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We quantified plant diversity patterns according to changes in species composition, floristic richness, and species diversity in various plant communities in the Shilin karst area (24°38′– 24°58′ N, 103°11′– 103°29′ E, altitude 1600–2203 m) of central Yunnan, China, in which the previous land use had been documented. Cluster analysis of floristic similarity of all the stands showed that plant species composition and diversity were primarily influenced by the legacies of land use (as coppices, pastures, and plantations). The DCA (detrended correspondence analysis) grouped 14 sampling transects into 3 plant communities, including a shrubland, a mixed deciduous and evergreen broad-leaved stand (secondary forest), and a premature semihumid evergreen broad-leaved stand (natural premature forest), along a disturbance gradient. We also analyzed Pinus plantations. While plant species diversity was particularly low in the Pinus plantation, stands developing (secondary forest) on former coppice sites were becoming increasingly similar to the natural premature forest. The results would indicate that vegetation and plant species diversity is more efficiently restored by letting degraded vegetation regrow rather than establishing plantations.

Introduction

There are 620,000 km^2 of karst landforms in southwestern China, where various types of evergreen broad-leaved forests grow across a wide climatic range (Wu 1980). These karst ecosystems are known to be extremely vulnerable to erosion due to large-scale tree cutting, pasture creation, slash-and-burn agriculture, and collection of fuelwood (Cao et al 2003; Wang and Liu 2004; Zhang et al 2006). Karst rock resulting from land degradation—mainly induced by a rapid reduction of vegetation cover—as well as soil degradation in the fragile eco-geo-environment have led to depletion of biodiversity and destruction of habitats (La Moreaux et al 1997; Pan et al 2002; Academic Divisions of CAS 2003).

Biodiversity is a key element of vegetation dynamics during succession (Faliński 1986; Knapp 1986) and has been recognized as an important component of sustainable development (O'Riordan 2002). The ways in which plant species respond to disturbances can lead to recommendations for the recovery of forest ecosystems (Bazzaz 1983; Oliver and Larson 1990; Foster et al 1999).

Previous studies of secondary forests have revealed that plant communities under various degrees of human disturbance can be considered spatially and temporally dynamic patches of vegetation, showing recovery toward the original natural vegetation (Wang et al 2007; Fukushima et al 2008; Tang et al 2010).

A government policy of "returning the agricultural land to the forests" was implemented between the mid-1980s and late 1990s in China, including a vast project of sowing Pinus seeds from airplanes. Since then the secondary plant communities (also called the naturally regenerated plant communities) have been in the process of succeeding toward the state of original natural forests (Tang et al 2007; Tang 2010; Tang et al 2010). Secondary plant communities may act as reservoirs for recolonization and as corridors between remaining primary forest fragments.

It is essential to examine the current state of biodiversity in secondary plant communities to provide guidance for the management of conservation areas, for nature-friendly land use, and for the restoration of the forests (Wang et al 2006). Forests under local user group

management can be restored from highly degraded states (Webb and Khurshid 2000; Webb and Gautam 2001). At present, the plant diversity patterns in these karst areas are poorly understood and scantily documented. The land-use history in the Shilin karst area in Yunnan reflects varying degrees of human disturbance. In this study, we aim to document floristic richness and diversity of both woody and herbaceous species in various natural secondary stands now in the process of recovery, and to include, for comparison, the diversity found in monospecific plantations in the same area.

Methods

Study area

This study was carried out in the Shilin karst area ($24°38'$–$24°58'$N, $103°11'$–$103°29'$E, alt. 1600–2203 m) of central Yunnan (Figure 1). The area covers about 900 km^2 underlain by Permian carbonate rocks, of which more than 400 km^2 have developed into karst and related landforms. At an altitude of 1680 m, the mean annual precipitation is 967.9 mm, 80% of which falls between May and October. The mean annual temperature is 16.2°C, mean maximum temperature is 20.7°C (July), and mean minimum temperature is 8.2°C (January). The land consists of rock gaps, rock ditches, small rock caves, and rock slots, all of which are surrounded by soil. The soil is shallow and patchily distributed on or between these various rock surfaces. The ratio of outcrops to soil ranges from 0.3 to 1.3.

