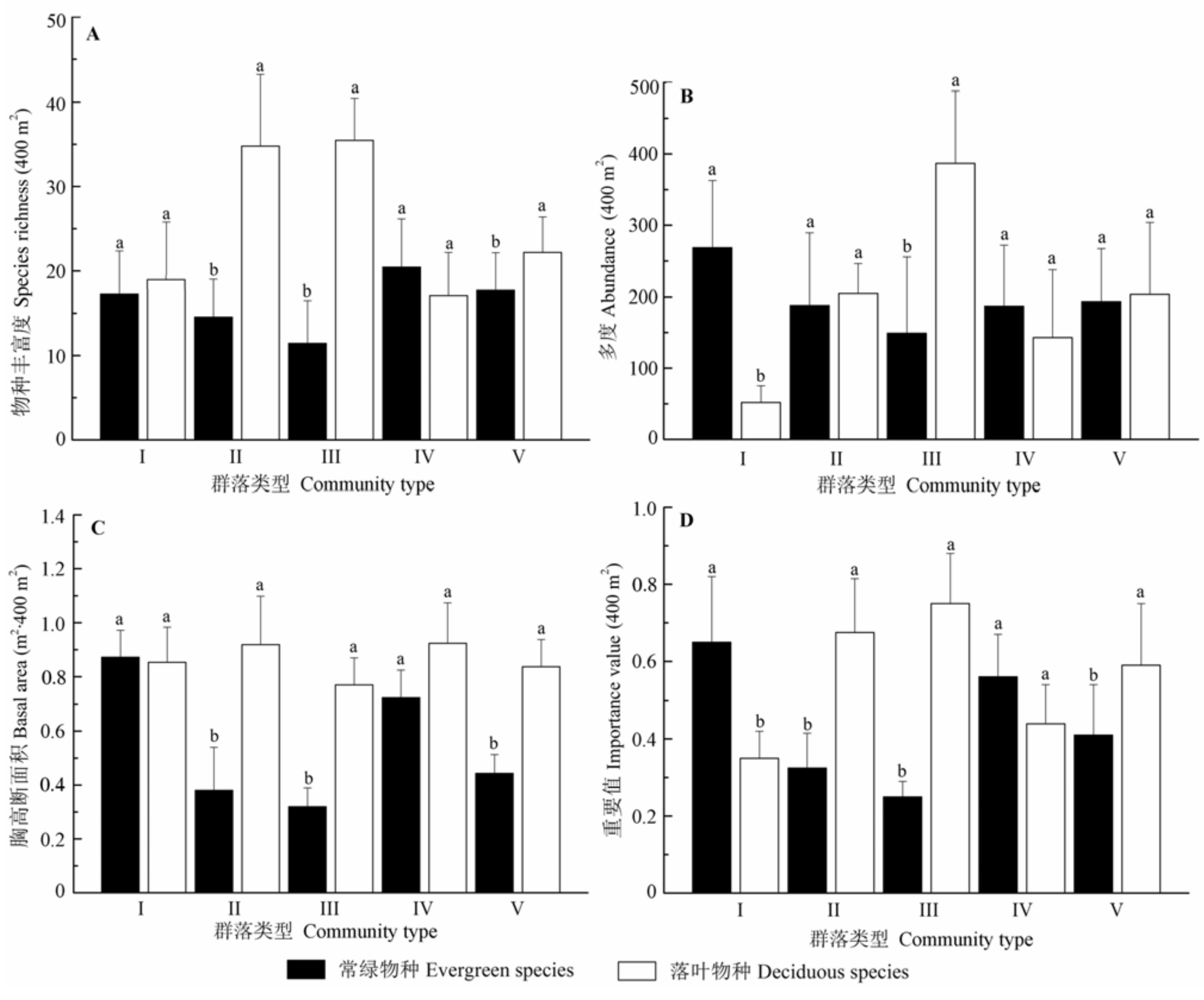

图3　鄂西南两个保护区亚热带常绿落叶阔叶混交林5种群落类型的常绿和落叶物种丰富度、多度、胸高断面积和重要值(平均值±标准偏差)。不同小写字母(a, b)表示显著差异(p < 0.05)。I、II、III、IV、V分别为青冈-翅柃+尖连蕊茶群落, 川陕鹅耳枥+青冈-翅柃群落, 川陕鹅耳枥+青冈-水马桑群落, 光叶水青冈+多脉青冈-翅柃群落和川陕鹅耳枥+交让木+包果柯-翅柃群落。

