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Article

Understory Structure and Vascular Plant Diversity in Naturally Regenerated Deciduous Forests and Spruce Plantations on Similar Clear-Cuts: Implications for Forest Regeneration Strategy Selection

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Abstract: The active effect of natural regeneration on understory vegetation and diversity on clear-cut forestlands, in contrast to conifer reforestation, is still controversial. Here we investigated differences in understory vegetation by comparing naturally regenerated deciduous forests (NR) and reforested spruce plantations (SP) aged 20–40 years on 12 similar clear-cuts of subalpine old-growth spruce-fir forests from the eastern Tibetan Plateau. We found that 283 of the 334 vascular plant species recorded were present in NR plots, while only 264 species occurred in SP plots. This was consistent with richer species, higher cover, and stem (or shoot) density of tree seedlings, shrubs, and ferns in the NR plots than in the SP plots. Moreover, understory plant diversity was limited under dense canopy cover, which occurred more frequently in the SP plots. Our findings implied that natural deciduous tree regeneration could better preserve understory vegetation and biodiversity than spruce reforestation after clear-cutting. This result further informed practices to reduce tree canopy cover for spruce plantations or to integrate natural regeneration and reforestation for clear-cuts in order to promote understory vegetation and species diversity conservation.

Keywords: understory vegetation; plant diversity; natural regeneration; reforestation; spruce plantation; Tibetan Plateau; generalized linear mixed-effect models (GLMMs)

1. Introduction

Species composition, diversity, and structure of understory vegetation are keys to providing complex structure and conserving indigenous floras within forests [1,2]. The understory can provide habitat and food for faunal communities [3], and act as a driver of nutrient cycling [4], stand productivity [4,5], and forest regeneration and succession [6–8]. Thus, the understory community and biodiversity are focal objectives for sustainable forest management, effective forest biodiversity conservation, and successful forest restoration [4,6,9]. However, the effects of different strategic applications for forest regeneration on understory vegetation and species diversity on clear-cuts remains controversial, advocating further study [9–12]. It is a challenge for forest managers to promote forest regeneration, while conserving indigenous biodiversity in a large area of clear-cut forestlands.

Natural regeneration and conifer reforestation on clear-cuts are two major regeneration strategies that have been long employed in the northwestern Sichuan Province, China [13], and globally [14]. Natural regeneration without artificial reforestation often depends on remnant vegetation, its seed pool, and dispersals surrounding vegetation and involves the synchronous development of both native trees and other plant forms together with their abiotic environment. It usually leads to a mix of tree species and unevenly-aged individuals, which exhibit connectivity among their components and are self-organized into hierarchies and cycles [15,16]. In contrast to natural regeneration, artificial reforestation schemes are designed with targets for establishing overstory structure and satisfying production demands, and they often repress vegetation with the potential to hinder target tree growth. They are also designed to achieve a stand of individuals that are even-aged and regularly spaced. Thus, artificial reforestation efforts usually do not include activities that are conducive to developing understory biodiversity [14]. This is true depending on the extent to which a site is prepared for planting, which has not been addressed [11,12,17] up to now. A substantial body of research has compared species composition and diversity between coniferous plantations and naturally regenerated forests or secondary forests worldwide (for reviews see Brockerhoff *et al.*, 2008; Bremer & Farley, 2010) [11,12]. However, results vary and are even contradictory. Reforested plantations might have similar, or significantly lower or higher, vascular plant species richness and diversity of understory vegetation in comparison with naturally regenerated forests [10–12,18–21]. Consequently, the effects remain unpredictable and differ according to the manner and intensity of disturbance from different regeneration pathways [11,12].