The original vegetation in the area was semihumid evergreen broad-leaved forest dominated by evergreen species of Fagaceae. Most of this forest had previously been utilized as coppices for fuelwood or pastures, but since the 1980s, some of these have been replanted by plantations of

Pinus yunnanensis. Other remnant coppices and pastures were abandoned in the 1980s and have since regenerated naturally, with secondary stands consisting of evergreen and deciduous broad-leaved trees or shrubs. These secondary woodlands and *Pinus* plantations have been unmanaged since they were planted or were later abandoned. The landscapes appear as dynamic habitats consisting of mosaics of diverse stands at various stages of vegetation recovery.

Data collection and analysis

The plant communities are heterogeneous in structure and species composition. We surveyed all the vegetation patches in the area. Based on the topography, we randomly selected 4–5 transects for each patch in Soyishan, Yuehu, Naigushan, and Songlinhoushan. A transect of arbitrary length was selected and divided into 10 m × 10 m quadrats. In total, we made 14 transects for natural secondary plant communities and 4 transects for plantations to analyze the plant diversity pattern. In view of the relationship between the minimal area of a transect and the maximum number of species, our quadrat sampling was continued at each transect until no new species were encountered in three contiguous quadrats. In total, 2.32 ha were sampled. In studying the overstory of the plant communities, a tree inventory was carried out for all the individuals at least 1.3 m high in each quadrat. All were tagged with number tape, recorded with species name, whether living or dead, diameter at breast height (DBH) (including all stem stumps and sprouts), and tree height (H). We randomly selected two 2 m × 2 m plots in each quadrat to investigate the woody species (H < 1.3 m) in the understory. For herbaceous species investigation, we randomly selected two 1 m × 1 m subplots in each

quadrat. All the species were identified and the number of individuals counted. In this study, herbs included forbs, ferns, graminoids, and herbaceous lianas.

The species basal area (BA, cm^2) of plants was calculated from DBH (diameter at breast height) data for all the stems of woody species, and the relative proportion of BA (RBA) was calculated for the species (%). To determine which woody species were dominant, a dominance analysis (Ohsawa 1984) was carried out.

For each transect, the diversity indices were calculated using the Shannon index, $H' = -\Sigma(n_i/N)Ln(n_i/N)$, where N is total number of individuals, and n_i is the number of ith species (Pielou 1969), and Fisher's alpha, $S = \alpha*Ln(1 + n/\alpha)$, where S is number of taxa, n is number of individuals, and α is Fisher's alpha (Williams 1947). For all the transects in each plant community type combined, the Jaccard index (beta diversity) was used to compare each of the different nonnatural plant communities to the natural forest: $Cj = j/(a + b - j)$, where Cj is the Jaccard index, a and b are the total number of species for the two communities, and j is the number of common species among the two communities.

Plant communities excluding plantations were delineated using detrended correspondence analysis (DCA; Hill 1979). The PCORD program (McCune and Mefford 1999) was used to perform the analysis. In this paper, natural premature forest is considered as one of the natural secondary plant community types due to its partial cutting in the past. Differences in floristic richness and diversity indices among the natural secondary plant communities and plantations were tested by analysis of variance (ANOVA) and the Tukey-Kramer test for unequal sample sizes. The statistical analyses were performed using a package, STATISTICA (StatSoft, USA).

Results

Vegetation
From the floristic similarity dendrogram of 18 transects obtained by cluster analysis, the transects were classified into 4 community types: natural premature forest (NF), secondary forest (SF), shrubland (SL), and *Pinus* plantations (PP) (Figure 2A). Natural premature forest was dominated by evergreen *Cyclobalanopsis glauca*, *Neolitsea homilantha*, *Olea yunnanensis*, and accompanied by deciduous *Ilex macrocarpa*, *Pistacia weinmannifolia*, and *Carpinus mobeigiana*, constituting a premature stage of a typical semihumid evergreen broad-leaved forest in central Yunnan. This type of plant community was partially cut for fuelwood 25 years ago, but there has been no human activity since then. True primary forests are practically nonexistent in the area. The secondary forest was dominated by *Cyclobalanopsis glauca*, *Olea yunnanensis*, and *Pistacia weinmannifolia*, representing a natural process formed from an abandoned coppice that was utilized for fuelwood cutting until 1990. The shrubland was dominated by *Neolitsea homilantha*, which began to grow after the abandonment of a pasture in 1989. The *Pinus* plantation was exclusively dominated by *Pinus yunnanensis*, which grew after seed dispersal by airplanes in 1980.