Fig. 3　Species richness, abundance, basal area and importance value of the five forest types in the subtropical evergreen-deciduous broadleaved mixed forest across two nature reserves in Southwest Hubei, China (mean ± *SD*). Different lowercase letters (a, b) indicate significant differences at the level of 0.05. I, II, III, IV, V indicate different community types: *Cyclobalanopsis glauca-Eurya alata + Camellia cuspidata, Carpinus fargesiana + Cyclobalanopsis glauca-Eurya alata, Carpinus fargesiana + Cyclobalanopsis glauca-Weigela japonica, Fagus lucida + Cyclobalanopsis multinervis-Eurya alata, Carpinus fargesiana + Daphniphyllum macropodum + Lithocarpus cleistocarpus-Eurya alata.*

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3.3 不同径级的常绿和落叶物种丰富度、多度、胸高断面积及重要值比例的变化

除群落I外，所有群落类型内的常绿和落叶物种丰富度比例均随胸径级的增加而下降(图4A)。除群落IV内1–5 cm的径级外，其他群落类型各径级中的落叶物种丰富度均大于常绿物种。

除群落I外，常绿和落叶物种多度在群落内所占的比例随径级的增加而逐渐下降(图4B)。除群落III外，各群落内1–5 cm径级的常绿物种多度均大于落叶物种，在5–10 cm的径级内，群落I和群落IV的常绿物种多度大于落叶物种，群落II、群落III和群落V的落叶物种多度大于常绿物种。除群落I外，各群落的落叶物种多度在≥10 cm的径级内均大于常绿物种。

各群落类型内常绿物种和落叶物种的胸高断面积比例均随着径级的增加而升高(图4C)。群落II、群落III和群落V中落叶物种的胸高断面积比例在1–5 cm和5–10 cm的径级内大于常绿物种，群落I和群落IV中则呈现相反的趋势。各群落胸径≥10 cm的落叶物种比例均大于常绿物种。

除群落III外，常绿物种的重要值在1–5 cm径级内均大于落叶物种(图4D)。在5–10 cm的径级内，群落I和群落IV的常绿物种重要值大于落叶物种，群落II、群落III和群落V的落叶物种重要值大于常绿物种。各群落胸径≥ 10 cm的落叶物种重要值均大于常绿物种。

