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RESEARCH ARTICLE

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Changes in species composition and diversity in the restoration process of sub-alpine dark brown coniferous forests in western Sichuan Province, China

Abstract By adopting the concept of space as a substitute for time, we analyzed the dynamics of species composition and diversity of different restoration sequences (20, 30, 40, 50 years) in two secondary forest types in western Sichuan Province, distributed in a northerly or northwesterly direction. The analysis was based on the results of measurements of 50 plots located at elevations between 3100–3600 m. The forests originated from natural regeneration in combination with reforestation of spruce when the old-growth bamboo-dark brown coniferous forests and moss-dark brown coniferous old growth forests were harvested. Similar old-growth dark brown coniferous forests at ages ranging between 160 and 200 years were selected as the reference forests for comparisons. We recorded 167 species of vascular plants from 44 families and 117 genera. There was no significant difference in terms of the number of species among secondary forests. But the importance values of dominant species varied during the restoration processes. The dominant species in the secondary forests is *Betula albo-sinensis*, while *Abies faxoniana* is the dominant species in old-growth dark brown coniferous forests. Species richness increased significantly with restoration processes. It increased quickly in secondary forests during the period from 30 to 40 years, but decreased significantly in the old-growth dark brown coniferous forests. The species richness among growth forms decreased in the following order: herb layer > shrub layer > tree layer. The maximum value of the evenness index occurred in secondary forests at age 40 and remained relatively stable in the bamboo-birch forests, but the evenness index tended to decrease in moss-birch forests and slightly increased in the old-growth moss-dark brown coniferous forests. There was a statistically significant difference in the evenness index between the tree and shrub layers as well as between the tree layer and the herb layer, but there was no significant difference between the shrub layer and the herb layer. The value of the Shannon index increased over restoration time. In bamboo-birch forests, the maximum value of the Shannon index was 3.80, recorded at age 50. In moss-birch forests, the maximal value was 3.65, reached in this forest at age 30. The value of the Shannon index of old-growth dark brown coniferous forests was recorded between younger secondary and older secondary forests. The value of the dominance index of communities varied. At the first stage of restoration, it increased, and at the end it was decreased. The dominance index of the tree layer had a similar trend as that of the community dominance index, but was more variable. The minimum value of the dominance index of the tree layer in the moss-birch forests reached 20 years earlier than that of the bamboo-birch forests. There was a significant difference among restoration sequences in the α diversity indices except for the dominance index. No significant differences between the two secondary forest types were detected. Over age, the value of the Bray-Curtis index between secondary forest and old-growth dark brown coniferous forest increased.

Keywords species composition, species diversity, degradation, dark brown coniferous forests, forest restoration, sub-alpine, western Sichuan

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1 Introduction

Community diversity is an important research area in community ecology, indeed in all areas of ecology (Shi et al., 2002b). Any community or ecosystem has characteristics of species diversity, which is the biological basis on which to maintain ecosystem functions (Tilman and Downing, 1994; Grime, 1997; Zhang et al., 2004). Study on species diversity could embody the type of structures, the organizational level, the development phase, the degree of stability and site differences in the community or ecosystem (Yan et al., 2001). Restoration of species diversity has become an important characteristic of ecosystem restoration (Lin et al., 2001). The maintenance and development of biodiversity are two main objectives in ecosystem restoration (Young, 2000; Zerbe and Kreyer, 2006). In many restoration practices, diversity is regarded as one of the main indicators in evaluating the restoration effects (Ruiz-Jaen and Aide, 2005). When species composition and diversity are studied, the relations between elevation gradients, the process of forest restoration and species diversity are usually the main issues in the research (He and Chen, 1997; Guariguata et al., 1997; Vázquez and Givnish, 1998; Wen, 1998; Wu et al., 2001; Bao et al., 2002; Hao et al., 2002a; Shi et al., 2002a; Zhao et al., 2002; Ishida et al., 2005).