The community structure varied among the four community types (Figure 2B). The maximum height and DBH in the natural premature forest (NF) were 25 m and 68.2 cm, respectively. In the secondary forest (SF) trees were 14 m tall and 33.4 cm DBH; in the shrubland (SL), they were 8.5 m tall and 9 cm DBH; and in the *Pinus* plantation (PP), they were 15 m tall and 26.8 cm DBH. Basal area density was 19.2 m^2/ha in the natural premature forest, 11.3 m^2/ha in the secondary forest, 1.3 m^2/ha in the shrubland, and 4.7 m^2/ha in the planted *Pinus* forest. The secondary forest had higher stem density (3748 stems/ha) than the others (2437 stems/ha for NF, 881 stems/ha for SL, and 594 stems/ha for PP). Many sprouts in the secondary forest were the result of fuelwood cutting in the past.

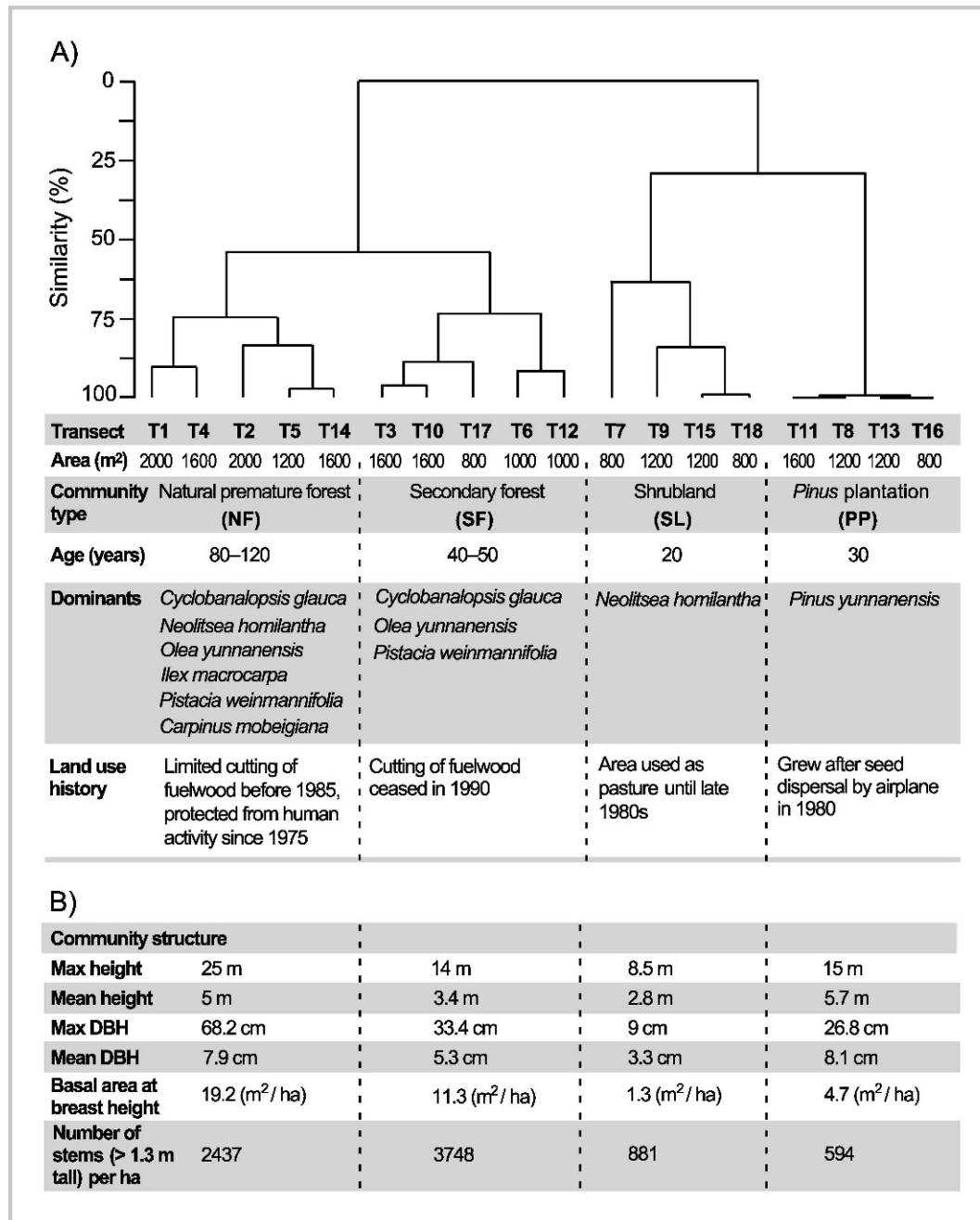### Ordination of natural secondary plant communities
The DCA ordination of all transects except those of the *Pinus* plantation (Figure 3) shows an eigenvalue for the first axis of 0.660 and the second axis of 0.266. This order reflects a varying intensity of human disturbance and the resulting status of the plant communities. From right to left along the first axis, the scatter corresponds to various degrees of past human disturbance (from total removal to create pastureland, to intense cutting for fuel, to limited cutting for fuel).