3.4 群落物种组成与环境因子的关系

基于距离矩阵的多元回归分析(MRM)结果表明：环境因子可以解释物种组成变化的59%，海拔、坡度、坡向、土壤全氮、土壤全磷、土壤碱解氮、

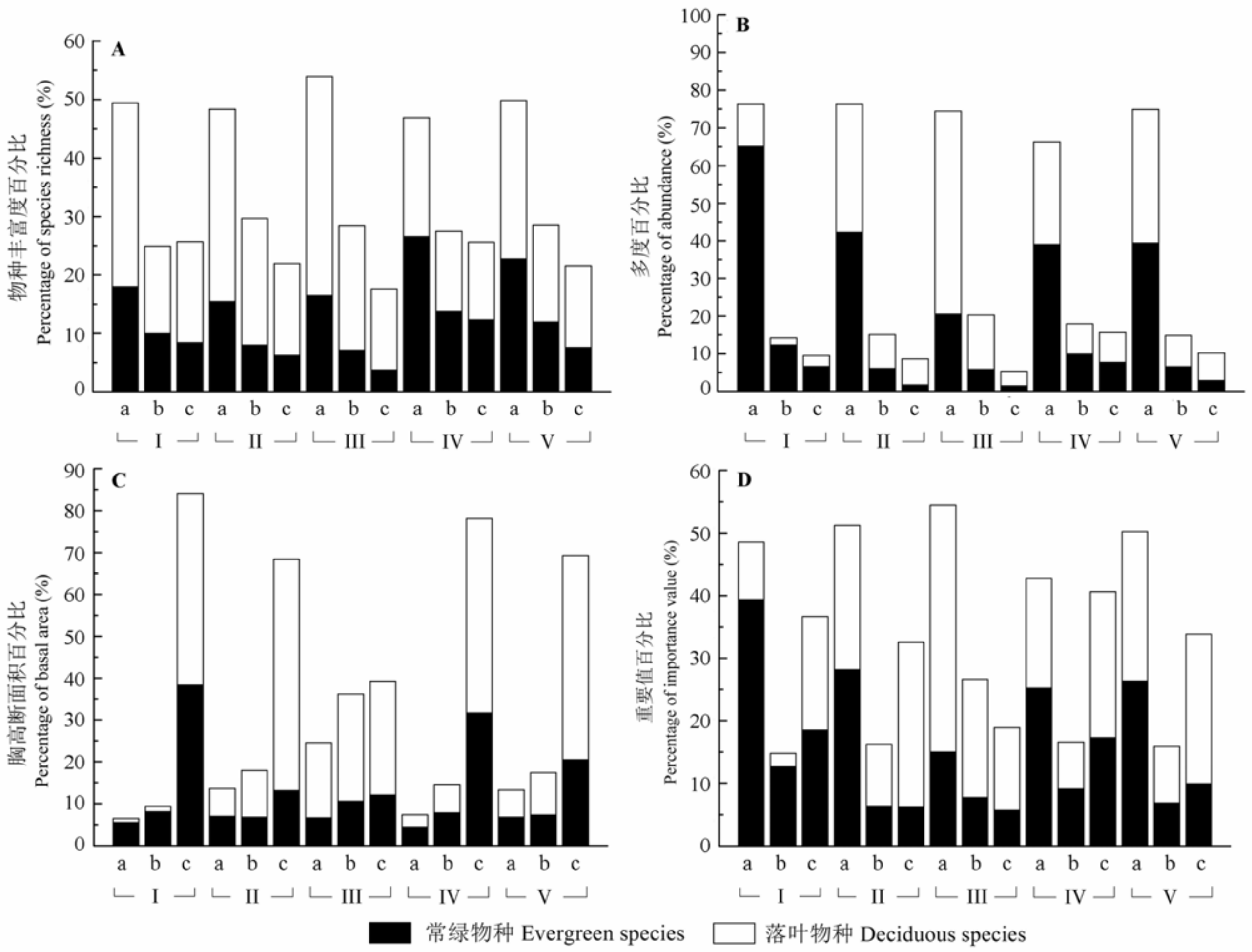

图4 鄂西南两个保护区亚热带常绿落叶阔叶混交林5种群落类型的常绿和落叶物种不同径级的物种丰富度、多度、胸高断面积和重要值比例。a, 胸径1–5 cm; b, 胸径5–10 cm; c, 胸径≥10 cm。I–V同图3。

Fig. 4 Evergreen/deciduous ratio of species richness, abundance, basal area and importance value with size class in subtropical evergreen-deciduous broadleaved mixed forest across two nature reserves in Southwest Hubei, China. a, *DBH* 1–5 cm; b, *DBH* 5–10 cm; c, *DBH* ≥10 cm; *DBH*, diameter at breast height. I–V see Fig. 3.

表2　鄂西南两个保护区亚热带常绿落叶阔叶混交林内环境因子对物种分布的影响

Table 2　Effects of environmental factors on species distribution in subtropical evergreen-deciduous broadleaved mixed forest across two nature reserves in Southwest Hubei, China

环境因子 Environmental variables	R^2	p
海拔 Elevation	0.126 7	0.001***
坡度 Slope	0.028 5	0.001***
坡向 Aspect	0.002 4	0.014*
土壤含水量 Soil water content	0.001 7	0.071
pH	0.002 9	0.059
土壤有机质 Soil organic matter	0.000 7	0.092
土壤全氮 Total nitrogen	0.001 1	0.002**
土壤全磷 Total phosphorus	0.036 4	0.001***
土壤碱解氮 Available nitrogen	0.017 8	0.001***
土壤速效磷 Available phosphorus	0.245 7	0.001***

*, 在0.05水平上显著相关; **, 在0.01水平上显著相关; ***, 在0.001水平上显著相关; R^2, 决定系数。

*, difference is significant at 0.05 level; **, difference is significant at 0.01 level; ***, difference is significant at 0.001 level; R^2, coefficient of determination.