The conflicting results presented in the literature regarding species richness and understory vegetation structure are due to several inconsistent factors used when making comparisons: different historical origins of previous vegetation [12], distinct initial site condition [22,23], different successional stage or forest age [16,24,25], target tree identity and mixture [10,11], and site degradation intensity and management [11,12,14,22]. To reach reliable conclusions on the effects of different regeneration methods on understory vascular plant composition and diversity requires controlling variability among study sites. Moreover, it is also necessary to consider the sampling design and the accompanying statistical methodology. During sampling design and the investigation of species composition, different scales (stand, plot, and quadrats) have long been widely used by researchers. Recently, systematical sampling has become more popular [25,26]. Quadrats are often nested plots, and plots are often nested stands during the systematical sample process. However, these data are usually not independent [27,28] and may also be non-normal. These are troubling issues for many researchers who are used to applying independent tests in their studies. The generalized linear mixed-effect models (GLMMs) is an extension of generalized linear models (GLMs), including random effects to deal with correlated data structures, in particular, with clustered structures [28,29]. This model also provides a more flexible approach for non-normal data [30]. However, it has not been widely used in studies that utilize nested data to explore differences in understory vascular plant structure and biodiversity between naturally and artificially regenerated forests [29,31].

In the current study, we aimed to evaluate the understory community structure and plant composition over the same regeneration period in two stand types: naturally regenerated deciduous forest and planted spruce forest, originating from similar clear-cuts of old-growth spruce-fir forests in the eastern Tibetan Plateau. GLMMs were applied to explore the difference of understory vegetation between the two regenerating forests. We addressed three questions: (1) Which regeneration strategies result in higher vascular plant diversity in the forest understory: natural regeneration or spruce reforestation? (2) How do the vascular plant groups (tree seedlings, shrubs, ferns, forbs, and graminoids) differ in species composition, richness, and community structure between the understory of the two forests? (3) What are the differences in structures of the overstory and understory and their relationships between the two forests? We hypothesized that: (H1) The naturally regenerated forests would host higher species diversity compared to the planted spruce forests, with woody plant diversity being the key driver of the diversity difference; and (H2) the tree canopy structure of the two forests disparately influences the structure and species diversity of the understory.

2. Materials and Methods

2.1. Study Area

This study was conducted in the Aba Tibetan and Qiang Autonomous Prefecture (30°35′ N–34°19′ N, 100°30′ E–104°27′ E), which is an area of approximately 80,000 km^2 in the northwestern Sichuan Province, China. This region is located in the northeastern Hengduan Mountains region, a famous biodiversity hotspot known in China and worldwide. It is also part of the Southwestern National Forest Region in China [13]. The forested elevations range from 2400 m to 3900 m, and the climate is temperate with an annual rainfall of 800–1000 mm and a mean annual temperature of 6–10 °C. The frost-free period in this region is less than 100 days. Mountain brown soil (luvisols) is the major soil type [32,33].

The old-growth coniferous forests are dominated by one to three species of firs (*Abies* spp.), spruces (*Picea* spp.), or larches (*Larix* spp.). They are widely distributed in the subalpine region and harbor a very high biodiversity with over 6000 species of vascular plants [13]. There is large-scale clear-cut logging in the primary coniferous forests beginning in the 1960s and ending with the Natural Forest

Protection Program in 1998. As a result of forest harvest, there are large numbers of clear-cuts with patch sizes of 3–10 ha throughout the national forestland in the studied regions. Most clear-cuts were reforested with a single native species, spruce (*Picea asperata* Mast.), in accordance with the manual [32]. Four-year-old spruce seedlings were planted at an initial density of at least 3300 stems per hectare. Once or twice in the initial two to five years following, planting management activities, including weeding and cutting shrubs, were employed to reduce competition and promote target seedling growth. After these initial treatments, no further management was applied. During this period, some clear-cut patches left to regeneration naturally succeeded towards deciduous broad-leaved forests dominated by *Betula albo-sinensis* Burk., *B. platyphylla* Suk., *Acer mono* Maxim., *A. maximowiczii* Pax, *A. davidii* subsp. *grosseri* (Pax) P. C. de Jong, *Populus davidiana* Dode, *Sorbus koehneana* Schneid, *S. setschwanensis* Schneid, and *S. hupehensis* Schneid [13,33]. As a result, the study area is a mosaic of spruce plantations of various ages and naturally regenerated forest patches [13]. The naturally regenerated deciduous broad-leaved forest accounts for approximately 25% of the forested area in the region, and the reforested spruce forest accounts for >40% [13]. The large area of secondary forest allowed us to select paired stands of the same ages, one reforested and the other resulting from natural regeneration, to explore the difference of understory structure and vascular plant diversity between the two forest regeneration strategies.

