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ORIGINAL PAPER

Regeneration strategies influence ground bryophyte composition and diversity after forest clearcutting

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Abstract

• ***Context*** Natural regeneration with broadleaved species and reforestation with coniferous trees are two widely practiced forest regeneration strategies after timber harvesting. They lead to different tree species composition and may cause different understory biodiversity, but the effects on ground bryophyte composition and diversity are not well-known.

• ***Aims*** We tested whether natural regeneration with broadleaved species and reforestation with spruce induced different diversities of the ground bryophyte populations 20–40 years after old-growth spruce forest clearcutting in the subalpine regions of southwestern China.

• ***Methods*** Differences between natural stands and plantations were compared through the analysis of 13 paired stands, with 78 plots, 390 shrub/herb quadrats, and a total of 1,560 bryophyte quadrats.

• ***Results*** Naturally regenerated forests were characterized by lower density and cover and lower tree height but higher herbaceous plant height, shrub cover, and bryophyte diversity. They also harbored many more ground bryophytes. The species richness of pleurocarpous mosses and fans, mats, and turfs were significantly higher in naturally regenerated forests. Frequency difference analysis demonstrated that more bryophyte species preferred ground habitats in naturally regenerated forests than in plantations (116 vs. 48 species). The canonical correspondence analysis indicated that stand structure attributes were more important determinants of ground bryophyte diversity and abundance.

• ***Conclusion*** Natural regeneration and reforestation resulted in large differences in ground bryophyte populations. A larger diversity was observed in the former case, and natural regeneration practices can be an effective measure for the protection of ground bryophyte diversity after clearcutting.

Keywords Bryophyte · Regeneration strategy · Planted forest · Clearcutting · Natural forest · Biodiversity conservation

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1 Introduction

Bryophytes are important components of forest biodiversity and play important roles in ecosystem processes and functions (Humphrey et al. 2002; Vellak and Ingerpuu 2005). Because of their poikilohydric features, bryophytes, especially liverworts, depend greatly on local microclimates and microhabitats (Frelich et al. 2003; Proctor 2008). This further implies that many bryophytes are sensitive to forest management practices (Lesica et al. 1991; Ódor and Standovár 2001; Ross-Davis and Frego 2002; Vellak and Ingerpuu 2005) that directly affect forest microclimates and substrates (Chen et al. 1999; Ross-Davis and Frego 2002).

Continuous loss and degradation of old-growth forests are accelerating and account for the majority of global forest losses from 2000 to 2010 (FAO 2011); deforestation and forest degradation remain the primary threats to biological diversity. Alternative modes of forest regenerations significantly affect the original biodiversity of old-growth forests, such as the loss of species that are highly associated with old-growth forests (McClellan et al. 2000). Development of alternative regeneration strategies following the clearing of a forest is of great concern worldwide (e.g., Brockerhoff et al. 2008; Rudolphi and Gustafsson 2011). A critical challenge for foresters who seek a balance between production and biodiversity conservation is how to reasonably promote forest regeneration and in situ biodiversity conservation in a large area of degraded forest lands, such as clearcuts, that have been widely practiced in our study region and elsewhere. However, scientific evidence showing the effects of different forest regeneration strategies on bryophyte composition and biodiversity are sparse and sporadic in contrast to the large amount of research conducted on vascular plant diversity (Barbier et al. 2008; Brockerhoff et al. 2008).

Natural regeneration and reforestation are the two most common regeneration strategies and have been widely adopted on harvested lands worldwide (FAO 2011). For the majority of cutovers, coniferous trees (e.g., pine and spruce) are often used for establishing plantations. Homogeneous habitats were created by the establishment of a monospecific, even-aged tree layer, together with silvicultural treatments used for plantation management (e.g., site preparation). In naturally regenerated stands, complex microhabitats were created by exhibiting a mosaic pattern of overstory canopy (Tullus et al. 2013). Therefore, differences in the understory vegetation biodiversity might be expected between plantations and naturally regenerated stands. Many authors have concluded that natural regeneration was an effective strategy in conserving ground bryophyte biodiversity, although the regeneration duration appeared responsible for the extent of biodiversity conservation (Rudolphi and Gustafsson 2011; Yan and Bao 2011). However, several evidences supported that afforestation or reforestation play positive roles in conserving vascular plant biodiversity (Brockerhoff et al. 2008; Bremer and Farley 2010). China has the largest area of forest plantations in the world, and is expanding the areal extent of these plantations in order to strengthen the nation's ecological security (FAO 2011). In the past several decades, these efforts have predominantly relied on reforestation as opposed to natural regeneration (Liu 2002). Coniferous plantations account for 71 % of the total plantations in China. Given the large plantation area and expected future enlargement, it is critical to understand the consequences of different regeneration strategies (e.g., in bryophyte biodiversity conservation) so that the conservation of biological diversity can be effectively included in future management plans.

In this study, we examined the effects of natural regeneration with broadleaved species and reforestation with spruce on ground bryophyte assembly on harvested areas in the subalpine regions of southwestern China. Our taxa focal points were chosen because bryophytes are common and abundant in old-growth forests and often change abruptly after forest harvesting (Ross-Davis and Frego 2002). Additionally, bryophytes are more sensitive than most vascular plants to habitat and microclimate changes (Haeussler et al. 2002), i.e., they serve as good indicators to assess the biodiversity effect of habitat changes resulting from different regeneration pathways. Humphrey et al. (2002) found that bryophyte richness was similar between spruce plantations and semi-natural oak forests in Britain. However, spruce plantations had lower bryophyte species richness, evenness, and diversity than those sites within naturally regenerated forests in eastern Canada (Ross-Davis and Frego 2002). There have not been field studies directly comparing plantations and naturally regenerated deciduous broadleaved forests in China. This study also compares young spruce plantations with early naturally regenerated forests rather than old growth forests as in most of the studies cited above to examine the effect of different forest regeneration strategies on bryophyte composition and diversity in similarly degraded cutovers.

Our objective in the current study was to evaluate the effects of different forest regeneration strategies on bryophyte composition and diversity following clearcuts of old-growth spruce forests. The regeneration strategy is treated as a comprehensive factor, including disturbance, tree species, stand structure attributes, soil, species pools, local climate, and the effects of various regeneration strategies. Therefore, other major factors, such as regional climate, topography, and stand development stage, should be excluded. We hypothesized that alternative forest regeneration strategies on similar clearcuts will produce significantly different results in ground bryophyte composition and diversity. More specifically, naturally regenerated forests will harbor many more bryophytes (i.e., higher diversity) than planted forests. This prediction was largely based on the fact that reforestation, as a further disturbance on clearcuts, can directly destroy remnant bryophyte assemblies and their microhabitats (Yan and Bao 2008). Our hypothesis is also supported by the fact that changes in stand structural differentiation following alternative strategies distinctly modulate the microclimate and substrates that directly affect bryophyte distribution, growth, mortality, and other population demographic features (Fenton and Frego 2005; Márialigeti et al. 2009). Additionally, bryophytes have distinct life-history strategies and may respond differently to habitat alterations resulting from natural disturbances and management (Fenton and Frego 2005; Yan and Bao 2008). Therefore, the following questions were addressed. (1) Do ground bryophyte composition and diversity indices differ between naturally regenerated forests and planted forests? (2) How do

phylogenetic and growth-form groups of bryophytes vary in response to the applications of different forest regeneration strategies? (3) What is the relative contribution of stand structure and topography variables to the total variance of bryophyte biodiversity?

2 Materials and methods

2.1 Study region

The study area is located in the Aba Tibet and Qiang Autonomous Prefecture (30°35′ N–34°19′ N, 100°30′ E–104°27′), northwestern Sichuan Province, southwestern China. It is within the well-known program of the Southwestern Forest Management Region and is a hotspot for biodiversity conservation both in China and globally (Liu 2002). The altitude ranges from 2,200 to 3,900 m; the climate in the forest region is temperate with annual rainfall of 800–1,100 mm and a mean annual temperature of 6–10 °C; the soil is luvisol developed from metamorphic rocks of phyllite, slate, and schist (Bao et al. 2009). Large-scale timber harvesting using clearcuts on the old-growth coniferous forests occurred from the 1960s to 1990s, leaving harvested areas of an average size of ~5 ha. Most clearcuts were reforested with a monospecific indigenous species of spruce (*Picea asperata*) following the national alpine reforestation manuals (Yang 1985), i.e., 4-year-old seedlings at an initial density of 3,300 stems/ha. Some small cutovers were left to naturally regenerate and later become deciduous broadleaved forests dominated by *Betula albo-sinensis*, *Populus davidiana*, *Sorbus hupehensis*, *Sorbus koehneana* and *Sorbus setschwanensis*. The naturally regenerated deciduous broadleaved forests account for ~25 % of the forested area in the region, while the planted spruce forests account for >40 %. Most of these forests are <45 years old.