Floristic composition
We recorded 222 species, including 109 woody species (trees, shrubs, and lianas) and 113 herbaceous species (forbs, ferns, graminoids, herbaceous lianas), of 183 genera in 79 families in the 14 transects of natural secondary plant communities and the 4 transects of the *Pinus* plantation.

Overstory (H ≥ 1.3 m tall): Sixty-four woody species (trees and shrubs) in the overstory (H ≥ 1.3 m tall) were found in the three natural secondary plant communities and the *Pinus* plantation (*Supplemental material*, Appendix S1; http://dx.doi.org/10.1659/MRD-JOURNAL-D-10-00021.S1). The one-time plantation was dominated by light-demanding coniferous *Pinus yunnanensis* in PP. In the shrubland (SL), 18 species were found. Light-demanding evergreen broad-leaved *Neolitsea homilantha* dominated SL, along with evergreen *Olea yunnanensis*, and deciduous *Pistacia weinmannifolia*. In the secondary forest (SF), 26 species were found, dominated by shade-tolerant evergreen *Cyclobalanopsis glaucoides*, *Oleas yunnanensis*, and light-demanding deciduous *Pistacia weinmannifolia*. In the natural premature forest (NF), 53 species were found, dominated by shade-tolerant evergreen trees *Cyclobalanopsis glaucoides* and *Olea yunnanensis*, along with evergreen *Neolitsea homilantha* and deciduous *Pistacia weinmannifolia*, *Ilex macrocarpa*, *Pistacia chinensis*, and *Carpinus mobeigiana*. The RBA of shade-tolerant species increased

FIGURE 2 Similarity dendrogram using Sørensen's relative similarity index and group average clustering (A), and community structural features (B).

A)

Transect	T1	T4	T2	T5	T14	T3	T10	T17	T6	T12	T7	T9	T15	T18	T11	T8	T13	T16
Area (m²)	2000	1600	2000	1200	1600	1600	1600	800	1000	1000	800	1200	1200	800	1600	1200	1200	800
Community type	Natural premature forest (NF)					Secondary forest (SF)					Shrubland (SL)				*Pinus* plantation (PP)			
Age (years)	80–120					40–50					20				30			
Dominants	*Cyclobanalopsis glauca* *Neolitsea homilantha* *Olea yunnanensis* *Ilex macrocarpa* *Pistacia weinmannifolia* *Carpinus mobeigiana*					*Cyclobanalopsis glauca* *Olea yunnanensis* *Pistacia weinmannifolia*					*Neolitsea homilantha*				*Pinus yunnanensis*			
Land use history	Limited cutting of fuelwood before 1985, protected from human activity since 1975					Cutting of fuelwood ceased in 1990					Area used as pasture until late 1980s				Grew after seed dispersal by airplane in 1980			