2.2. Field Investigation and Data Collection

The field investigation occurred in the summers of 2006 and 2007. Forest management records from local forest management centers were used to select suitable sites with paired stands of reforested spruce forest (SP) and naturally regenerated forest (NR). Each pair originated from similar clear-cuts with a same harvested time and with a similar topography. Twelve sites (each with a pair) from three counties with 20-40-year-old stands were selected. We systematically set three plots in the NR and three plots in the SP stands at each site. Evaluation, aspect, and slope were measured for each plot, and the stand age was also recorded according to forest management records. Each plot was the same size, 20 m × 20 m. We further systematically placed nine 2 m × 2 m shrub quadrats to investigate shrubs, and nine 1 m × 1 m herb quadrats were fixed to the upper left corner of each shrub quadrat to investigate herbs in each plot. Overall, 12 stands, including 36 plots, 324 shrub quadrats and 324 herb quadrats from naturally regenerated sites, and another paired 12 stands, also including 36 plots, 324 shrub quadrats, and 324 herb quadrats from reforested spruce plantations, were examined.

We defined tree canopy cover as the proportion of the forest floor covered by the vertical projection of tree crowns and carefully estimated the projected canopy cover and total shrub cover (including tree seedlings) for each quadrant following the method used by Strong (2011) [25]. Then, for all shrubs present in a quadrat, we recorded the species name, measured its average height, counted the stems, and estimated the cover. A similar investigation was implemented for each herb quadrat as well. To improve the estimation, a grid (the size of the shrub or herb quadrat) with 20 cells was used to estimate the total cover and that of each species. Specimens of dominant or unknown species for each of the stands were collected in the field and identified in a laboratory using various volumes of *Flora Popularis Republicae Sinicae* (Chinese version of Flora of China, China) [34]. All specimens are stored in the herbarium at the Chengdu Institute of Biology of the Chinese Academy of Sciences.

2.3. Statistical Analysis

In the study, we focused on the difference of species composition, structure, and species richness between the naturally regenerated forests and reforested spruce plantations based on the same background, but different forest management strategies. Hence, we checked for differences at the site level (n = 12) of the altitude, aspect class, slope, and time elapsed since clear-cutting between the NR and the SP stands by employed an independent t-test. The two stands did not differ significantly in altitude, aspect, slope, and stand ages (Table A1).

We then compared the difference between the NR and the SP and investigated the effects of canopy and shrub cover on the structure and species richness of the understory vegetation by applying GLMMs analysis based on the following facts: (1) nested data structure was not independent; (2) response variables were not fitted to normal distribution; and (3) there were many zeroes in our data because of the presence or absence of some group or species in each quadrat. During GLMMs analysis, treatment (NR *vs.* SP) was introduced as a fixed factor and stands (12 *vs.* 12) as a random factor, with three plots nested in each stand, and nine quadrats nested in each plot. Poisson error distribution, using a log-link function, was recommended for cover, average height, density, and species richness during GLMMs analysis.

Except for directly comparing species composition and total species richness between the NR and the SP forests, we classified all species into five species groups by growth form (tree seedlings, shrubs, ferns, forbs, and graminoids). The graminoids included species from Poaceae, Cyperaecae, and Junacaceae. The difference of each growth form group was analyzed by GLMMs. Poisson error distribution, using a log-link function, was also used for cover, average height, density, and species richness. We compared differentiation in vascular plant richness or abundance between the two forests for species group analysis as well. First, we categorized each species into one of three frequency-tendency distribution groups according to their occurrence tested by GLMMs model. The three identified species groups were: (1) reforestation species group (RES): species exclusively or more frequently found in the SP; (2) natural regeneration species group (NRS): species found exclusively or more frequently in the NR; and (3) generalist species group (GES): species that are recorded synchronously in the NR and SP, but do not show significant differences in occurrence (Tables A2 and A3). We postulated that with a background of the same origins (similar clear-cuts of the same old-growth spruce-fir forests) and regional species pools, the two forests provided different habitats and environments due to two regeneration strategies and, consequently, early stand succession. Thus, vascular plants with higher occurrence frequency in either the NR or the SP could indicate stronger habitat preference.