2.2 Sampling selection and data collection

We selected 13 sites with pairs of planted and naturally regenerated stands of various ages (i.e., 20–40 years) to conduct our investigation. A total of 26 stands with similar topographical characteristics (e.g., elevation, slope degree, and slope aspect), clearcut prescriptions, and developmental phase were chosen across three adjacent counties covering an area of more than 16,300 km^2, totalling 13 planted stands and 13 naturally regenerated stands ranging from 2,769 to 3790 m in altitude and from 21 to 38 years in forest age (Appendix Table 6). Because topographical characteristics in the subalpine region are very complex, the most similar stands in terms of topography were chosen for our study. The field investigation was performed in the summer of 2007. Because of the high spatial heterogeneity within the stand, three 10×10 m plots were placed on three slope positions (i.e., upper, middle, and lower) at each of the stands to represent the entire stand. Topography variables (i.e., elevation, slope degree, and slope aspect) were recorded for each plot. Slope and aspect were converted using the class method with 45° intervals, ranging from 1 (247.5°–292.5°) to 8 (67.5°–112.5°). Tree canopy cover was visually estimated, and the height was measured for each tree ≥3 m. The density of all trees, coniferous trees, and deciduous trees were tallied by plot. Five 2×2 m quadrats were installed at the four corners and the center of each plot, and the average shrub height and cover were measured in each quadrat. At the upper-right corner in each of the five shrub quadrats, one 1×1 m quadrat was installed to measure the average herbaceous height and litter cover. Finally, twenty 0.25 m^2 (50×50 cm) quadrats with every 2.5 and 2 m along contours, and the slope aspect for each plot were systematically installed in order to conduct a bryophyte community survey. Within each of the quadrats, bryophytes and their percent covers were estimated by species, and the sample was collected for species identification. In total, we obtained data from 26 stands, 78 plots, 390 shrub/herb quadrats, and 1,560 bryophyte quadrats. The >3,900 bryophyte samples were microscopically examined for species (or subspecies) identification in the laboratory according to the Flora Bryophytorum Sinicorum. All vouchers were kept in the herbarium at the Chengdu Institute of Biology, Chinese Academy of Sciences.

2.3 Statistical analyses

We aggregated three plots in each stand to avoid pseudoreplication and then used the 26 independent stands in the final analyses. Forest structure variables were also averaged by three replicated plots. Topography and forest structure differences between the two forests were tested separately using the nonparametric Mann–Whitney test.

In addition to the direct comparisons of total species composition and richness, we applied species group analysis to compare differentiation in bryophyte richness or abundance between the two forests. First, we categorized each species to one of three frequency–tendency distribution groups according to their occurrence, tested by the chi-square and Fisher's exact tests (Nagaike 2002; Ross-Davis and Frego 2002). The three identified species groups were the following: (1) reforestation species group, species exclusively or more frequently found in plantations; (2) natural regeneration species group, species found exclusively or more frequently in natural stands; and (3) generalist species group, species that are recorded synchronously in natural stands and plantations but do not show significant differences in occurrence (Appendix Table 7). We postulated that with a background of the same origins (similar clearcutting of the same old-growth spruce forests) and regional species pools, the two forests provide different habitats and environments due to the two different regeneration strategies

and consequently early stand succession. Thus, bryophytes with higher occurrence frequency in either the natural stands or plantations can indicate stronger habitat preferences. We also classified all bryophytes into seven growth forms (turfs, cushions, wefts, mats, fans, dendroids, and pendants) and three phylogenetic groups (liverworts, acrocarpous moss, and pleurocarpous moss) according to morphological trait classification. The richness and cover of different species groups for each stand were calculated. The differences for each species group between the two forests ($n=13$) were tested separately using the nonparametric Mann–Whitney test.

To determine the differences in dominant species composition between the two forests, the important value (IV) of each bryophyte was calculated as: (relative cover+relative frequency)/2 (Appendix Table 7). Three diversity indices (species richness, Shannon–Wiener index, and Pielou's evenness) and the cover of the ground bryophyte community at stand level were calculated following Magurran (1988). The Shannon–Wiener index was calculated using the IV of each species for their probabilities. A nonparametric Mann–Whitney test was also applied to check the difference of the four bryophyte indices between the two forest types.

A nonparametric analysis was applied to determine the correlation between topography variables, forest structure variables, and bryophyte community diversity based on Kendall's coefficient. A multiple response permutation procedure (MRPP) test was applied to determine if regeneration strategy (natural stands vs. plantations) affected bryophyte composition. The canonical correspondence analysis (CCA) was applied to explore the contribution of stand structural and topographical variables on bryophyte composition. Furthermore, the partial CCA (pCCA) was used to estimate the contribution amount of the potential influence for the total variance. Considering the potential effect of topographical characteristics, all topographical factors were included in all subsequent analyses. All important independent variables were classified into two categories: (1) forest structure variables, including nine parameters, e.g., stand age and tree density, tree canopy cover and the average height, shrub cover and height, herbaceous cover and height, and litter cover; and (2) topographical variables, including three parameters, e.g., elevation, slope degree, and slope aspect. Because preliminary analyses showed that the densities of coniferous trees and broadleaved trees were not significantly correlated with ground bryophyte diversity indices, the total tree density was used in further analysis. The contributions of forest structure variables, topography variables, and their interactions were approximated as the constrained inertia of the sum of total inertia. All statistical analyses were performed using the statistical program SPSS 13.0 for Windows (SPSS, Chicago, IL, USA), except for MRPP, CCA, and pCCA in a vegan package (Oksanen et al. 2011), which were performed in R 2.14.0.

3 Results

3.1 Topography and forest structure

There were no significant differences in elevation, slope aspect, or slope degree between the plantations and natural stands (Table 1), implying a sound experimental design. The plantations had significantly higher stand density, coniferous tree density, and tree height but significantly lower broadleaved tree density, shrub cover, and herbaceous plant height compared to the natural stands (Table 1). No differences in litter cover, herbaceous cover, shrub height, or stand age were found.

3.2 Ground bryophyte composition

In total, 232 bryophytes (28 liverworts, 103 acrocarpous mosses, and 101 pleurocarpous mosses, same as below), belonging to 45 families and 114 genera, were recorded in the investigated stands (Appendix Table 7). Overall, 205 bryophytes (28, 86, and 91) and 157 bryophytes (19, 76, and 62) were recorded in the natural stands and the plantations, respectively. The natural stands harbored 48 bryophytes more than the plantations, including 9 liverworts, 10 acrocarpous mosses, and 29 pleurocarpous mosses.

A total of 75 bryophytes (9, 27, and 39) were recorded only in the natural stands and 27 species (0, 17, and 10) were recorded only in the plantations. There were 130 species (19, 59, and 52) co-occurring in the plantations and the natural stands, but 41 species (9, 13, and 19) were found more frequently in the natural stands, 21 species (3, 8, and 10) were found more frequently in the plantations, and another 68 species (7, 38, and 23) did not present a significant difference in frequency between the plantations and natural stands (Appendix Table 7).

The two types of forest also presented some differences in species dominance. Twenty-five species were dominant in the two types by IV≥1, but only 11 of those were dominant in both forest types: *Actinothuidium hookeri*, *Entodon concinnus*, *Eurhynchium coarctum*, *Hylocomium splendens*, *Kindbergia arbuscula*, *Mnium lycopodioides*, *Plagiomnium acutum*, *Plagiomnium ellipticum*, *Plagiomnium rhynchophorum*, *Rhytidiadelphus triquetrus*, and *Thuidium cymbifolium* (Appendix Table 7). Additionally, most of the 75 bryophyte species recorded only in the natural stands and another 27 species only in the plantations had low occurrence frequencies (i.e., <10 times in 780 quadrats).