The western Sichuan sub-alpine forest is an extension of the Qinghai-Tibet Plateau towards southeastern China and one of the major areas of biodiversity research (Yang et al., 2003). The major component of the western Sichuan sub-alpine forest is the dark brown coniferous forest (Zhang et al., 2005a). Forests in this area has been over-exploited on a large scale since the 1950s, leading to a rapid decrease in vegetation coverage, the loss of some species and degradation in the functioning of the ecosystem (Liu et al., 2001). The restoration of the sub-alpine dark brown coniferous forest is very necessary and pressing. Most of the research in this area has been focused on structural and functional changes in plantations. Much less researches have been directed towards the dynamics of a series of secondary forest structures in different forest restoration efforts after the dark brown coniferous forests were clear-cut. The only research mentioned on this aspect has been that of woodland hydrological effects (Zhang et al., 2005b). In order to study the changes in species composition and diversity in the restoration process of these sub-alpine dark brown coniferous forests, with important consequences for understanding the ecological processes and mechanisms, we must evaluate the forest restoration process and accelerate restoration of the degraded dark brown coniferous forest ecosystem. We have used the α and β diversity indices to analyze the changes and characteristics of different forests restoration efforts in western Sichuan. This would provide a reference for the conservation of biodiversity and a synthesis of ecosystem management of these degraded dark brown coniferous forests.

2 Study site

Study sites were located in the Miyaluo Forest Region (31°24′–31°55′N, 102°35′–103°4′E, elevation of 2200 to 5500 m) of western Sichuan, with an extension to the Qinghai-Tibet Plateau towards southeastern China. The climate is characterized by dry cold winters and wet cool summers. Mean monthly temperatures, at the elevation of 2760 m, are the highest in July at 12.6°C and the lowest in January (−8°C). Annual precipitation is 700–1000 mm and the annual evaporation 1000–1900 mm. The annual accumulated temperature ⩾10°C is between 1200 and 1400°C. The terrain is steep, deeply dissected and complex. Forest soils in the Miyaluo region consist mainly of mountain brown and mountain dark brown soils.

Affected by ridges and the undulating topography of the Qing-Tibet Plateau, its thermal pattern, water distribution, microclimate, soil and vegetation vary greatly along vertical elevation gradients (Jiang, 1963a). There is a sub-alpine needle-broadleaf forest belt below 2700 m elevation. At elevations between 2700 and 4000 m, there are sub-alpine coniferous forests and a sparse alpine forest belt. Above 4000 m, there are alpine meadows, alpine deserts and a snow zone (Jiang, 1963b). In the sub-alpine dark brown coniferous forest belt, a number of forests are derived from bamboo-conifer forest types, distributed at the northern or northwestern slopes at elevations between 3100 and 3500 m. However, other groups of forests are derived from moss-conifer types, distributed at the northern or northwestern slopes, or at moist valley bottoms, at elevations between 3300 and 3600 m. Bamboo and moss-conifer forests are the major forest types in the sub-alpine dark brown coniferous forest belt. Usually, forests derived from the same forest types and have been disturbed, e.g., by logging, undergo the same long-term successional process. For example, when bamboo or moss-conifer forests are logged, they form bamboo-birch forests or moss-birch forests at an early forest restoration stage.

Forest in the Miyaluo region experienced large scale logging between 1950 and 1978. After 1978, the yield decreased gradually and stopped altogether in 1998, when the Protection of Natural Forest in China was promulgated. The logging sites, largely between elevation 2800 and 3600 m, were the main sites of old-growth, sub-alpine dark brown coniferous forests (Zhang et al., 2005b). These sites provide a chance to study the restoration of degraded dark brown coniferous forest at various stages in the progression of forest succession. The dominant tree of the remaining old-growth dark coniferous forest is *Abies faxoniana*. The most abundant tree species of the secondary forests in the study area is *Betula albo-sinensis*. The following shrub species are present: *Sinarundinaria chungii*, *Rhodoendron* spp., *Rosa* spp., *Euonymus* spp., *Lonicera* spp., *Ribes* spp., *Cotoneaster* spp., *Berberis* spp., *Acanthopanax gracilithlus* and the herbage species are *Smilacina japonica*, *Streptopus obtusatus*, *Allium ovalifolium*, *Girardinia suborbiculata*, *Smilax* spp., *Asarum himalaicum*, *Circaea alpine*, *Parasenecio* spp., *Thalictrum* spp., *Anemone rivularis*, *Oxalis graffiti* and *Clintonia udensis*.