B)

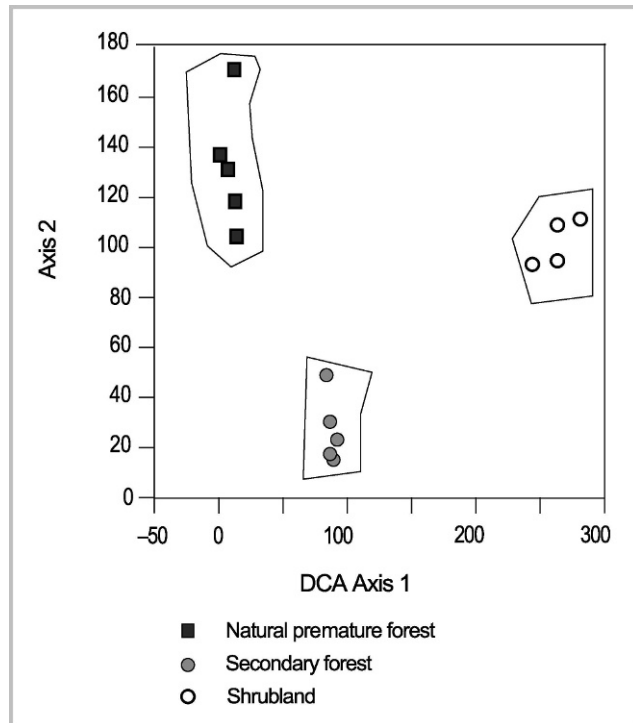| Community structure				
Max height	25 m	14 m	8.5 m	15 m
Mean height	5 m	3.4 m	2.8 m	5.7 m
Max DBH	68.2 cm	33.4 cm	9 cm	26.8 cm
Mean DBH	7.9 cm	5.3 cm	3.3 cm	8.1 cm
Basal area at breast height	19.2 (m²/ha)	11.3 (m²/ha)	1.3 (m²/ha)	4.7 (m²/ha)
Number of stems (> 1.3 m tall) per ha	2437	3748	881	594

while the RBA of light-demanding species decreased in the overstory from the shrubland, to the secondary forest, and finally to the natural premature forest along the past disturbance gradient (Figure 4).
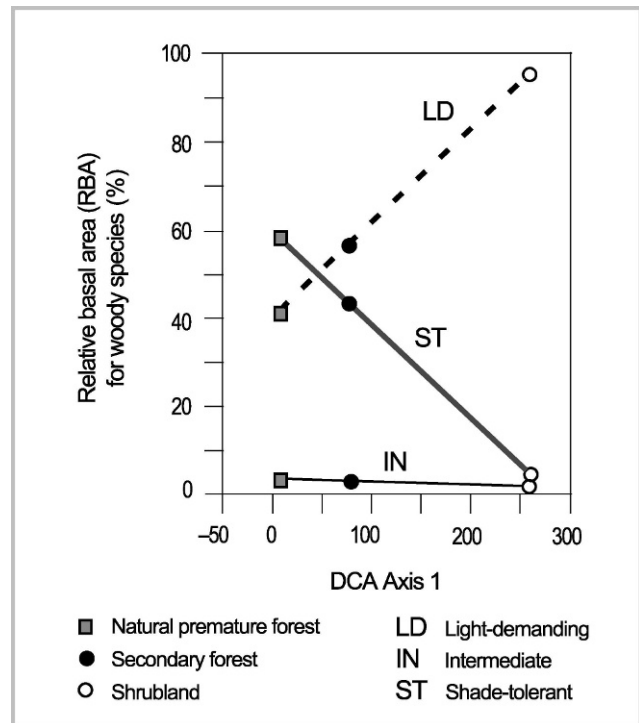
Understory

1. Woody species (H < 1.3 m tall): Eighty-seven woody species were present in the understories of the three natural secondary plant communities and the *Pinus* plantation. The highest number (57) of species was found in the shrubland (SL). All of them were light-demanding shrub species, except for 5 intermediate and 3 shade-tolerant species. As for the relative number of seedlings of the dominant trees in each plant community, the secondary forest (SF) reached

FIGURE 3 Ordination of the 14 transects of natural secondary plant communities using detrended correspondence analysis (DCA).