3.3 Bryophyte species groups

The generalist species group, the natural regeneration species group, and the reforestation species group had 68, 116, and 48 species recorded in the investigated plots, respectively. Furthermore, the natural regeneration species group contained

Table 1 Topographical and forest structural characteristics (mean±SE) of the naturally regenerated deciduous stands and the plantations in northwestern Sichuan, China

Variables	Natural stands ($n=13$)	Plantations ($n=13$)	F	P value
Topography				
Elevation (m)	3,248.54±88.11	3,204.08±56.32	1.57	0.674
Slope aspect	2.23±0.26	2.31±0.38	2.9	0.869
Slope degree (°)	29.31±1.42	31.77±1.52	0.004	0.248
Forest structure				
Stand age (year)	29.31±3.91	32.08±2.11	8.29	0.540
Stand density (stem ha^{-1})	1,000.90±183.29^b	2,266.67±259.93^a	1.29	0.001
Coniferous tree density (stem ha^{-1})	194.87±70.33^b	2,066.67±234.03^a	8.11	<0.001
Broadleaved tree density (stem ha^{-1})	803.21±155.67^a	197.44±109.22^b	2.07	0.004
Tree height (m)	5.74±0.97^b	9.02±1.1^a	0.73	0.035
Shrub height (cm)	99.78±8.63	70.36±16.16	4.64	0.121
Herbaceous height (cm)	13.71±0.94^a	9.65±0.78^b	0.11	0.003
Tree canopy cover (%)	42.87±7.32^b	63.35±4.05^a	2.85	0.022
Shrub cover (%)	28.56±3.90^a	12.68±3.87^b	0.41	0.008
Herbaceous cover (%)	29.32±3.47	32.17±4.83	2.64	0.637
Litter cover (%)	42.85±3.50	47.69±4.53	0.08	0.406

The superscript letters indicate the significant differences between the two stands (nonparametric Mann–Whitney test, $P<0.05$)

higher species ratios of liverworts and pleurocarpous mosses than the reforestation species group (liverworts, 15.5 vs. 6.3 %; pleurocarpous mosses, 50.0 vs. 41.7 %). The phylogenetic group analysis showed that the pleurocarpous moss group presented significantly higher species richness in the natural stands than in the plantations, but there were no significant differences for liverworts and acrocarpous mosses (Fig. 1a). We also found no significant difference in cover between the plantations and natural stands for the three groups, but the pleurocarpous moss group exhibited higher cover than the other two groups for both forest types ($P<0.01$; Fig. 1b). Altogether, there were seven growth forms recorded in the plantations and natural stands in total (Appendix Table 7), but only three growth forms (fans, mats, and turfs) had significantly higher species richness in the natural stands than the plantations (Fig. 1c). Two growth forms (fans and mats) also presented significantly higher cover in the natural stands than in the plantations, but only the wefts showed higher values in the plantations relative to the natural stands (Fig. 1d).

3.4 Ground bryophyte diversity and cover

Mann–Whitney tests revealed that the natural stands had higher values of species richness and Shannon–Wiener and Pielou's evenness indices, but lower ground bryophyte cover than the plantations (Table 2).

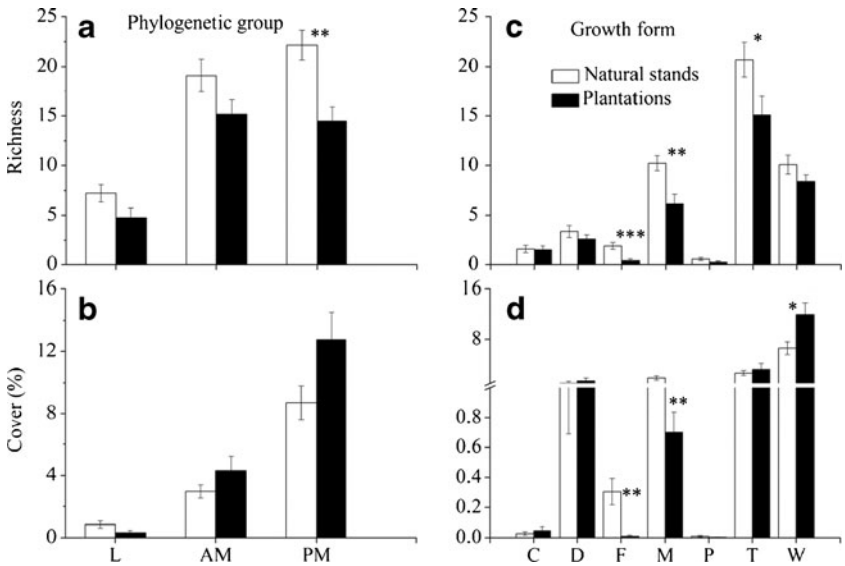

Fig. 1 Difference in species richness and cover (mean±SE) of ground bryophyte phylogenetic and growth form groups between naturally regenerated deciduous stands and the plantations in northwestern Sichuan, China. *Asterisks* indicate significant differences between the two stands based on the nonparametric Mann–Whitney test ($n=13$) (*$0.01<P<0.05$; **$0.001<P<0.01$). Phylogenetic group: *L* liverwort, *AM* acrocarpous moss, *PM* pleurocarpous moss; growth form: *C* cushions, *D* dendroids, *F* fans, *M* mats, *P* pendants, *T* turfs, *W* wefts

Table 2 Ground bryophyte diversity indices (mean±SE) in the naturally regenerated deciduous stands and the plantations in northwestern Sichuan, China

	Natural stands (n=13)	Plantations (n=13)	F	P
Species richness	48.46±2.91[a]	34.38±2.82[b]	0.11	0.002
Shannon–Wiener	3.02±0.07[a]	2.42±0.12[b]	3.19	<0.001
Pielou's evenness	0.79±0.01[a]	0.69±0.02[b]	1.89	0.001
Cover (%)	12.51±1.38[b]	17.38±1.38[a]	0.14	0.020

Different superscript letters indicate significant differences between the two stands (nonparametric Mann–Whitney test, P<0.05)

3.5 Influences from topography and forest structure

The MRPP test showed that the regeneration strategy resulted in significantly different outcomes between the plantations and natural stands on ground bryophyte composition (A= 0.03, P=0.02). The CCA bi-plot of 26 stands, constrained by all environmental variables, also classified the 26 stands into 2 groups: the natural stands and the plantations, with the stand structural and topographical features explaining 21 % of total variance on ground bryophyte composition (Fig. 2). Ground bryophyte composition was only significantly correlated with the elevation of three topographical parameters (Table 3). Of the nine stand structural variables, only litter cover and shrub height and its cover were not significantly correlated with ground bryophyte composition (Table 3). The amount of variation explained by all significant variables was

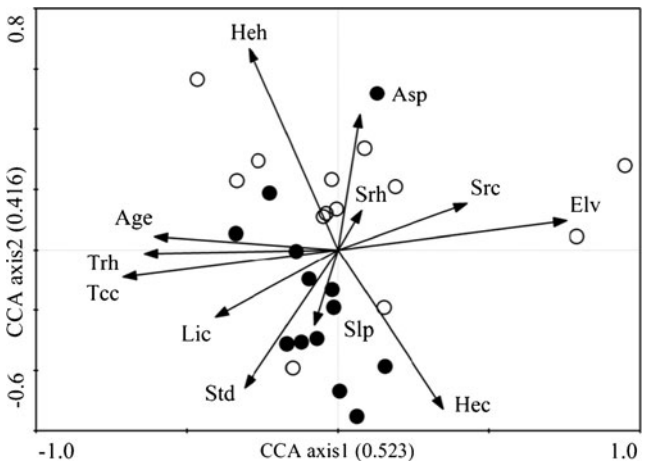

Fig. 2 Bi-plot of the 26 stands (*hollow circles* naturally regenerated deciduous stands; *solid circles* plantations) by canonical correspondence analysis (CCA) according to all environmental variables (with eigenvalue in *brackets*). The sum of all canonical eigenvalues is 4.544. The first two axes account for 21 % of the variation in species–environment relationships. Environmental variables include forest structure (*age* stand age, *Std* stand density, *Tcc* tree canopy cover, *Trh* tree height, *Src* shrub cover, *Srh* shrub height, *Hec* herbaceous cover, *Heh* herbaceous plant height, *Lic* litter cover) and topography (*Elv* elevation, *Asp* slope aspect, *Slp* slope degree)

Table 3 Statistical results of the canonical correspondence analysis (CCA) and topography/forest structure variables of 26 stands of the naturally regenerated deciduous forests and the plantations in northwestern Sichuan, China

	CCA1	CCA2	r^2	P
Topography				
Elevation (m)	0.995	−0.101	0.538	<0.001
Slope aspect	0.139	−0.99	0.188	0.079
Slope degree (°)	−0.278	0.961	0.062	0.474
Stand structure				
Herbaceous height (cm)	−0.424	−0.905	0.499	<0.001
Tree canopy cover (%)	−0.994	0.100	0.476	0.001
Tree height (m)	−0.999	−0.006	0.383	0.001
Herbaceous cover (%)	0.566	0.824	0.379	0.001
Stand age (year)	−0.995	−0.097	0.347	0.004
Stand density (stem ha^{-1})	−0.558	0.830	0.275	0.026
Litter cover (%)	−0.887	0.463	0.196	0.079
Shrub cover (%)	0.949	−0.316	0.188	0.071
Shrub height (cm)	0.507	−0.862	0.02	0.792

55.7 %, in which the stand structural variables contributed 39.5 % of the total and much more for the topographical variables and the interactions (Table 4). Of all the investigated factors, the relative contributions from all of the variables can be ranked as follows: elevation>herbaceous plant height>tree canopy cover>tree height>herbaceous cover>stand age> stand density (Fig. 2).