GLMMs analysis was also utilized to identify the effects of canopy and shrub cover on the structure and species richness of understory vegetation. Structure and species richness of the understory vegetation were selected as dependent variables. Canopy and/or shrub cover was selected as an explanation variable and stand as a random factor, with three plots nested in each stand, and nine quadrats nested in each plot. In both cases, Poisson error distribution with log-link function was selected in GLMMs.

Moreover, the total percentage of cover for each quadrat was ranked into six classes to draw a frequency distribution, and the cover classification was followed by a modified Braun-Blanquest cover abundance scale, as described by Hurst and Allen 2007 [26], including Cover Classes 1 (<1%), 2 (1%–5%), 3 (6%–25%), 4 (26%–50%), 5 (51%–75%), and 6 (76%–100%) (Figure 1). We also compared the distributions of species numbers within quadrats (species density) between the two forests (Figure 2).

Figure 1. Frequency distribution for covers of tree canopy, shrubs, and herbs at four m^2 shrub quadrats (**a**,**b**) and at one m^2 herb quadrat (**c**) within the naturally regenerated forests (NR, n = 324) and the reforested spruce forests (SP, n = 324) originating from clear-cuts in the eastern Tibetan Plateau. Cover classification was followed by a modified Braun-Blanquest cover abundance scale, as described by Hurst and Allen (2007) [26], including Cover classes 1 (<1%), 2 (1%–5%), 3 (6%–25%), 4 (26%–50%), 5 (51%–75%), and 6 (76%–100%).

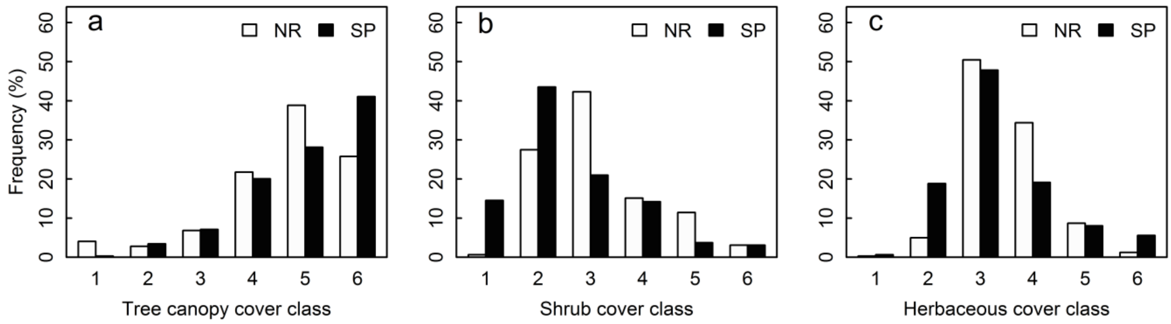
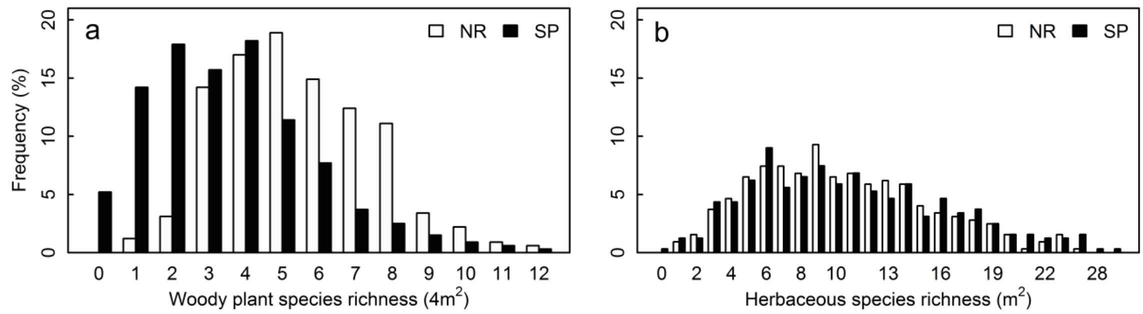


Figure 2. Frequency distribution of species density for woody plant species in four m^2 quadrats (**a**) and for total herbaceous species in one m^2 quadrats (**b**) within the naturally regenerated forests (NR) and reforested spruce forests (SP) originating from similar clear-cuts in the eastern Tibetan Plateau.