土壤速效磷是影响研究区群落分布的主要因子(表2)。

整体来看, 群落I主要分布在坡度大、全磷、全氮含量高、海拔在1 538 m左右的阴坡; 群落II主要分布在坡度较大、速效磷含量低、海拔在1 470 m左右的阴坡和半阴坡; 群落III主要分布在坡度较小, 全磷含量较高、海拔在1 762 m左右的阳坡和半阳坡; 群落IV主要分布在碱解氮和全氮含量高、海拔在1 587 m左右的阴坡和半阴坡; 群落V主要分布在坡度小、速效磷含量高、全磷和碱解氮含量低、海拔在1 406 m左右的半阴坡。

采用多元逐步回归分析对各群落常绿和落叶物种丰富度与环境因子关系的研究(表3)表明, 除土壤含水量和有机质之外, 其他环境因子在不同群落类型间与常绿和落叶物种呈现显著的相关性($p < 0.05$)。海拔高度与群落III和群落V的落叶物种显著相关。坡度与群落I和群落IV的落叶物种显著负相关。坡位与群落I、群落III和群落IV显著相关。土壤氮与群落I、群落II、群落III和群落IV显著相关。土壤磷与群落II和群落V显著负相关。

4　讨论

4.1　亚热带常绿落叶阔叶混交林群落的数量分类与排序

通过TWINSPAN及DCA方法对鄂西南木林子自然保护区和星斗山自然保护区的亚热带常绿落叶阔叶混交林进行数量分类和排序, 将两个保护区的92个样地分成了5个群落类型。TWINSPAN划分出的群落类型在DCA排序图上能明显地区分开, 说明排序与分类结果基本吻合, 数量化的分类结果是可信的。

植被分类是植被生态学研究中最复杂的一个问题, 直到现在还没有植被学家们认同的统一分类原则和分类系统(宋永昌, 2004)。而我国亚热带地区植

表3　鄂西南两个保护区亚热带常绿落叶阔叶混交林5种群落常绿和落叶物种丰富度与环境因子的多元逐步回归分析

Table 3　Multiple regression analysis between species richness and environmental variables in the five forest types in subtropical evergreen-deciduous broadleaved mixed forest across two nature reserves in Southwest Hubei, China

类型1) Type1)	物种丰富度2) Species richness2)	环境变量3) Environmental variables3)										参数4) Parameter4)	
		E	S	A	SWC	pH	SOM	TN	TP	AN	AP	AIC	p
I	ESR			–0.26		–1.16		1.11				–46.83	0.020*
	DSR		–1.55									–32.35	0.329
II	ESR							1.26	–4.31	2.54	–0.95	–55.14	0.008*
	DSR											–55.29	0.007*
III	ESR											–41.90	0.019*
	DSR	7.85		0.29						–0.68		–64.30	0.032*
IV	ESR			–0.13				4.16		1.96		–11.01	0.021*
	DSR		–1.98									–24.49	0.053
V	ESR								–0.67		–0.57	–107.40	0.022*
	DSR	–2.32										–129.68	0.005*

1) I–V同图3。2) DSR, 落叶物种丰富度; ESR, 常绿物种丰富度。3) A, 坡向; AN, 土壤碱解氮; AP, 土壤速效磷; E, 海拔; pH, 土壤pH值; S, 坡度; SOM, 土壤有机质; SWC, 土壤含水量; TN, 土壤全氮; TP, 土壤全磷。4) AIC, 赤池信息准则。*, 显著相关($p < 0.05$)。

1) I–V see Fig. 3. 2) DSR, deciduous species richness; ESR, evergreen species richness; 3) A, aspect; AN, available nitrogen of soil; AP, available phosphorus of soil; E, elevation; pH, pH value of soil; S, slope; SOM, soil organic matter; SWC, soil water content; TN, total nitrogen of soil; TP, total phosphorus of soil. 4) AIC, Alkaike information criterion. *, statistical is significant at 0.05 level.