We also found that the three investigated tree canopy parameters had negative relationships with the diversity indices, except the stand age and broadleaved tree density, whereas shrub height and cover had positive relationships with the diversity index (Table 5). Kendall's correlation analysis suggested that only herbaceous plant height and shrub cover were significantly and positively correlated with ground bryophyte species richness. Stand density, coniferous tree density, and herbaceous cover had a significant negative correlations with ground bryophyte diversity (P<0.05), whereas herbaceous plant height had a significant positive correlation with ground bryophyte diversity (P<0.01). Stand density and coniferous

Table 4 Results of the partial canonical correspondence analysis (pCCA) variation partitioning in determining the relative influence of forest structure and topography on the overall ground bryophyte species composition of 26 stands in northwestern Sichuan, China

Category	Contribution (%)
Topography | forest structure	14.29
Forest structure | topography	39.52
Topography ∩ forest structure	1.85
Unexplained	44.33

Table 5 Kendall's correlation indices between topography/forest structure variables and ground bryophyte diversity indices of 26 stands in northwestern Sichuan, China

	Species richness	Shannon–Wiener	Evenness
Topography			
Elevation (m)	−0.025	0.025	0.086
Slope aspect	0.039	0.151	0.207
Slope degree (°)	0.147	0.038	−0.107
Forest structure			
Stand age (year)	0.025	0.025	0.025
Stand density (stem ha^{-1})	−0.263	−0.309*	−0.383**
Coniferous tree density (stem ha^{-1})	−0.353*	−0.355*	−0.367**
Broadleaved tree density (stem ha^{-1})	0.259	0.163	0.050
Tree height (m)	−0.044	−0.019	−0.068
Shrub height (cm)	0.240	0.262	0.225
Herbaceous height (cm)	0.365**	0.465**	0.403**
Tree canopy cover (%)	−0.269	−0.148	−0.099
Shrub cover (%)	0.296*	0.262	0.225
Herbaceous cover (%)	−0.243	−0.277*	−0.203
Litter cover (%)	−0.095	−0.175	−0.250

*$0.01<P<0.05$; **$0.001<P<0.01$

tree densities were both significantly and negatively correlated with ground bryophyte evenness ($P<0.01$), whereas a significantly positive correlation was found between herbaceous plant height and ground bryophyte evenness ($P<0.01$). Herbaceous plant height was significantly and negatively correlated with ground bryophyte cover ($P<0.05$) (Table 5).

4 Discussion

This study underscores the importance of the reasonable selection of forest regeneration strategy following degraded clearcuts for in situ conservation of bryophyte diversity. Our results clearly suggest that the uses of two regeneration strategies on similar cut sites produced distinct stand structures, including tree, shrub and herbaceous layers, and, consequently, understory habitats and vegetation (Table 1). This implies that monospecific reforestation can be more effective and swift in the establishment of canopy structure by faster tree growth both in height and the diameter at breast height, thus enhancing stand productivity (Fitzsimmons 2003), but limiting understory vegetation development (Brockerhoff et al. 2008). It is also clear that the dense tree canopy significantly affected the organizational structure of the understory vegetation in the plantations in comparison with the natural sites (Tables 1 and 5), which inevitably influences the understory plant composition and biodiversity (Humphrey et al. 2002; Bao et al. 2009).

4.1 Regeneration strategy and bryophytes

We found that a greater ratio of bryophyte species (130 species) co-occurred in both forests (82.8 % in plantations and 63.4 % in natural stands). Furthermore, some important late-successional species, such as *A. hookeri*, *H. splendens* and *R. triquetrus*, which are possibly remnants of clearcuts from the old-growth spruce forests (Bao et al. 2009), can also be dominant within the two forests. This suggested that forest regeneration, regardless of natural regeneration or reforestation, could to a certain extent effectively promote and conserve native ground bryophyte composition on cutovers, which supports the insight that reforestation with indigenous trees may play an important role in biodiversity conservation (Humphrey et al. 2002; Brockerhoff et al. 2008; Bremer and Farley 2010).

We also found that the plantations and natural stands had significantly different ground bryophyte species composition and richness, with 48 more species found in natural stands than plantations (205 vs. 157 species). Almost two thirds of the species (75 species) in the natural stands were not found in the plantations (Appendix Table 7), implying that fewer species occurring only in the plantations was the primary reason for the low richness observed in the plantations. The natural stands also had higher bryophyte diversity indices than the plantations (Table 2). This was consistent with a study by Ross-Davis and Frego (2002), which was based on surveys of various substrates (rocks, stumps, and twigs). Our results are strictly from the investigation of the same substrate (ground soil), nevertheless, it seems that even when the same substrate is present, the reforestation strategy would result in less ground bryophyte richness than natural regeneration. Moreover, we found that the natural stands had significantly higher pleurocarpous moss species richness than the plantations (Fig. 1a), suggesting that the lower diversity in the plantations compared to the natural stands could be mainly due to the absence of some liverworts and pleurocarpous mosses (Ross-Davis and Frego 2002). Our results further highlighted that natural regeneration can promote the establishment and survival of pleurocarpous moss and liverworts on harvested sites (Lesica et al. 1991; Márialigeti et al. 2009). Thus, we conclude that a natural regeneration strategy is better than a reforestation strategy in promoting the conservation of ground bryophyte biodiversity, which supports the initial hypothesis.

Finally, the growth form of a bryophyte does not only reflect a partial life-history strategy of the species but also mirrors the habitat quality (Oishi 2009). For example, because the fans are often found in high-shade habitat (During 1990), the present work also showed a higher species richness of fans, mats, and turfs (Fig. 1c) and significantly higher covers of the fans and mats ($P<0.05$, Fig. 1d) in the natural stands than in the plantations. This evidence supports the conclusion that bryophyte distribution and assembly induced by a regeneration strategy

are due to the combined effects from habitat quality change and species biological traits (e.g., life history).

4.2 Factors influencing ground bryophytes

It is known that ground bryophyte communities and species composition can be strongly influenced by forest management activities (e.g., Newmaster and Bell 2002; Astrom et al. 2005) and the interaction with bryophyte life-history strategy (During 1990; Ross-Davis and Frego 2002; Ramovs and Roberts 2005). Reforestation activities are currently a common choice to restore forest resources worldwide (FAO 2011) and, as a direct agent responsible for bryophyte settlement and community assembly, have often resulted in the decline of some sensitive bryophytes at the early stages (Newmaster and Bell 2002; Ross-Davis and Frego 2002; Yan and Bao 2008; Bao et al. 2009). Compared to natural regeneration without further disturbances at a harvest site, reforestation activities, such as site preparation, pit digging, seedling planting, initial weeding, and seedling tending, directly destroy the indigenous plant cover and can further expose the soil surface (Newmaster and Bell 2002; Yan and Bao 2008). Consequently, those activities deteriorate microhabitats and their quality into "more hostile environments" for shade-tolerant species (e.g., liverworts), whereas they increase the opportunities for pioneers or disturbance species (e.g., *Brachythecium* spp., *Bryum* spp., *Munium* spp., *Polytrichum* spp. and *Tortella* spp.; Newmaster and Bell 2002; Bao et al. 2009). Such disturbances associated with reforestation practices also hinder remnant bryophyte establishment and population development, especially shade-tolerant pleurocarpous mosses and liverworts, such as *Bazzania bidentula*, *Jungermannia brevicaulis*, *Rhytidiadelphus subpinnatus*, and *Sanionia unicinata*, but promote the successful settling of soil-dwelling acrocarpous mosses (Appendix Table 7). Obviously, this will result in fewer liverworts and pleurocarpous mosses to colonize harvested sites because of their intolerance to ground disturbance and limited capabilities to cope with rigorous habitats (During 1990; Astrom et al. 2005; Oishi 2009). By contrast, on the naturally regenerated sites, no further disturbances have occurred since clearcutting; consequently, those remnant shrubs were not further destroyed and they had an opportunity to swiftly enlarge their populations because of radiation release and increased soil fertility after clearcutting. Thus, shrubs could sustainably provide relatively better shade habitats for those remnant forest floor bryophyte species populations, which are mainly liverworts and pleurocarpous mosses. Rapid shrub development can occupy exposed habitats and also hinder the invasion of acrocarpous mosses to some extent because of the lack of further habitat exposure after clearcutting (Yan and Bao 2008; Bao et al. 2009). All of this eventually results in a differing ground bryophyte assembly between naturally regenerated and reforested stands in the early stand stage (20–40 years old) after clearcutting. Logically, we propose that during forest management decision making, attention should be given to the conservation of these sensitive forest floor bryophyte populations during reforestation or afforestation practices.