All statistical analyses were performed using R software (version 2.13.1; R Development Core Team, 2011, R Foundation for Statistical Computing, Vienna, Austria); some packages were used for these analyses, including lme4 [35], lattice [36], Matrix [37], *etc.*

3. Results

3.1. Structural Parameters

The paired (NR *vs.* SP) stands with similar ages had similar topographical conditions (Table A1). However, they had different structural parameters at the understory both in the nested 2 m × 2 m shrub quadrats and the 1 m × 1 m herbaceous quadrats, except for the herbaceous species richness in the unit of square meters (Table 1). Furthermore, the two stands also displayed various frequency distribution patterns in covers of tree canopy, shrubs, and herbaceous plants (Figure 1). Higher average tree canopy cover was presented in the SP than the NR, both in the shrub quadrats (Table 1; Figure 1a) and the herb quadrats (Table 1). The frequency distributions demonstrated that most quadrats in both forests had higher tree canopy cover and more frequently presented between 50% and 100% (Classes 5 and 6, respectively). However, comparatively, the tree canopy cover was more frequently at class 6 (76%–100%) and less often at class 1 (<1%), 4 (26%–50%), and 5 (51%–75%) in the SP than in the NR (Figure 1a). Significantly less shrub cover both at shrub and herb quadrats, lower stem density, and shorter average height of shrubs at the shrub quadrats presented in the SP than in the NR (Table 1). The frequency distributions also revealed that the SP had more quadrats with shrub cover of less than 5% (Cover Classes 1 and 2), but the NR had more quadrats with cover between 6% and 75% (Cover Classes 3 - 5) (Figure 1b). Furthermore, the SP had less cover and shorter average shoot heights, but greater shoot density for herbaceous plants than those of the NR (Table 1). The SP also had higher frequency in herbaceous cover presenting both at the lowest two classes (1 and 2, <5%) and the highest cover class (6, >75%); whereas the higher frequency in the NR was presented at the medium cover class (Classes 3 and 4, 6%–50%) (Figure 1c).

Table 1. Structure and species density (mean ± SE) in shrub and herb layers from the naturally regenerated forests (NR) and the reforested spruce forests (SP) originating from similar clear-cuts in the eastern Tibetan Plateau. The difference between the NR and the SP was tested by generalized linear mixed-effects models (GLMMs). Treatment (NR *vs.* SP) was introduced as a fixed factor and stands (12 *vs.* 12) as a random factor, with three plots nested in each stand, and nine quadrats nested in each plot. In each case, Poisson error distribution with log-link function was selected in GLMMs. * indicated that shrub included shrub and tree seedlings.