3 Methods

3.1 Field survey

By adopting the concept of space as a substitute for time, six plots represented, respectively, a bamboo-broadleaf forest (20–40 years), a bamboo-needle-broadleaf mixed forest (50 years), a bamboo-old-growth dark brown coniferous forest (160–200 years); a moss-broadleaf forest (20–40 years), a moss-needle-broadleaf mixed forest (50 years) and a moss-old-growth dark brown coniferous forest (160–200 years). These plots are located on shaded or half-shaded slopes with gradients between 20° and 40° at elevations between 3100 and 3600 m. We sampled 5–10 quadrats in each plot. Fifty tree-quadrats (20 m × 20 m each), 200 shrub-quadrats (10 m × 10 m each) and 500 herb-quadrats (1 m × 1 m each) were selected. Specific names, number of trees, diameter at breast height (*DBH*) and height of each tree were recorded and mapped from the tree quadrats. Specific names, coverage, mean height of shrubs and abundance, number of shrubs and clonal shrubs were recorded in the shrub- and herb-quadrats. We also counted the number of snags ($DBH \geqslant 5$ cm) and stacks of logs.

3.2 Importance value

Hao et al. (2002b) defined the concept of importance value for trees and shrubs or herbs.

Importance value of a tree = (relatively abundance + relatively dominance + relatively frequency)/3

Importance value of shrub or herb = (relatively height + relatively coverage + relatively frequency)/3

3.3 Measurement of α diversity

We used the Shannon index (H') to study species diversity and the number of species (S) to study species abundance (Hao et al., 2002a, 2002b). The formula for calculating H' is as follows:

$$H' = -\sum_{i=1}^{S} p_i \ln p_i \quad (1)$$

where p_i denotes the relatively importance value of species i, and S the number of species in the samples.

The formula for evenness index (J) is as follows (Hao et al., 2002a):

$$J = \frac{H'}{\ln S} \quad (2)$$

We used the Simpson index (D) to measure community dominance. The formula of the Simpson index is:

$$D = \sum_{i=1}^{S} P_i^2 \quad (3)$$

Based on the importance value, these indices account for diversity, evenness and dominance (Peng, 1996; Hao et al., 2002a).

3.4 Measurement of β diversity

We used the Bray-Curtis index to account for β diversity. The formula is as follows:

$$C_N = \frac{2j_N}{a_N + b_N} \quad (4)$$

where a_N denotes the number of species in sample A, b_N the number of species in sample B and j_N the total number of relatively small, individual community species in samples A and B.

The importance values were used as measurement indicators to calculate the Bray-Curtis index. This index is based on the Sorenson index (Ma et al., 1995; Gao et al., 1998).

3.5 Statistical analysis

Data were analyzed statistically using SPSS (version 12.0) and SigmaPlot (version 10.0) to draw the figures.