Furthermore, reforestation also significantly and directly shaped forest structure and prolonged stand dynamics in comparison to the natural regeneration process (Table 1). Through modifications of resource availability (light, water, and soil nutrients) and habitat quality (Moora et al. 2007), it also indirectly modulated ground bryophyte species composition and diversity development (Table 2). Several stand structure variables were strongly correlated with ground bryophyte composition and diversity (Tables 3, 4, and 5) and can explain 21 % of the ground bryophyte community differences together with topographical variables (Table 4). Notably, stand structure played a stronger role in influencing bryophyte community composition than did topography in the current study (Table 4). It is widely known that vascular plant species composition and forest structure change with topography (e.g., Xu et al. 2000) because elevation, slope, and aspect determine resource availability at the landscape scale, which indirectly influences plant distribution and vegetation dynamics. Lee and La Roi (1979) found that bryophytes have wider tolerances to elevation-correlated factors, including temperature, and, for most species, habitats are narrow along the moisture gradient and broad along the elevation gradient in rocky mountains. The most immediate drivers for bryophytes are microhabitat quality and heterogeneity formed by small topographic relief, dead wood, snags, and canopy gaps within forests (Ódor and Standovár 2001; Humphrey et al. 2002; Frelich et al. 2003; Moora et al. 2007; Márialigeti et al. 2009). These fine-scale microhabitat features that are greatly managed by stand structure, as shown in our results (Table 5), play significant roles in bryophyte distribution. It should be noted that we largely excluded the effects of topography factors, but the potential effects of elevation still influenced our results (Table 3; Fig. 2). Actually, it is difficult to disentangle the effects of different factors that contribute to bryophyte diversity in the mountain region. If the topographical effects were not intentionally excluded, the actual effects of topography on bryophyte assembly would be more important than we reported for the subalpine forest regions that we focused on. Therefore, it will be necessary to understand the actual effects of topography and its interaction with regeneration strategy on bryophyte assembly.

Forest canopy characteristics (e.g., tree species composition and mixture) can play indispensable roles in influencing bryophyte species composition and diversity during forest regeneration. Our work showed that tree species proportions were quite different; naturally regenerated deciduous broadleaved forests had a small proportion of coniferous trees, and plantations are almost always mono-specific spruces (Table 1). Mixing of deciduous and coniferous tree species generally affects

understory diversity (including bryophytes), but in almost all cases, the maximum understory diversity has been observed in mono-specific stands instead of multiple-species forests (Barbier et al. 2008). In a temperate-mixed forest, Márialigeti et al. (2009) demonstrated that bryophyte species richness increased with tree species number and stand structural diversity, arguing that overstory species diversity was responsible for providing more favorable conditions for bryophytes. In our study, the two forests were both at their early successional stages (Liu 2002). Although there were large differences in stand densities of the coniferous and the deciduous species (Table 1), we did not find a strong correlation between ground bryophyte richness and coniferous tree density in the naturally regenerated deciduous forests ($R=0.121$, $P=0.576$) or with deciduous tree density in the spruce forest ($R=0.228$, $P=0.315$). Our results thus rejected the insight that the presence of deciduous trees in conifer-dominated stands increases bryophyte diversity, whereas the presence of conifers in the deciduous stands is equally important (Márialigeti et al. 2009), most likely because of only having a small mixed proportion in both of the two young forests in the present study (Table 1). Moore (2012) reported that for those forests planted in historically or currently unwooded areas, the number of woodland species supported can be enhanced by maintaining adequate below-canopy light levels by planting broadleaves. However, a recent study in Northern and Eastern Europe found that the bryophyte layer of naturally regenerated stands had higher species richness, diversity, and number of forest bryophyte species than planted birch stands (Tullus et al. 2013). Thus, we speculate that a plantation of broadleaved species in our study area would probably have resulted in similar differences. We found that tree canopy cover was greater in planted forests than naturally regenerated forests, and canopy cover significantly influenced ground bryophyte composition (Tables 1 and 3). Thus, we can conclude that tree species and the resulting difference in canopy cover were probably the driving forces for the observed bryophyte community patterns.

Several authors have suggested that the direct factors responsible for distinct bryophyte composition in forests are microclimate and habitat heterogeneity created by distinct stand structure (Lee and La Roi 1979; Ross-Davis and Frego 2002; Márialigeti et al. 2009). Canopy tree identity controls the understory microclimate, which, in turn, regulates bryophyte regeneration and survival (Fenton and Frego 2005; Vellak and Ingerpuu 2005). For example, Lemenih et al. (2004) found that broadleaved species have significantly lower canopy cover and leaf area index, higher understory air temperature, and higher soil temperature as well as higher diurnal temperature fluctuations than conifers (also see Chen et al. 1999). Furthermore, our results definitely suggested that the understory shrub and herbaceous layers at fine-scale levels in those young forests can also produce contrasting effects on bryophyte diversity: positive roles from shrubs and negative roles from herbaceous cover (Tables 3 and 5). In temperate deciduous forests, the effects are likely positive because of the shading effects (i.e., modification of local abiotic conditions that favor growth) (Márialigeti et al. 2009). Consequently, broadleaved forests have richer bryophyte and vascular plant species (Humphrey et al. 2002; Lemenih et al. 2004). Therefore, natural stands provide a more suitable habitat (i.e., higher quality) for a wider range of native species to settle than the plantations, resulting in many more bryophyte species exclusively or more frequently existing in the natural stands according to frequency-tendency tests (116 vs. 48 species).

5 Conclusions and implications

Conservation and maintenance of bryophyte diversity is often neglected in forestry practices worldwide, perhaps because these tiny plants are difficult to identify and their economic value is not well known. We conducted the current study in the managed subalpine region in southwestern China to explore the effects of natural regeneration and reforestation strategy on ground bryophyte assembly in harvested areas. We found that the two forest regeneration strategies indirectly and directly resulted in significantly different ground bryophyte communities in the early forest regeneration stage. Although reforestation may eventually restore the forests and conserve ground bryophyte diversity to some extent, natural regeneration resulted in a much higher number of bryophytes, especially liverworts and pleurocarpous mosses that are sensitive to habitat alteration. We identified the stand structure as the most important variable influencing bryophyte composition and diversity, whereas the homogenous habitats created by clear-cuts following silvicultural practices seemed to be responsible for the relatively low diversity in the planted forest. These findings suggest that reduction of the overstory canopy could be an effective approach in strengthening habitat heterogeneity for bryophytes in plantations and that integrating natural regeneration into reforestation would be an alternative management option for enhancing both productivity and in situ conservation of bryophyte diversity.

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Appendix

Table 6 Basic site information of 13 naturally regenerated deciduous stands and 13 plantations investigated in the northwestern Sichuan, China

Site	Regeneration strategy	Forest type	Density (stem ha^{-1})	Clear-cutting time	Elevation (m)	Aspect	Slope degree (°)	Coordinates
Barkam	Naturally	Natural forest	780	1990s	3,150	NW30°	33	31°49′19.77″ N, 102°17′29.79″ E
Barkam	Naturally	Natural forest	1,813	1980s	3,558	NE20°	21	31°48′19.27″ N,102°17′51.23″ E
Barkam	Naturally	Natural forest	870	1970s	3,043	NE50°	35	31°49′31.44″ N, 102°17′04.21″ E
Jinchuan	Naturally	Natural forest	1,944	1990s	3,765	NW25°	28	31°26′33.90″ N, 101°50′39.10″ E
Jinchuan	Naturally	Natural forest	1,667	1990s	3,790	NW25°	26	31°26′40.00″ N, 101°50′52.80″ E
Jinchuan	Naturally	Natural forest	1,925	1980s	3,405	NW20°	36	31°28′22.40″ N, 101°50′47.90″ E
Jinchuan	Naturally	Natural forest	1,625	1960s	2,769	NW10°	30	31°32′00.10″ N, 101°52′28.80″ E
Li	Naturally	Natural forest	1,389	1990s	3,217	E	34	31°41′37.39″ N, 102°45′36.81″ E
Li	Naturally	Natural forest	1,137	1990s	3,260	NE40°	35	31°47′37.16″ N, 102°42′11.27″ E
Li	Naturally	Natural forest	1,180	1970s	3,277	NE60°	22	31°41′52.22″ N, 102°45′15.11″ E
Li	Naturally	Natural forest	1,430	1970s	3,195	NW50°	30	31°40′39.95″ N, 102°46′24.50″ E
Li	Naturally	Natural forest	1,135	1960s	2,938	NE40°	27	31°39′35.76″ N, 102°47′37.75″ E
Li	Naturally	Natural forest	1,117	1960s	2,864	NE30°	24	31°39′35.51″ N, 102°48′17.70″ E
Barkam	Reforestation	Plantation	3,000	1980s	3,668	NE60°	31	31°43′12.10″ N, 102°16′37.50″ E
Barkam	Reforestation	Plantation	2,500	1980s	3,281	NE69°	35	31°47′52.08″ N, 102°17′30.11″ E
Iinchuan	Reforestation	Plantation	3,700	1980s	3,360	NW15°	29	31°28′15.00″ N, 101°50′50.00″ E
Jinchuan	Reforestation	Plantation	2,566	1980s	3,330	NW14°	43	31°28′24.70″ N, 101°50′44.90″ E
Jinchuan	Reforestation	Plantation	1,933	1970s	3,170	NE19°	36	31°30′24.00″ N, 101°50′58.90″ E
Jinchuan	Reforestation	Plantation	1,000	1970s	3,014	NW13°	31	31°31′30.40″ N, 101°51′51.20″ E
Jinchuan	Reforestation	Plantation	1,233	1970s	3,010	NW20°	23	31°31′34.50″ N, 101°51′59.90″ E
Jinchuan	Reforestation	Plantation	767	1970s	2,990	NE28°	31	31°32′18.10″ N, 101°52′44.30″ E
Li	Reforestation	Plantation	3,767	1990s	3,277	NE60°	35	31°41′21.91″ N, 102°44′39.04″ E
Li	Reforestation	Plantation	2,800	1980s	2,940	E	25	31°41′43.20″ N, 102°44′43.80″ E
Li	Reforestation	Plantation	2,133	1970s	3,108	W	25	31°41′28.92″ N, 102°45′05.39″ E
Li	Reforestation	Plantation	2,267	1960s	3,357	NW60°	34	31°40′32.35″ N, 102°45′46.96″ E
Li	Reforestation	Plantation	1,800	1960s	3,141	NW60°	35	31°40′27.96″ N, 102°45′42.51″ E