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被具有复杂多样、次生性强和过渡类型多等特点，更增加了该地区植被分类的困难(赖江山等, 2010)。传统的植物群落分类多根据群落的外貌特征及群落的种类组成划分群落类型，个人经验对分类结果的影响比较大(刘海江和郭柯, 2003; 刘万德等, 2010)。随着植被研究的精度要求不断提高，提供客观归类和划分结果的数量分类方法在植被分类中越来越重要(袁秀等, 2013)。目前数量生态学中的分类和排序方法已成为现代植被生态学研究中必不可少的手段，双向指示种分析法(TWINSPAN)和除趋势对应分析法(DCA)已广泛应用于森林和草地等植物群落分析(Ozinga *et al*., 2005; 孙菊等, 2009; 廉凯敏等, 2015)。本研究也证实了TWINSPAN分类与DCA排序这两种方法相结合应用于亚热带常绿落叶阔叶混交林植被数量分析是可行的，而且可以相互补充和交叉检验。

4.2 常绿和落叶物种比例随群落类型的变化及其环境解释

由于叶片是植物光合作用的主要场所，因而叶片的物候过程对于群落外貌、林下环境、凋落物分解和生态系统生产力具有重要作用(Bohlman *et al*., 1998; Quigley & Platt, 2003)。落叶是物种适应环境胁迫的一种重要策略，通过落叶可以回避不利生境对树木生长造成的伤害和不利影响(Poorter & Markesteijn, 2008)，低温和水分胁迫是阔叶树种落叶的重要原因(Lechowicz, 1984; Reich *et al*., 2004)。与热带部分地区树种因土壤水分亏缺而出现旱季落叶的情况不同(Williams *et al*., 2008; de Faria Lopes *et al*., 2012)，亚热带常绿落叶阔叶混交林的形成更多受到海拔升高而形成的低温胁迫的影响(Oliveira-Filho *et al*., 2006; 白坤栋等, 2010; 宋坤, 2012)。回归分析中土壤含水量与常绿和落叶物种分布并无显著的相关性，这个结果证明了研究区常绿和落叶物种的变化与土壤水分无关。温度是限制植物组成、生长、繁殖和分布的重要因子(Woodward, 1987)。研究地区冬季气温较低，一些喜温且生长迅速竞争能力强的常绿阔叶树种受到限制，但绝对低温尚较高，因此较耐寒的常绿阔叶树与落叶阔叶树均能生长，最终在该地段形成了亚热带常绿落叶阔叶混交林(吴征镒, 1980)。

从物种组成和群落结构来看，研究区各群落类型常绿和落叶物种存在一定的差异。群落I和群落IV的常绿和落叶物种在群落内的差异多不显著或者常绿物种大于落叶物种，而群落II、群落III和群落V则表现为落叶物种大于常绿物种。造成这种差异的主要原因可能是环境差异和人为干扰。环境是影响物种组成的决定性因素，环境因子组成的变化产生了不同的生境，从而引起不同地带及区域的物种差异(Toledo *et al*., 2011)。而人为干扰能够显著地改变群落结构和物种组成，从而影响群落的发展方向(Lomolino, 2001; Haberl *et al*., 2007; Nogués-Bravo *et al*., 2008)。群落III位于海拔较高的阳坡，随着海拔的升高，气温逐渐降低，光照强度增加，较低的气温和阳坡较好的光照条件促进落叶物种的生长(Malhi *et al*., 2010)。充足的光照也促进土壤种子库萌发，使群落内幼苗和幼树的密度较大。同时，群落III位于保护区森林防火隔离带附近，较频繁地受到了人为的干扰，干扰提高了林下的光照条件，导致群落内喜光的落叶树种增加和耐阴的常绿树种减少(Hawthorne, 1996; Bongers *et al*., 2009)。群落II和群落V分布于低海拔地区，长期受到人类樵采等活动的影响，林下的光照条件较好，群落内的落叶物种大于常绿物种。群落I和群落IV主要位于阴坡，且人为干扰较少，林内光照条件较差，适宜常绿物种的生长。