4 Results

4.1 Species composition at different forest restoration sequences

In the bamboo-birch forest, located in shaded or half-shaded slopes at elevations between 3100 and 3500 m and the moss- birch forest, also in shaded or half-shaded slopes at elevations between 3300 and 3600 m, 167 species of vascular plants were recorded from 44 families and 117 genera, found in the fifty 20 m × 20 m quadrats. There were no significant differences in terms of the number of species of these two secondary forests. But the importance value of the dominant species varied with the sequence during the restoration processes. *Betula albo-sinensis* and *Abies faxoniana* constitute the main species in the tree layer of the secondary forests. *Sorbus koehneana*, *Prunus tatsienensis* and *Acer* spp. occur mainly in the bamboo-birch forest, while *Sorbus hupehensis* and *Prunus pilosiuscula* occur largely in the moss-birch forest. *Rosa omeiensis*, *Lonicera nervosa* and *Euonymus porphyreus*, as the common species, occur in the shrub layer of both the bamboo-birch and the moss-birch forests. There are some other dominant shrub species in the two secondary forests. For example, *Sinarundinaria chungii*, *Cotoneaster dielsianus*, *Smilax stans*, *Berberis diaphana*, *Acanthopanax gracilithlus* and others are found in the bamboo-birch forest, as well as such warm adaptation species as *Acer mono*, *Acer laxiflorum* and *Helwingia japonica*. However, in the moss-birch forest, there are fewer shrub species, such as *Ribes glaciale*, *Cotoneaster davaricatus* and a small number of other species. In the herb layer of both forest types, the common species are *Girardinia suborbiculata*, *Smilacina japonica*, *Asarum himalaicum*, *Allium ovalifolium*, *Parasenecio otopteryx* and *Parasenecio palmatisectus*. Besides these, *Streptopus obtusatus*, *Smilacina henryi*, *Ophiopogon japonicus*, *Rodgersia aesculifolia*, *Geranium henryi* and *Galium bungei* are found in the bamboo-birch forests as well as *Oxalis griffitii*, *Galium* spp., *Iris* spp., *Picris hieracioides* and a few others. *Abies faxoniana* is the dominant species in the tree layer of old-growth dark brown coniferous forests. In the shrub layer, besides the common species such as *Ribes glaciale*, *Lonicera nervosa* and *Cotoneaster foveolatus*, there are a few dominant species such as *Sinarundinaria chungii* in the old-growth bamboo-dark coniferous forests. In the herb layer, species such as *Girardinia suborbiculata* and *Circaea alpina* and a few others occur. *Betula albo-sinensis*, as a shade intolerant species with a life span of 160 years, could dominate the crown canopy for a long time and maintain a considerable effect on forest communities. Shade tolerant and semi-tolerant species occur in the forest communities quite frequently.

4.2 α diversity at different forest restoration sequences

From Fig. 1 and Table 1, it is seen that species richness increased significantly with the progress of the restoration processes. The maximum value of species richness in secondary forests occurs at age 50. The number of species in the 50-year-old bamboo-birch forest is 77 and there are 67 species in 50-year-old moss-birch forests. Species richness increased quickly in the secondary forests between ages 30 and 40. After that, the index gradually reached a peak value that was maintained at this level in the old-growth dark brown coniferous forests. Table 2 shows a significant difference in species richness among growth forms at different forest restoration sequences. The species richness among growth forms decreased in the following order: herb layer > shrub layer > tree layer, and reflects the interspatial distribution pattern of species diversity in the communities. The time required for species richness to reach its maximum value among the various growth forms is not the same. In the two forest types, the maximum value of species richness in the tree layer occurred at age 40 in the bamboo-birch forest and in the moss-birch forest at age 30. The maximum value of species richness in the shrub layer occurred at age 50 in the bamboo-birch forest