Table 7 Species list, their occurrence, mean cover, and important value (IV) in the naturally regenerated deciduous stands and the plantations in the northwestern Sichuan, China

	Natural stands (n = 780)			Plantations (n = 780)					
	Occurrence	Mean cover (%)	IV	Occurrence	Mean cover (%)	IV	Phylogenetic group	Growth form	Frequency–tendency distribution
Present only in natural stands									
Anastrepta orcadensis	15	1.21	0.366	–	–	–	L	T	NRS
Anoectangium aestivum	1	0.05	0.019	–	–	–	AM	T	NRS
Anoectangium stracheyanum	5	0.222	0.09	–	–	–	AM	T	NRS
Anoectangium thomsonii	4	0.133	0.064	–	–	–	AM	T	NRS
Atrichum rhystophyllum	1	0.3	0.063	–	–	–	PM	T	NRS
Bazzania bidentula	1	0.2	0.046	–	–	–	L	T	NRS
Blepharostoma trichophyllum	2	1.805	0.342	–	–	–	L	W	NRS
Brachymenium muricola	1	0.1	0.028	–	–	–	AM	T	NRS

Table 7 (continued)

	Natural stands (n = 780)			Plantations (n = 780)					
	Occurrence	Mean cover (%)	IV	Occurrence	Mean cover (%)	IV	Phylogenetic group	Growth form	Frequency–tendency distribution
Brachythecium buchananii	9	2.189	0.48	–	–	–	PM	M	NRS
Brachythecium rutabulum	4	1.925	0.383	–	–	–	PM	M	NRS
Brachythecium thraustum	2	5.95	1.08	–	–	–	PM	M	NRS
Brotherella falcata	4	2.48	0.482	–	–	–	PM	M	NRS
Bryoerythrophyllum yunnanense var. *yunnanense*	1	0.1	0.028	–	–	–	AM	T	NRS
Bryum billarderi	16	0.949	0.33	–	–	–	AM	T	NRS
Bryum cellulare	1	0.01	0.012	–	–	–	AM	C	NRS
Bryum lonchocaulon	2	0.105	0.039	–	–	–	AM	C	NRS
Calypogeia trichomanis	8	0.154	0.108	–	–	–	L	T	NRS
Cirriphyllum cirrosum	1	1.7	0.313	–	–	–	PM	M	NRS
Cyrto-hypnum bonianum	1	0.01	0.012	–	–	–	PM	W	NRS
Dicranodontium denudatum	3	0.107	0.049	–	–	–	AM	T	NRS
Dicranum cheoi	1	7.7	1.382	–	–	–	AM	T	NRS
Dicranum drummondii	17	2.064	0.539	–	–	–	AM	T	NRS
Dicranum japonicum	9	4.934	0.97	–	–	–	AM	T	NRS
Dicranum majus	11	1.219	0.328	–	–	–	AM	T	NRS
Didymodon rufidulus	8	0.269	0.128	–	–	–	AM	T	NRS
Didymodon vinealis	6	0.46	0.142	–	–	–	AM	T	NRS
Ditrichum pallidum	1	0.01	0.012	–	–	–	AM	T	NRS
Encalypta rhaptocarpa	1	0.2	0.046	–	–	–	AM	T	NRS
Encalypta spathulata	2	0.105	0.039	–	–	–	AM	T	NRS
Entodon micropodus	1	1.2	0.224	–	–	–	PM	W	NRS
Entodon viridulus	1	0.3	0.063	–	–	–	PM	W	NRS
Eurhynchium eustegium	5	1.54	0.325	–	–	–	PM	M	NRS
Eurhynchium laxirete	6	0.433	0.137	–	–	–	PM	M	NRS
Forsstroemia producta	1	0.3	0.063	–	–	–	PM	W	NRS
Gollania neckerella	3	0.917	0.193	–	–	–	PM	M	NRS
Gollania robusta	15	1.383	0.397	–	–	–	PM	M	NRS
Herbertus angustissimus	5	3.1	0.603	–	–	–	L	T	NRS
Hymenostylium recurvirostrum var. *recurvirostrum*	11	0.721	0.239	–	–	–	AM	C	NRS
Hyophila involuta	1	0.2	0.046	–	–	–	AM	T	NRS
Hypnum fujiyamae	10	1.207	0.316	–	–	–	PM	M	NRS
Hypnum hamulosum	3	0.073	0.043	–	–	–	PM	W	NRS
Hypnum plumaeforme	4	0.015	0.043	–	–	–	PM	M	NRS
Hypopterygium aristatum	1	0.05	0.019	–	–	–	PM	D	NRS
Isopterygium bancanum	1	0.05	0.019	–	–	–	PM	M	NRS
Jungermannia brevicaulis	2	6.75	1.223	–	–	–	L	T	NRS
Leptodontium flexifolium	7	0.393	0.14	–	–	–	AM	T	NRS
Leucodon secundus	1	0.2	0.046	–	–	–	PM	M	NRS
Leucodon sinensis	3	0.2	0.066	–	–	–	PM	M	NRS
Lindbergia sinensis	2	0.105	0.039	–	–	–	PM	M	NRS
Lophozia cornuta	11	0.715	0.238	–	–	–	L	T	NRS
Meteorium subpolytrichum	2	0.15	0.047	–	–	–	PM	P	NRS
Mnium thomsonii	1	6.5	1.168	–	–	–	AM	T	NRS

Table 7 (continued)