除地形因子和人为干扰之外，土壤养分也对常绿和落叶物种比例的变化产生了一定的影响。落叶物种分布区的土壤氮含量常被认为高于常绿物种分布区，其原因是落叶物种比常绿物种具有更高的氮矿化速率(Aerts & Chapin, 1999; Cornwell *et al*., 2008)，然而也有研究表明常绿和落叶物种的氮矿化速率并无显著差异(Reich *et al*., 2001; Booth *et al*., 2005)。本研究发现土壤氮含量在多数群落内与常绿物种丰富度显著正相关，这可能与不同群落类型的物种属性及真菌差异有关(Mueller *et al*., 2012)。总体来看，研究区常绿物种更易受土壤养分的影响。关于土壤养分对各群落内常绿和落叶物种分布的影响有待进一步深入分析。

4.3 常绿和落叶物种比例随胸径级的变化

除群落III外，各群落类型小径级(1–5 cm)内落叶物种的物种丰富度高于常绿物种，但多度、胸高断面积和重要值却表现为落叶物种小于常绿物种，这主要与常绿和落叶物种的生活型属性有关。研究区群落内小径级个体的生活型主要是小乔木和灌

木, 而大乔木个体密度相对较低。这些小乔木和灌木物种以常绿树种为主, 因此出现了小径级内落叶物种丰富度高但多度、胸高断面积和重要值低的现象。较高强度的干扰能够提高落叶树种在群落中的比例(丁易和臧润国, 2008), 群落III的小径级在各个指标上都是落叶树种占优势, 这可能说明人为干扰和环境条件显著影响了该群落的更新和发展方向, 导致该群落在未来一段时间内都将以落叶物种为主。大径级(≥10 cm)的落叶物种在多数群落内的物种丰富度、多度、胸高断面积和重要值均大于常绿物种, 表明落叶树种在林冠层占据显著的优势, Chabot和Hicks (1982)的研究也发现, 光照条件较好的林冠层落叶物种更多。林冠层落叶树种占据优势能够显著影响林下光照条件, 从而影响森林更新和物种多样性(Quigley & Platt, 2003)。落叶物种具有更高的资源养分利用效率(Kloeppel *et al*., 2000), 能够利用夏季良好的水热条件迅速获得碳水化合物完成高生长, 在与常绿树种的竞争过程中居于优势地位(Antúnez *et al*., 2001)。同时, 落叶物种采取了落叶的策略来适应研究区的冬季低温胁迫, 而常绿物种则保留叶片越冬, 低温可能损害常绿树种的气孔和光合速率而使常绿植物生长受到严重制约(Wyka & Oleksyn, 2014), 且较大的季节性温差所引起的冰凌和雪灾也可能造成常绿植物受到伤害从而限制其在林冠层的优势(白坤栋等, 2010)。林下的常绿树木由于林冠层的郁闭而受到光强的限制。尽管在林冠层落叶期间(晚秋到早春), 林下光照条件可以由于林冠层的落叶而得到改善, 但低温限制了林下常绿树木的生长。这种竞争最终形成了林冠层以落叶阔叶树为主和林下层以常绿树种为主的格局。

有关常绿、落叶物种随群落类型变化的具体机制还需要进一步深入细致研究, 如群落所处的具体小生境(土壤、地形和小气候等因子)、不同物种的生理生态特性与生态适应性等方面。这些研究将随着鄂西南地区森林动态样地监测平台的建设逐步开展。通过长期定位观测和基础研究, 阐明该地区常绿落叶阔叶混交林的恢复动态规律, 可为该地区基于生态系统功能的恢复实践提供重要的理论依据。

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附录1 鄂西南星斗山和木林子自然保护区亚热带常绿落叶阔叶混交林各样地物种名录

Appendix 1 List of species of the subtropical evergreen-deciduous broadleaved mixed forest across two national nature reserves in Southwest Hubei, China

http://www.plant-ecology.com/appendix/CJPE2015-10-A1.pdf