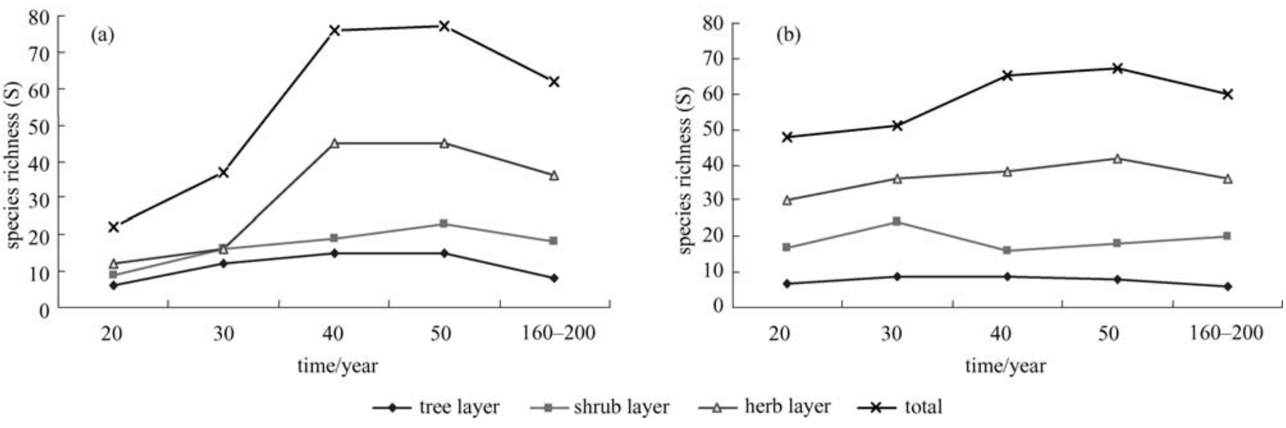

Fig. 1 Species richness at various stages of restoration. (a): Bamboo–birch forests and old-growth bamboo–dark coniferous forests; (b): Moss–birch forests and old-growth moss-dark coniferous forests. The same explanations apply to Figs. 2–4.

Table 1 ANOVA (*F* values) of species diversity at different restoration sequences

item	species richness index (*S*)	evenness index (*J*)	Shannon index (*H'*)	dominance index (*D*)
restoration sequences	6.96*	4.52*	8.98*	0.29
forest types	0.23	3.11	0.71	0.29
interaction	3.11	1.60	2.38	1.17

Note: * means $p < 0.05$.

and at age 30 in the moss-birch forest. The maximum value of species richness in the herb layer occurred at age 50 in both bamboo-birch and moss-birch forests.

Table 2 Difference test of species diversity of different growth forms (*t* values) among restoration sequences

diversity index	tree vs. shrub	tree vs. herb	shrub vs. herb
S	−6.188**	−10.665**	−5.624**
J	−3.758*	−2.146*	−1.145
H′	−7.534**	−6.443**	−2.440*
D	6.238**	2.567*	−0.721

Note: * means $p < 0.05$, and ** $p < 0.01$.

The evenness index implies a degree of equality in abundance or importance value of each species. From Fig. 2, it can be seen that the maximum value of the evenness index occurred at age 40 in both secondary forests. After that, the evenness index in the bamboo-birch forests, stabilized at a value of about 0.87 and in the moss-birch forests, the maximum value of the evenness index was 0.90. The value of the evenness index decreased in these secondary forests after age 50 and slightly increased in old-growth moss-dark brown coniferous forests. There are significant differences in the evenness indices among forest restoration sequences, but not between the two forest types (Table 1). The *t* test in Table 2 shows that there are statistically significant differences in the evenness indices between the tree and shrub layers and between the tree and herb layers. There are no significant differences between the shrub and herb layers.

From Fig. 3, it is seen that the value of the Shannon index shows an increasing trend over restoration time. In the bamboo-birch forests, the maximum value of the Shannon index was 3.80, which occurred in this secondary forest at age 50. In the moss-birch forests, the maximum value of the Shannon index was 3.65, occurring at age of 30. The Shannon index was 3.56 and 3.40, respectively, in the old-growth bamboo and moss-dark brown coniferous forests. There was a significant difference in the Shannon index among the forest restoration sequences and growth forms, but again no significant difference between the two forest types (Figs. 1 and 2). The Shannon index among these secondary forests varies from 2.69 to 3.80, with average values of 3.47 and 3.48 in the old-growth dark brown coniferous forests, slightly higher than in the secondary forests. The Shannon index has similar trends as the