	Natural stands (n = 780)			Plantations (n = 780)					
	Occurrence	Mean cover (%)	IV	Occurrence	Mean cover (%)	IV	Phylogenetic group	Growth form	Frequency–tendency distribution
Neckeropsis nitidula	19	0.885	0.348	–	–	–	PM	F	NRS
Orthomnion yunnanense	6	0.01	0.062	–	–	–	AM	D	NRS
Palamocladium leskeoides	1	5.5	0.99	–	–	–	PM	W	NRS
Palamocladium nilgheriense	5	0.01	0.052	–	–	–	PM	W	NRS
Plagiomnium cuspidatum	2	0.605	0.128	–	–	–	AM	D	NRS
Plagiothecium euryphyllum var. *brevirameum*	2	0.255	0.066	–	–	–	PM	F	NRS
Plagiothecium handelii	2	0.01	0.022	–	–	–	PM	M	NRS
Plagiothecium nemorale	3	1.567	0.309	–	–	–	PM	F	NRS
Pleuroziopsis ruthenica	4	0.9	0.201	–	–	–	PM	D	NRS
Pleurozium schreberi	2	4.85	0.884	–	–	–	PM	W	NRS
Pohlia hyaloperistoma	4	0.01	0.042	–	–	–	AM	T	NRS
Polytrichastrum emodi	9	0.774	0.228	–	–	–	PM	T	NRS
Porella oblongifolia	34	1.983	0.695	–	–	–	L	M	NRS
Pseudochorisodontium setschwanicum	1	1	0.188	–	–	–	AM	T	NRS
Regmatodon longinervis	2	0.01	0.022	–	–	–	PM	M	NRS
Rhynchostegiella japonica	3	0.667	0.149	–	–	–	PM	W	NRS
Rhynchostegium ovalifolium	2	3.25	0.599	–	–	–	PM	W	NRS
Rhynchostegium serpenticaule	1	0.8	0.153	–	–	–	PM	W	NRS
Sanionia unicinata	46	5.346	1.415	–	–	–	PM	M	NRS
Scapania nemorea	3	0.237	0.072	–	–	–	L	T	NRS
Thamnobryum sandei	1	3	0.545	–	–	–	PM	F	NRS
Tortula planifolia	1	0.01	0.012	–	–	–	AM	C	NRS
Ulota sp.	1	0.2	0.046	–	–	–	PM	C	NRS
Present only in plantations									
Amblystegium serpens var. *serpens*	–	–	–	2	0.2	0.067	PM	M	RES
Atractylocarpus alpinus	–	–	–	5	0.064	0.075	AM	T	RES
Brachythecium populeum	–	–	–	2	6.3	1.368	PM	M	RES
Brachythecium salebrosum	–	–	–	23	2.422	0.799	PM	M	RES
Bryoerythrophyllum alpigenum	–	–	–	2	0.2	0.067	AM	T	RES
Bryoerythrophyllum rubrum	–	–	–	1	8	1.719	AM	T	RES
Bryum dichotomum	–	–	–	1	0.2	0.055	AM	T	RES
Cyrto-hypnum vestitissimum	–	–	–	7	7.129	1.606	PM	W	RES
Dicranella schreberiana	–	–	–	1	0.01	0.014	AM	T	RES
Dicranella varia	–	–	–	1	0.1	0.034	AM	T	RES
Didymodon asperifolius	–	–	–	1	0.01	0.014	AM	T	RES
Didymodon fallax	–	–	–	2	0.35	0.099	AM	T	RES
Gollania schensiana	–	–	–	2	3.5	0.771	PM	M	RES
Grimmia fuscolutea	–	–	–	1	1	0.226	AM	C	RES
Habrodon perpusillus	–	–	–	1	2	0.439	PM	W	RES
Leucodon subulatus	–	–	–	1	3	0.652	PM	M	RES
Mnium heterophyllum	–	–	–	9	0.928	0.308	AM	T	RES
Plagiomnium maximoviczii	–	–	–	19	4.229	1.135	AM	D	RES
Plagiomnium tezukae	–	–	–	1	0.01	0.014	AM	D	RES
Ptychomitrium formosicum	–	–	–	1	0.01	0.014	AM	C	RES

Table 7 (continued)

	Natural stands (n = 780)			Plantations (n = 780)					
	Occurrence	Mean cover (%)	IV	Occurrence	Mean cover (%)	IV	Phylogenetic group	Growth form	Frequency–tendency distribution
Pylaisiella extenta	–	–	–	20	0.644	0.383	PM	M	RES
Pylaisiella robusta	–	–	–	1	2	0.439	PM	M	RES
Racomitrium carinatum	–	–	–	9	0.402	0.196	AM	C	RES
Rhizomnium hattorii	–	–	–	6	0.15	0.106	AM	T	RES
Schistidium trichodon	–	–	–	3	0.233	0.087	AM	C	RES
Symblepharis reinwardtii	–	–	–	1	1	0.226	AM	T	RES
Taxiphyllum aomoriense	–	–	–	15	0.609	0.314	PM	M	RES
Ubiquitous									
Abietinella abietina	17	4.031	0.889	27	2.208	0.802	PM	W	GES
Anastrophyllum donianum	8	0.17	0.111	9	0.937	0.31	L	T	GES
Anomobryum auratum	2	0.01	0.022	3	0.15	0.069	AM	T	GES
Anomobryum julaceum	9	0.201	0.126	10	0.198	0.165	AM	T	GES
Atrichum undulatum var. *gravilisetum*	3	0.217	0.069	4	2.103	0.498	PM	T	GES
Bartramia subulata	2	0.075	0.033	4	0.553	0.167	AM	T	GES
Brachythecium plumosum	3	7.5	1.367	4	0.58	0.173	PM	M	GES
Brachythecium rivulare	7	0.693	0.194	4	0.525	0.161	PM	M	GES
Brotherella erythrocaulis	1	1.3	0.242	2	0.55	0.142	PM	M	GES
Bryum blindii	6	2.153	0.444	12	0.273	0.205	AM	T	GES
Bryum caespiticium	6	0.692	0.184	5	4.29	0.976	AM	C	GES
Bryum leptocaulon	1	0.2	0.046	1	0.01	0.014	AM	T	GES
Campylopus pyriformis	1	0.5	0.099	3	0.133	0.065	AM	T	GES
Campylopus durelii	6	0.893	0.219	6	1.25	0.34	AM	T	GES
Chiloscyphus minor	32	0.708	0.448	19	0.356	0.309	L	T	GES
Conocephalum conicum	8	0.681	0.202	17	0.262	0.265	L	W	GES
Dicranoweisia crispula	9	0.23	0.131	3	0.567	0.158	AM	C	GES
Dicranoweisia indica	1	0.5	0.099	2	0.01	0.027	AM	T	GES
Dicranum bonjeanii	2	0.105	0.039	7	0.731	0.242	AM	T	GES
Dicranum hamulosum	5	3.814	0.73	2	0.1	0.046	AM	T	GES
Dicranum leiodontium	7	1.443	0.327	7	1.307	0.365	AM	T	GES
Dicranum mayrii	1	0.3	0.063	1	0.4	0.098	AM	T	GES
Dicranum muehlenbeckii	6	0.075	0.074	3	0.213	0.082	AM	T	GES
Dicranum nipponense	2	0.2	0.056	1	0.01	0.014	AM	T	GES
Didymodon ditrichoides	4	0.28	0.09	10	0.293	0.185	AM	T	GES
Didymodon erosodenticulatus	3	0.503	0.12	2	0.1	0.046	AM	T	GES
Didymodon rigidulus	12	0.746	0.253	6	1.683	0.433	AM	T	GES
Entodon aeruginosus	33	2.522	0.781	29	2.227	0.831	PM	W	GES
Entosthodon buseanus	1	0.1	0.028	1	2.2	0.481	AM	T	GES
Eurhynchium coarctum	173	2.739	2.226	158	2.693	2.514	PM	W	GES
Eurhynchium longirameum	7	2.914	0.59	8	0.526	0.21	PM	W	GES
Fissidens anomalus	8	1.739	0.39	2	0.03	0.031	AM	T	GES
Fissidens polypodioides	1	0.05	0.019	5	0.246	0.114	AM	T	GES
Giraldiella levieri	6	0.055	0.07	3	0.103	0.059	PM	W	GES
Gollania cylindricarpa	7	2.193	0.461	3	1.003	0.251	PM	M	GES
Gollania japonica	25	1.619	0.54	18	2.786	0.815	PM	M	GES
Grimmia pilifera	1	0.01	0.012	3	0.283	0.097	AM	C	GES

Table 7 (continued)