FIGURE 4 Relative basal area (RBA) of woody species with different traits for the overstory (H $\geq$ 1.3 m high) of natural secondary plant communities along DCA axis 1.

45.4%, while the natural premature forest (NF) was at 40.2%, the shrubland (SL) at 5.3% and the *Pinus* plantation (PP) at 1%. In the SF, seedlings of light-demanding *Pistacia weinmannifolia* had the highest proportion (22.5%). The seedlings of the shade-tolerant evergreen tree *Cyclobalanopsis glaucoides* amounted to 9.3% in NF, 2.9% in SF, 0.04% in the SL, and none in the PP (Table 1).

2. Among the 113 herbaceous species, 61 were found in the natural premature forest (NF), 53 in the secondary forest (SF), 52 in the shrubland (SL), and 51 in the *Pinus* plantation (PP) (Table 2). The average abundance of herbs in the secondary forest (SF) was significantly lower than in the other 3 plant communities (Table 2). In total, 8 invasive species were found; most of them were in nonnatural premature stands, but 3, including *Ainsliaea bonatii*, *Eupatorium adenophorum*, and *Senecio scandens*, were also found in the natural premature forest (NF).

Floristic richness and diversity

The parameters of plant diversity of natural secondary plant communities and the *Pinus* plantation are shown in Figures 5 and 6. In floristic richness, including both woody and herbaceous species in terms of number of species, number of genera, and number of families in each transect, the natural premature forest had values significantly higher than the

shrubland and the secondary forest (Figure 5A–C). The secondary forest had a significantly higher number of species than did the shrubland. The shrubland had significant higher values than the *Pinus* plantation. The number of either woody or herbaceous species, using Shannon's H′ and Fishers' alpha, showed the secondary forest to be increasingly similar to the natural premature forest (Figure 6A–F). The number of woody species, using Shannon's H′ and Fisher's alpha of woody species in the shrubland, had significantly higher values than those of the *Pinus* plantation, while the numbers of herbaceous species, using Shannon's H′ and Fisher's alpha for herbs in the shrubland, were not significantly higher than those for the *Pinus* plantation

When the data for all the transects in each plant community were combined, Sørensen's similarity index (beta diversity) between the secondary forest (SF) and the natural premature forest (NF) was 34%; between the shrubland (SL) and the natural forest (NF), it was 18%; and between the *Pinus* plantation (PP) and the natural forest (NF), it was 7.6%.

Discussion

Change in species diversity during the recovery of vegetation

Biodiversity is in the process of being destroyed, and increasing numbers of species have been lost on a global