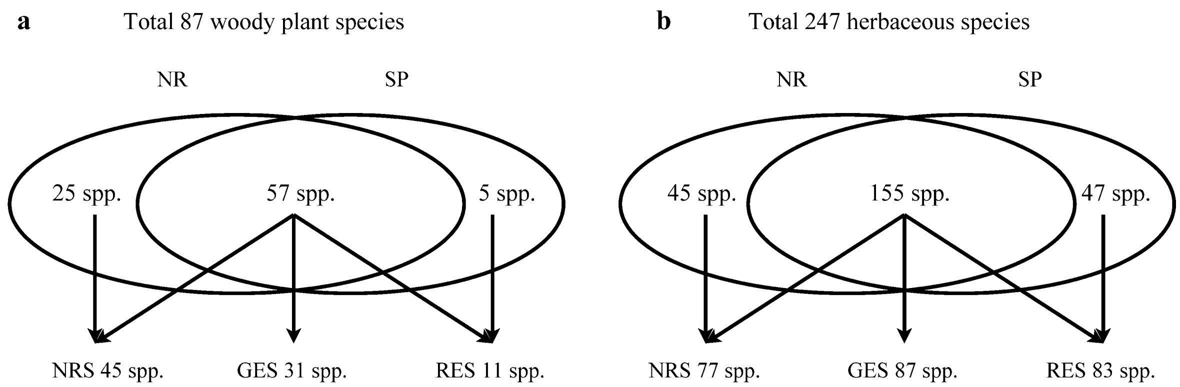
Stands	Parameters	NR	SP	Estimate	Z	Pr (>|z|)
Nested 2 m × 2 m shrub quadrats	Tree canopy cover (%)	57.42 ± 1.43	63.80 ± 1.41	0.100	9.91	<0.001
	Shrub cover (%) *	21.96 ± 1.27	14.36 ± 1.18	−0.424	−22.51	<0.001
	Average shrub height (cm)	72.69 ± 2.83	67.47 ± 4.10	−0.025	−2.657	0.008
	Shrub stem density (4 m^2)	31.51 ± 1.33	20.65 ± 1.53	−0.399	−25.33	<0.001
	Woody plant species richness (4 m^2)	5.48 ± 0.12	3.53 ± 0.13	−0.440	−11.59	<0.001
Nested 1 m × 1 m herbaceous quadrats	Tree canopy cover (%)	60.47 ± 1.55	66.38 ± 1.50	0.085	8.63	<0.001
	Shrub cover (%) *	21.80 ± 1.34	16.43 ± 1.39	−0.284	−15.677	<0.001
	Herbaceous cover (%)	27.18 ± 1.01	24.42 ± 1.30	−0.112	−7.199	<0.001
	Average herb height (cm)	14.81 ± 0.37	8.93 ± 0.27	−0.421	−17.61	<0.001
	Herbaceous shoot density (1 m^2)	58.98 ± 2.41	64.86 ± 4.00	0.273	26.05	<0.001
	Herbaceous species richness (1 m^2)	10.40 ± 0.28	10.88 ± 0.31	0.045	1.878	0.0603

3.2. Understory Species Richness and Composition

We recorded a total of 334 vascular plant species in the understories of both the SP and the NR stands (Tables A2 and A3). Fewer species occurred in the SP than in the NR (264 *vs.*

283 species) (Figure 3). A total of 87 woody plant species, including shrubs, tree seedlings, and saplings less than three meters high were recorded in the understory, but fewer species were in the SP than the NR (62 *vs.* 82) (Figure 3a). Fifty-seven woody species co-occurred in the two forests, making up a ratio of 69.5% in total woody plant species richness. A total of 247 herbaceous species were found in the two forests investigated, with 202 species in the SP and 200 species in the NR (Figure 3b). Many more herbaceous plant species (155 species, 63.2% of the totality) were commonly recorded in both forest types.

Figure 3. Species richness of totality and frequency tendency distribution species groups occurring under the naturally regenerated forests (NR) and the reforested spruce forest (SP) originating from similar clear-cuts in the eastern Tibetan Plateau. (**a**) woody plant species classification; and (**b**) herbaceous species classification. Frequency tendency distribution: natural regeneration species group (NRS), species only present or more frequent in naturally regenerated forests relative to reforested spruce plantations; reforestations species group (RES), species only or more frequent in reforested spruce plantations species relative to natural stands; generalist species group (GES), common in both forests, and with no significant difference in frequency between the two forests. The difference of frequency for each species between the NR and the SP was tested by generalized linear mixed-effects models (GLMMs). Treatment (NR *vs.* SP) was introduced as a fixed factor and stands (12 *vs.* 12) as a random factor, with three plots nested in each stand, and nine quadrats nested in each plot. In common species, a binomial error distribution with logit-ling function for presence (1) and absence (0) of each species in each quadrat was selected in GLMMs.



The two forests also differed in species richness within nested 2 m × 2 m shrub quadrats and 1 m × 1 m herbaceous quadrats (Table 1 and Figure 2). The SP had significantly less woody plant species richness, but similar herbaceous species richness in comparison to the NR (Table 1). The frequency distribution of shrub species richness in a unit of four square meters showed that the SP quadrats often had less than three species, whereas, the NR quadrats usually contained more than five species in each four m^2 quadrat (Figure 2a). Comparatively, the frequency distribution of herbaceous species density was similar to that of the NR (Figure 2b). The GLMMs analysis further showed a significant difference in frequency tendency distribution for common species between the NR and the SP stands for both woody species and herbaceous species (Tables A2 and A3). Except for those species existing either in the NR or the SP, there were 20 woody species and 32 herbaceous species with higher frequency in the NR than the SP; in contrast, there were six woody species and 36 herbaceous species whose frequency was higher in the SP than the NR.