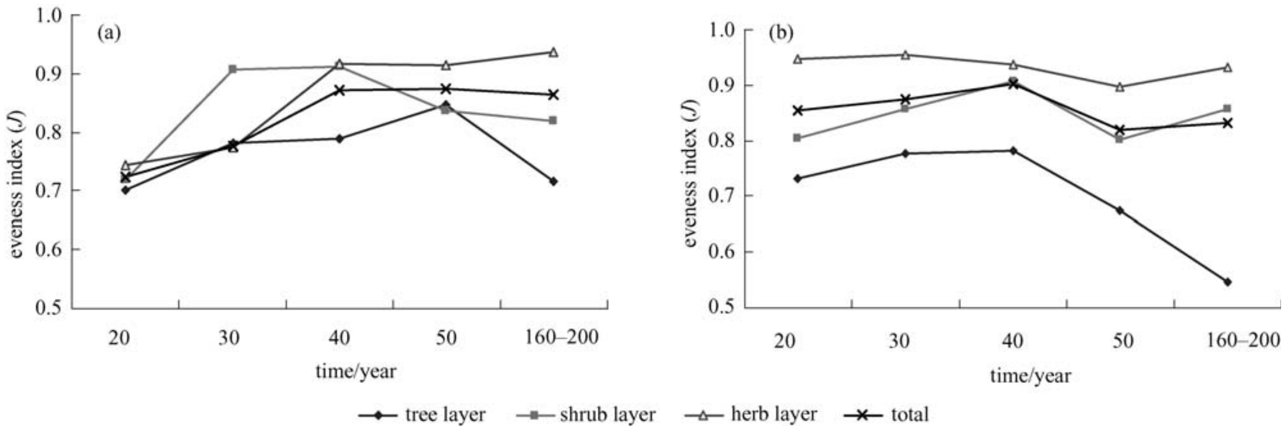

Fig. 2 Evenness at various stages of restoration

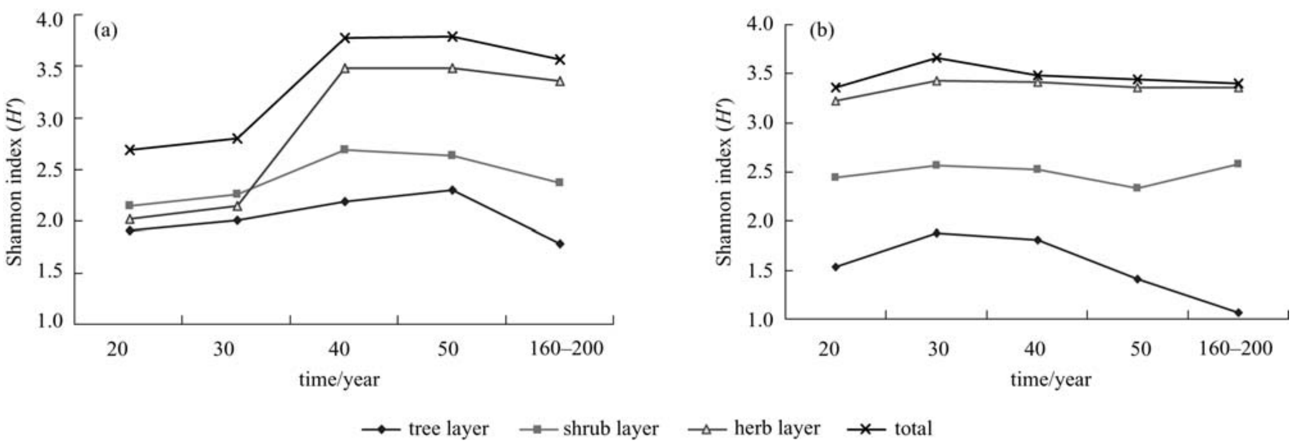

Fig. 3 Shannon index at various stages of restoration

species richness and evenness indices following forest restoration. This was to be expected because the Shannon index is affected by both species richness and evenness. The *t* test shows that there are significant differences among growth forms (Table 2). In general, the trend is as follows: herb layer > shrub layer > tree layer.

The value of the dominance index of communities varied. At first, it increased and then decreased, but the rate of change remained relatively small (Fig. 4). There was no significant difference in the dominance index among forest restoration sequences or between forest types (Table 1). There was a significant difference in the dominance index between tree and shrub layers and between tree and herb layers, but not between the shrub and herb layers (Table 2).