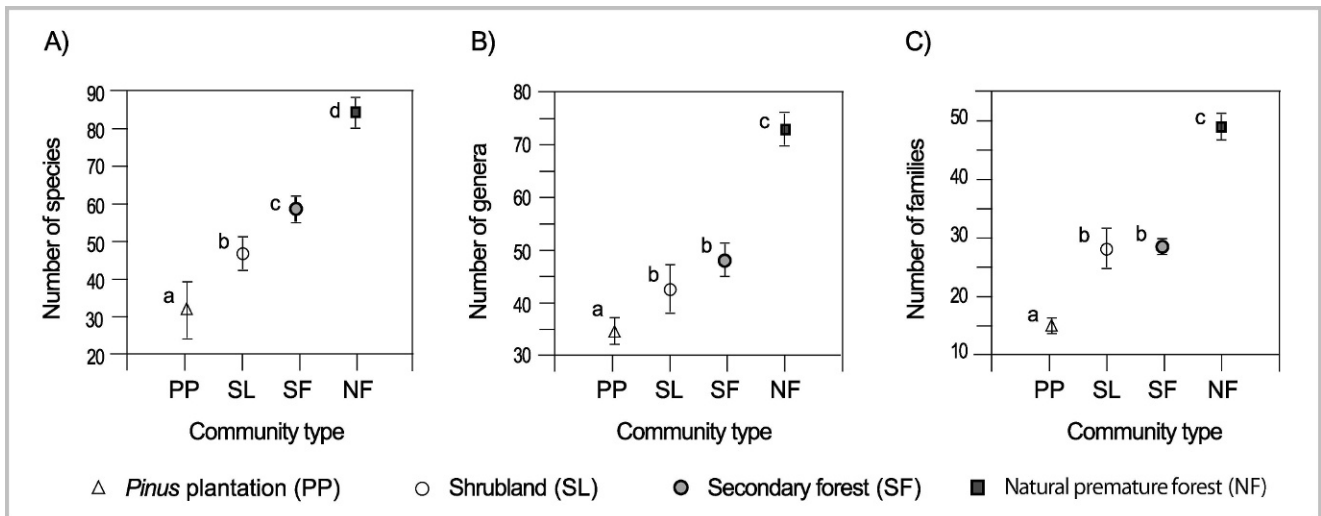**TABLE 1** Characteristics of the woody species in the understory of each plant community.[a]

Plant community	Plantation	Natural secondary plant communities		
	PP	SL	SF	NF
Total number of species	24	57	42	37
Relative number of individuals for seedlings of dominant trees (%)				
Pinus yunnanensis	0.98			
Neolitsea homilantha		2.76	8.35	6.42
Olea yunnanensis		1.53	11.54	11.59
Pistacia weinmannifolia		0.86	22.53	11.84
Pistacia chinensis		0.11	0.11	0.13
Cyclobalanopsis glaucoides		0.04	2.90	9.25
Carpinus mobeigiana				0.92

[a] PP, *Pinus* plantation; SL, shrubland; SF, secondary forest; NF, natural premature forest.
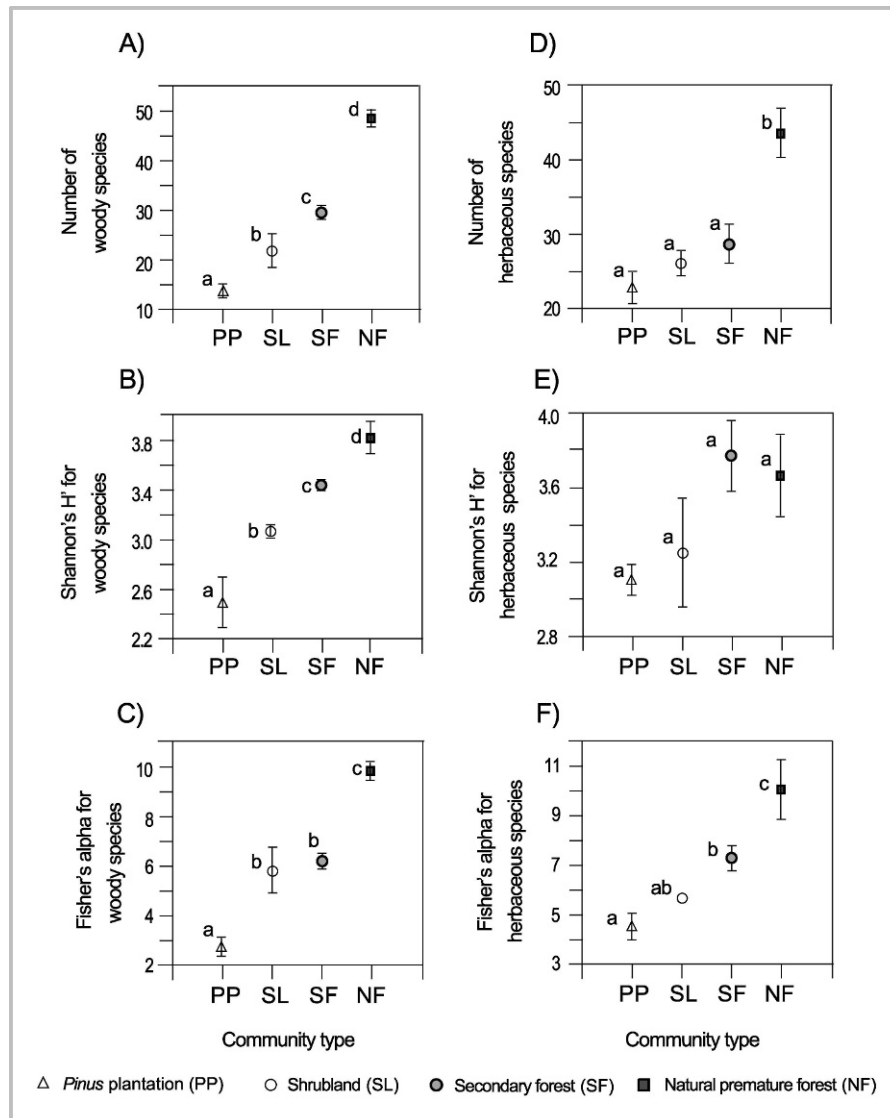
TABLE 2 Characteristics of herbaceous species in the understory of each plant community. Data in one-hundred 1 m × 1 m subplots were combined for each plant community.[a]