3.3. Species Groups

Species group analysis showed that higher woody plant species richness, but less herbaceous species, existed in the NRS group than the RES group (45 *vs.* 11; 77 *vs.* 83) (Figure 3), demonstrating that more woody species and fewer herbaceous species tended to live in the habitats under the naturally regenerated forests. The understory plant growth forms also displayed some differentiations in structure and species richness between the NR and the SP (Table 2). Three groups (tree seedlings, shrubs, and ferns) always had much higher presence frequency, cover, average height, stem or shoot density, and species richness under the NR than the SP. However, forbs only had higher average height but lower cover, shoot density, species richness per square meter, and total species richness; the graminoids only had slightly higher cover and average height under the NR than the SP. Comparatively, the NR had higher species richness from three growth form groups (tree seedlings, shrubs, and ferns) and less species richness from forbs and graminoids (Table 2).

Table 2. Species richness and structural parameter values (mean ± SE) of growth-form species groups and their differences in the naturally regenerated forests (NR) and the reforested spruce forests (SP) originating from similar clear-cuts in the eastern Tibetan Plateau. The difference between the NR and the SP was tested by generalized linear mixed-effects models (GLMMs). Treatment (NR *vs.* SP) was introduced as a fixed factor and stands (12 *vs.* 12) as a random factor, with three plots nested in each stand, and nine quadrats nested in each plot. In each case, Poisson error distribution with log-link function was selected in GLMMs, except binomial error distribution with logit-ling function for the presence (1) and absence (0) of each growth form.

Growth-forms	Parameters	NR	SP	Estimate	Z	Pr (>|z|)
Tree seedlings	Presence (absence)	260 (64)	213 (111)	−0.886	−4.510	<0.001
	Cover (%)	4.06 ± 0.50	2.63 ± 0.45	−0.437	−9.916	<0.001
	Average height (cm)	70.24 ± 5.25	40.07 ± 4.28	−0.529	−47.82	<0.001
	Density (stems/4 m^2)	4.89 ± 0.35	2.96 ± 0.26	−0.492	−11.993	<0.001
	Species richness (4 m^2)	1.65 ± 0.07	1.03 ± 0.06	−0.474	−6.790	<0.001
	Total species richness	28	21			
Shrubs	Presence (absence)	323 (1)	292 (32)	−3.795	−3.510	<0.001
	Cover (%)	11.72 ± 0.78	8.70 ± 0.94	−0.288	−11.553	<0.001
	Average height (cm)	65.52 ± 2.88	59.76 ± 4.23	−0.049	−4.869	<0.001
	Density (stems/4 m^2)	26.69 ± 1.33	17.80 ± 1.51	−0.380	−22.25	<0.001
	Species richness (4 m^2)	3.81 ± 0.10	2.76 ± 0.11	−0.323	−7.341	<0.001
	Total species richness	54	41			

Table 2. *Cont.*

Growth-forms	Parameters	NR	SP	Estimate	Z	Pr (>|z|)
Ferns	Presence (absence)	287 (37)	184 (140)	−3.845	−9.159	<0.001
	Cover (%)	8.88 ± 0.57	5.06 ± 0.49	−0.546	−17.589	<0.001
	Average height (cm)	14.95 ± 0.65	6.45 ± 0.49	−0.762	−28.787	<0.001
	Density (shoots/m^2)	13.27 ± 0.71	7.48 ± 0.61	−0.495	−19.218	<0.001
	Species richness (1 m^2)	1.68 ± 0.06	0.93 ± 0.05	−0.579	−8.070	<0.001
	Total species richness	22	12			
Forbs	Presence (absence)	323 (1)	321 (3)	−0.006	−0.004	0.997
	Cover (%)	17.54 ± 0.83	18.23 ± 1.23	0.042	2.236	0.0254
	Average height (cm)	13.18 ± 0.37	8.31 ± 0.28	−0.370	−14.81	<0.001
	Density (shoots/m^2)	40.90 ± 1.84	52.86 ± 3.76	0.456	37.20	<0.001
	Species richness (1 m^2)	7.85 ± 0.23	8.95 ± 0.28	0.140	5.153	<0.001
	Total species richness	159	167			
Graminoids	Presence (absence)	176 (148)	175 (149)	0.005	0.032	0.975
	Cover (%)	1.70 ± 0.23	1.24 ± 0.17	−0.314	−4.772	<0.001
	Average height (cm)	10.63 ± 0.77	7.46 ± 0.51	−0.296	−11.018	<0.001
	Density (shoots/m^2)	4.81 ± 0.47	4.51 ± 0.38	0.058	1.537	0.124
	Species richness (1 m^2)	0.88 ± 0.06	0.95 ± 0.06	0.085	1.030	0.303
	Total species richness	20	23			