4.3 β diversity at forest restoration sequences

β diversity is one of the most important elements in community diversity research. It can express the degree or speed of species substitution, the turn-over rate of species, the speed of biological change and other aspects of diversity. β diversity also reflects the difference in species composition among communities. The Bray-Curtis index is a broadly applied index that can be used to measure the β diversity of communities or sites. The higher the Bray-Curtis index value is, the more common species among the communities and the more similar in species composition. From Tables 3 and 4, it is seen that the maximum value of the Bray-Curtis index occurred in two adjoining forest restoration sequences, which shows that the greatest similarity occurred in these two forest communities. The larger the difference in forest age, the smaller the value of the Bray-Curtis index, which shows that the difference in communities or species composition increases with the increase in the age gap. Over age, the value of the Bray-Curtis index between secondary forests and old-growth dark brown forests increased.

5 Discussion

Because of deforestation, the intrinsic sites suffered from destruction, leading to a series of changes in species composition and community structure. With forest restoration, *Betula albo-sinensis* became the dominant population in the secondary forests restoration sequence and *Abies faxoniana* gradually reached into the tree layer. Some companion species occurred among the forest restoration sequence. Because the location of bamboo-birch forests is lower than that of the moss-birch forest, the companion species in the tree layer are mainly some semi-shade intolerant or warm species, e.g., *Prunus pilosiuscula* and *Sorbus hupehensis*. There was no difference in the kind of species found among forest restoration sequences of the same forest type, but the importance value of dominant species varied with forest restoration processes.

Species richness increased with forest restoration and increased quickly in secondary forests between the ages of 30 and 40. After that, it slowly reached a peak that was securely maintained at this level in the old-growth dark brown coniferous forests. Species richness among growth forms changed in a similar fashion, which agrees with

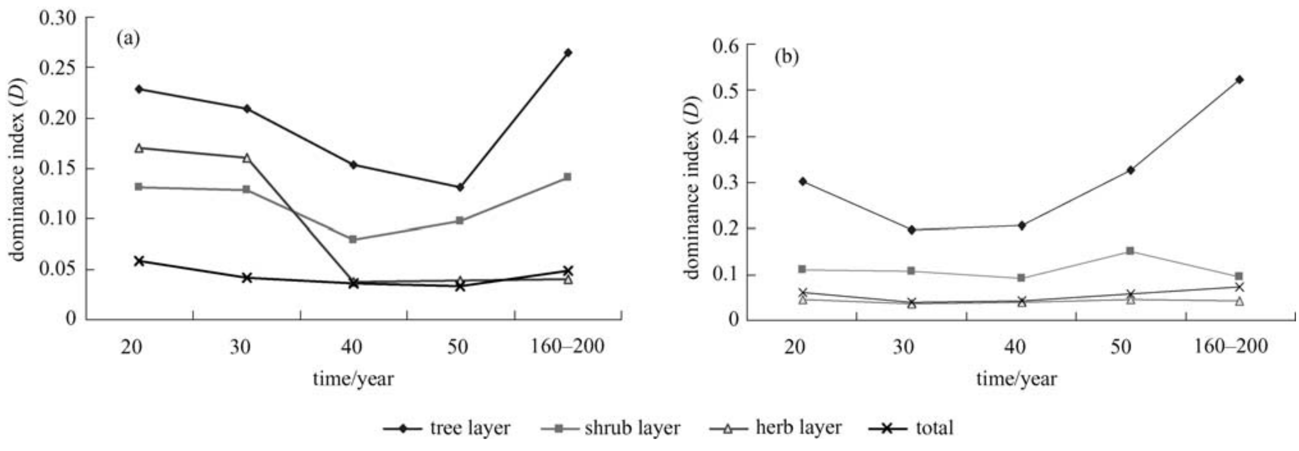

Fig. 4 Dominance index at various stages of restoration

Table 3 Bray-Curtis indices of communities in bamboo-birch forests and old-growth bamboo-dark coniferous forests

forest age	30 years	40 years	50 years	160–200 years
20 years	12.85	12.16	9.71	8.47
30 years		21.15	21.19	16.85
40 years			25.64	19.26
50 years				24.49