	Natural stands (n = 780)			Plantations (n = 780)					
	Occurrence	Mean cover (%)	IV	Occurrence	Mean cover (%)	IV	Phylogenetic group	Growth form	Frequency–tendency distribution
Hypnum cupressiforme var. *lacunosum*	1	2.5	0.456	1	0.05	0.023	PM	M	GES
Hypnum sakuraii	16	0.938	0.328	12	3.896	0.978	PM	T	GES
Kindbergia arbuscula	10	6.005	1.17	6	6.15	1.385	PM	D	GES
Kindbergia praelonga	31	2.907	0.829	34	0.616	0.549	PM	M	GES
Leucodon exaltatus	6	1.117	0.259	1	0.01	0.014	PM	M	GES
Lophozia fauriana	13	1.019	0.312	6	0.467	0.173	L	T	GES
Marchantia sp.	6	0.852	0.212	13	0.259	0.215	L	W	GES
Molendoa sendtneriana	1	0.15	0.037	2	0.03	0.031	AM	T	GES
Orthodicranum montanum	5	1.366	0.294	2	0.35	0.099	AM	T	GES
Orthotrichum hookeri	6	0.092	0.077	8	0.276	0.157	PM	C	GES
Orthotrichum laevigatum	3	0.01	0.032	1	0.05	0.023	PM	C	GES
Paraleucobryum enerve	17	2.017	0.53	14	0.851	0.353	AM	T	GES
Plagiochila microphylla	2	0.01	0.022	1	2.2	0.481	L	T	GES
Pogonatum subfuscatum	5	4.12	0.784	8	0.964	0.304	PM	T	GES
Pohlia elongata	5	0.442	0.129	2	1.4	0.323	AM	T	GES
Pohlia nutans	19	1.692	0.492	18	0.438	0.314	AM	T	GES
Pseudochorisodontium conanenum	6	2.112	0.437	2	0.53	0.138	AM	T	GES
Pseudosymblepharis duriuscula	13	1.028	0.314	5	2.892	0.678	AM	T	GES
Pylaisiella falcata	10	0.738	0.232	7	0.48	0.188	PM	M	GES
Rhodobryum ontariense	42	0.59	0.527	44	0.182	0.579	AM	D	GES
Rhynchostegiella laeviseta	1	1.2	0.224	1	0.05	0.023	PM	W	GES
Rhytidiadelphus squarrosus	25	1.051	0.438	19	7.284	1.787	PM	W	GES
Rhytidiadelphus triquetrus	55	2.837	1.058	52	2.135	1.094	PM	W	GES
Schistidium apocarpum	4	0.425	0.116	2	2.5	0.558	AM	C	GES
Tortella fragilis	6	0.31	0.116	3	3.033	0.684	AM	T	GES
Tortula yuennanensis	4	0.538	0.136	2	0.01	0.027	AM	C	GES
Trachycystis ussuriensis	48	1.761	0.796	45	1.165	0.801	AM	T	GES
Trichostomum hattorianum	25	1.381	0.497	27	1.579	0.668	AM	T	GES
Trichostomum tenuirostre	85	0.565	0.954	76	1.735	1.303	AM	T	GES
Tritomaria exsecta	8	0.635	0.194	3	0.01	0.039	L	T	GES
Weisia exserta	6	0.417	0.135	1	0.05	0.023	AM	C	GES
More frequent in natural stands relative to plantations									
Actinothuidium hookeri	96**	2.135	1.345	61**	3.033	1.396	PM	W	NRS
Apometzgeria pubescens var. *pubescens*	63**	0.41	0.707	22**	0.562	0.39	L	M	NRS
Bartramia halleriana	53**	1.318	0.767	21**	0.67	0.401	AM	T	NRS
Brachythecium coreanum	19**	1.468	0.452	2**	0.855	0.207	PM	M	NRS
Brachythecium garovaglioides	50**	1.603	0.788	6**	0.968	0.28	PM	M	NRS
Brachythecium pinnirameum	71**	1.641	1.006	33**	1.262	0.674	PM	M	NRS
Bryum argenteum	14**	0.656	0.258	3**	0.17	0.073	AM	T	NRS
Camptothecium auriculatum	98**	2.547	1.438	28**	0.895	0.535	PM	M	NRS
Chiloscyphus polyanthus	74**	0.337	0.803	21**	0.28	0.318	L	T	NRS
Climacium dendroides	33*	1.705	0.635	4*	0.955	0.253	PM	D	NRS
Dicranodontium filifolium	30**	3.095	0.853	11**	2.228	0.61	AM	T	NRS
Dicranodontium porodictyon	11**	1.945	0.457	1**	2.5	0.545	AM	T	NRS

Table 7 (continued)

	Natural stands (n = 780)			Plantations (n = 780)					
	Occurrence	Mean cover (%)	IV	Occurrence	Mean cover (%)	IV	Phylogenetic group	Growth form	Frequency–tendency distribution
Dicranum scoparium	7*	0.53	0.165	1*	0.01	0.014	AM	T	NRS
Gollania turgens	38**	1.802	0.703	10**	1.921	0.532	PM	M	NRS
Haplocladium angustifolium	21**	1.914	0.552	6**	0.702	0.223	PM	W	NRS
Homalothecium laevisetum	16*	1.418	0.413	5*	1.634	0.41	PM	W	NRS
Hylocomium splendens	91**	5.989	1.981	48**	10.385	2.804	PM	W	NRS
Hypnum calcicolum	25**	3.739	0.917	3**	0.433	0.129	PM	T	NRS
Hypnum tristo-viride	53**	1.435	0.788	20**	3.003	0.886	PM	M	NRS
Hypopterygium tenellum	39**	0.411	0.465	1**	0.01	0.014	PM	D	NRS
Jungermannia pumila	61**	0.69	0.736	7**	0.08	0.103	L	M	NRS
Lepidozia reptans	20**	4.442	0.992	1**	0.1	0.034	L	W	NRS
Metzgeria consanguinea	40**	0.343	0.463	13**	0.235	0.21	L	M	NRS
Mnium lycopodioides	207**	1.425	2.333	86**	1.541	1.384	AM	T	NRS
Mnium spinosum	109**	0.297	1.148	55**	0.795	0.845	AM	T	NRS
Neckera pennata	30**	0.8	0.444	3**	0.17	0.073	PM	F	NRS
Neodicladiella pendula	18*	0.391	0.25	7*	0.319	0.154	PM	P	NRS
Neodolichomitra yunnanensis	134**	4.954	2.229	36**	2.031	0.875	PM	W	NRS
Oncophorus virens	61**	0.699	0.737	26**	1.431	0.624	AM	T	NRS
Plagiochila perserrata	67**	0.761	0.808	40**	0.847	0.672	L	T	NRS
Plagiochila chinensis	39*	2.159	0.777	23*	5.185	1.388	L	T	NRS
Plagiochila delavayi	37**	1.02	0.553	1**	0.05	0.023	L	T	NRS
Plagiomnium ellipticum	293**	1.457	3.203	160**	5.78	3.197	AM	T	NRS
Plagiomnium medium	142**	1.442	1.683	40**	2.37	0.997	AM	D	NRS
Plagiothecium neckeroideum var. neckroideum	175**	1.069	1.948	28**	0.254	0.398	PM	F	NRS
Pohlia cruda	45**	1.057	0.64	9**	7.944	1.805	AM	T	NRS
Radula constricta	32**	2.767	0.814	11**	0.872	0.321	L	M	NRS
Rhizomnium magnifolium	11**	1.564	0.389	1**	0.01	0.014	AM	T	NRS
Rhynchostegiella acicula	14**	1.551	0.417	1**	1.2	0.268	PM	M	NRS
Rhytidiadelphus subpinnatus	67**	3.961	1.379	8**	1.326	0.381	PM	W	NRS
Symblepharis vaginata	41**	0.642	0.526	16**	1.781	0.576	AM	T	NRS
More frequent in plantations relative to natural stands									
Barbula subpellucida	1**	0.81	0.154	11**	1.674	0.492	AM	T	RES
Bryhnia serricuspis	17**	1.709	0.475	95**	5.167	2.268	PM	W	RES
Bryhnia trichomitria	7**	0.601	0.177	59**	4.628	1.711	PM	W	RES
Chiloscyphus latifolius	1*	10.8	1.934	7*	0.141	0.116	L	T	RES
Entodon caliginosus	49**	1.456	0.752	87**	3.74	1.866	PM	W	RES
Entodon concinnus	219**	1.466	2.461	467**	3.491	6.477	PM	W	RES
Eurhynchium savatieri	37**	1.296	0.603	89**	1.056	1.318	PM	M	RES
Gollania arisanensis	1**	0.05	0.019	11**	1.055	0.36	PM	M	RES
Haplocladium microphyllum	4*	0.675	0.16	14*	1.152	0.418	PM	W	RES
Mnium marginatum	86**	0.681	0.985	274**	1.576	3.7	AM	T	RES
Myuroclada maximowiczii	12**	1.599	0.405	55**	1.018	0.892	PM	M	RES
Plagiochila duthiana	4**	1.3	0.272	23**	0.979	0.491	L	T	RES
Plagiomnium acutum	93**	3.299	1.522	159**	4.097	2.826	AM	D	RES
Plagiomnium rhynchophorum	87**	1.392	1.122	121*	1.842	1.878	AM	D	RES
Porella chinensis	3**	0.537	0.126	15**	0.967	0.39	L	M	RES

Table 7 (continued)

	Natural stands ($n=780$)			Plantations ($n=780$)					
	Occurrence	Mean cover (%)	IV	Occurrence	Mean cover (%)	IV	Phylogenetic group	Growth form	Frequency–tendency distribution
Rhytidium rugosum	6**	0.267	0.108	34**	0.964	0.623	PM	W	RES
Thuidium cymbifolium	479**	4.219	5.563	631**	7.761	9.401	PM	W	RES
Timmiella diminuta	10**	0.487	0.187	29**	4.836	1.387	AM	T	RES
Tortella humilis	2*	0.075	0.033	9*	1.29	0.386	AM	T	RES
Tortella tortuosa	14*	0.254	0.186	31*	0.449	0.476	AM	T	RES
Tortula muralis	2**	0.01	0.022	13**	1.516	0.483	AM	T	RES

Frequency–tendency distribution group was developed based on species occurrence by the chi-squared and Fisher's exact tests: (1) Natural regeneration species group (NRS), (2) generalist group (GES), and (3) reforestation group (RES). For concurring species, the asterisk on right angle of occurrence value indicated significant difference in occurrence tested using χ^2

Growth form: *C* cushions, *D* dendroids, *F* fans, *M* mats, *P* pendants, *T* turfs, *W* wefts; phylogenetic group: *L* liverwort, *AM* acrocarpous moss, *PM* pleurocarpous moss

*$0.01<P<0.05$; **$0.001<P<0.01$

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