Plant community	Plantation	Natural secondary plant communities		
	PP	SL	SF	NF
Total number of species	51	52	53	61
Total abundance (no. of individuals)	6208	5447	2893	6456
Average abundance ± SD (plants per 1 m × 1 m)	57.8 ± 14.9*	53.3 ± 15.5*	39.8 ± 27.1**	63.3 ± 36.7*

[a] PP, *Pinus* plantation; SL, shrubland; SF, secondary forest; NF, natural premature forest. Asterisks denote significantly different means, $P < 0.05$.

FIGURE 5 Floristic richness for woody and herbaceous species among the *Pinus* plantation and natural secondary plant communities (A to C). Significantly different values are indicated by different letters, $P < 0.05$. Bars represent standard error.

FIGURE 6 Changes in diversity indices for woody and herbaceous species among the *Pinus* plantation and natural secondary plant communities (A to F). Significantly different values are indicated by different letters, $P < 0.05$. Bars represent standard error.

scale in recent years (Pimm et al 1995; Balmford et al 2003; Jenkins et al 2003). With the disappearance of almost all primary forests, secondary plant communities have become one of the ubiquitous vegetation types. In the secondary succession in the subtropical area in China, the middle successional stage—represented by secondary evergreen and deciduous broad-leaved forest or secondary conifer and broad-leaved forest—had higher species richness and diversity than the early successional stage, and sometimes than the late successional stage, because many species with different traits (light demanding, intermediate, and shade tolerant) occurred in the mixed forests (He et al 1998; Guo et al 1999; Jin 2002; Tang et al 2010). In the Shilin karst area, the species diversity in the secondary forest dominated by

evergreen *Cyclobalanopsis*, *Olea*, and deciduous *Pistacia* has not yet reached its peak. As time goes by, it is to be expected that the secondary forest will continue to increase in species diversity and in similarity to the natural semihumid evergreen broad-leaved forest.

Peng and Fang (1995) and Peng (2003) have reported that fast-growing single-species plantations can be generally regarded as a pioneer stage that accelerates the process of succession and improves the development of species diversity in tropical and subtropical areas of China. However, this study shows that a 30-year-old *Pinus* plantation had particularly low woody species diversity and poor regeneration quality in the understory, even when compared with a 20-year-old

shrubland that grew naturally from an abandoned pasture.

Conclusion

We conclude that secondary plant communities are also worth conserving, as we conserve the potential for natural mature forest. This study demonstrates that plantations of single species do not lead to efficient vegetation restoration, as indicated in the lack of plant diversity in plantations in the Shilin karst area. Our findings can be incorporated into management plans for sustainable management and conservation of biodiversity in the fragile mountainous karst areas in Yunnan.

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Supplemental data

APPENDIX S1 Woody species (H ≥ 1.3 m tall) composition in the overstory of each plant community. Values represent the relative basal area (RBA) for each species. Dominant species are shown in boldface.

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