Table 4 Bray-Curtis indices of communities in moss-birch forests and old-growth moss-dark coniferous forests

forest age	30 years	40 years	50 years	160–200 years
20 years	13.38	11.46	10.01	9.22
30 years		27.86	23.92	17.05
40 years			27.10	22.07
50 years				23.31

other research results (He and Chen, 1997; Wen, 1998). Species richness increased with forest restoration, which most likely was because large intrinsic species left behind pools of seeds after deforestation, which provided for an abundant seed source for forest restoration. The seedlings and saplings in the undergrowth grew into the crown canopy and the species richness increased gradually. After 30 years of forest restoration, many pioneer species still abound. However, at the same time, the sites provide suitable conditions for many shade tolerant species, leading to a temporary rapid rise in species richness. At the stage of the old-growth dark brown coniferous forest, many intolerant species disappeared and *Abies faxoniana* became the major dominant species, which maintained species richness at a secure level.

The community dominance index was shown as a trend of the inverse of the evenness index, the Shannon index and species richness. In general, at first, it had a tendency to decrease and in the end, to increase. The reason for the dominance index to decrease is most likely that in the process of forest restoration species, such as *Abies faxoniana*, *Sorbus* spp., *Pruns* spp., *Acer* spp., grow into the tree layer, thus increasing species biodiversity and weakening the importance of species, such as *Betula albo-sinensis* that is dominate in the early forest restoration period. At the stage of old-growth dark brown coniferous forests, species, such as *Abies faxoniana*, take absolute predominance and other species gradually disappear, leading to a rising dominance index. The time required for the dominance index of the tree layer to decrease to its minimum value was earlier in the moss-birch forests than that in the bamboo-birch forests, this was likely the result of the higher elevation of the moss-birch forests which, at these elevations, approach the reserve forests belt, where enough of a seed source is found to lead to a faster regeneration of *Abies faxoniana* in moss-birch forests than that in bamboo-birch forests. Consequently, in the moss-birch forests, a single dominant species, such as *Betula albo-sinensis*, starts to weaken earlier leading to a decrease in the dominance index of the tree layer. With progress in the regeneration sequence, the status of *Abies faxoniana* in the community gradually increased, forming a pattern of coexistence with *Betula albo-sinensis*, and finally replaced the birch and *Abies faxoniana* became the most important dominant species. The decrease in the dominance index of the tree layer shows a development pattern from small to large.

The objective of our research was to study the species composition and diversity of secondary forests formed after clear cutting of the old-growth bamboo-fir and moss-fir forests, which was distributed at elevations between 3100 and 3600 m in western Sichuan. Twenty to thirty years after clear cutting, strong shade intolerant species such as *Rubus* spp. gradually disappeared and pioneer species, semi-shade intolerant or medium-shade tolerant species, e.g., *Betula albo-sinensis*, *Lonicera* spp., *Sorbus* spp., and *Ribes* spp. invaded the communities. At the same time, seedlings and saplings of fir and spruce also appeared which agrees with species changes at early natural succession and artificial regeneration on bare land in this area (Shi et al., 1988; Bao et al., 2002). Given the results from our study, we conclude that, in general, the species diversity of secondary forests tends to increase with forest restoration, which is similar to the results obtained in the changes in species diversity in man-made conifer plantations in this area (Wu et al., 2001; Zhao et al., 2002). The species diversity seems to remain at a secure level with the restoration of the old-growth dark brown coniferous forests for 160 to 200 years. Elsewhere, the β diversity remained relatively low. The purpose of the use of the Bray-Curtis index was to measure the trend of inter-community similarity in forest restoration sequences. The use of the importance value as an indicator to account for the Bray-Curtis index is an objective reflection of the dynamics of β diversity along the sequence of forest restoration. In our study, the Bray-Curtis index shows an increased trend between secondary forests and old-growth dark brown coniferous forests with the progress in forest restoration. This is similar to the results of the change of inter-community similarity during vegetation restoration in the Damingshan Mountain obtained by Wen (1998).

The dynamics of species composition and diversity reflects environmental changes during ecosystem restoration and the response of biodiversity to these changes. A period of 50 years constituted the initial stage or metaphase of forest restoration relative to a longer forest restoration succession. It will require a very long time to entirely explore the rules of change in the species diversity of a complete forest restoration sequence from a secondary forest succession after clear cutting to a zonal climax community.

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