3.4. Relationships of the Tree Canopy Cover with the Structure and Species Richness of Understory Shrubs

The tree canopy cover in the NR and the SP presented different influences on structures and species richness of understory shrubs (Table 3). The tree canopy cover limited only covers of total shrub layer and tree seedlings under the NR; however under the SP, it significantly hindered not only covers, but also stem density and the average heights of tree seedlings and shrubs. It was noted that the tree canopy cover had no significant influence on species densities of both forests. Comparatively, the SP canopy cover had a more seriously negative influence on shrub assembly structure than that of the NR.

3.5. Relationships of the Tree Canopy Cover and Understory Shrubs with the Structures and Species Richness of Understory Herbs

The tree canopy cover in the NR and SP also showed different influences on structures and species richness of understory herbs (Table 4). The NR canopy cover insignificantly limited the herbaceous layer development; however, in contrast, the SP canopy cover significantly hindered herbaceous community development, including covers and shoot densities of totality and various growth form groups. Under the context of the tree canopy cover, in the SP, the shrub cover significantly influenced herbaceous cover and shoot density, fern shoot density, forbs cover and shoot density, and graminoids cover and shoot density, but only significantly affected the graminoids cover in the NR. Comparatively, the tree canopy cover in the SP had a more serious negative influence on herb community development than its shrub cover.

Table 3. Results of generalized linear mixed-effects models (GLMMs) for the effect of tree canopy cover on the understory shrub in the naturally regenerated forests (NR) and the reforested spruce forests (SP) on similar clear-cuts in the eastern Tibetan Plateau. Structure and species richness of the understory shrub were selected as dependent variables. Canopy cover was selected as an explanation variable and stand as a random factor, with three plots nested in each stand, and nine quadrats nested in each plot. In both cases, Poisson error distribution with log-link function was selected in GLMMs.

Dependent Variables	NR			SP		
	Estimate	Z	Pr (>|z|)	Estimate	Z	Pr (>|z|)
Total shrub layer cover (%)	−0.013	−6.084	<0.001	−0.022	−7.086	<0.001
Total shrub layer height (cm)	−0.002	−1.226	0.22	−0.013	−4.618	<0.001
Total shrub density (stems/4 m^2)	−0.002	−1.415	0.157	−0.008	−3.488	<0.001
Woody plant species richness (4 m^2)	−0.001	−1.001	0.315	−0.000	−0.225	0.822
Tree seedling cover (%)	−0.009	−2.136	0.033	−0.025	−3.515	<0.001
Tree seedling average height (cm)	−0.008	−1.575	0.115	−0.017	−2.257	0.024
Tree seedling species richness (4 m^2)	−0.001	−0.772	0.440	−0.001	−0.344	0.730
Shrub cover (%)	−0.004	−1.614	0.107	−0.018	−5.584	<0.001
Shrub average height (cm)	−0.003	−1.594	0.111	−0.012	−3.228	0.001
Shrub density (stems/4 m^2)	−0.003	−1.748	0.08	−0.007	−2.644	0.008
Shrub species richness (4 m^2)	−0.001	−0.628	0.530	−0.002	−1.048	0.294

Table 4. Results of generalized linear mixed-effects models (GLMMs) for the effects on the understory herbaceous layer by covers of the tree canopy and shrub in the naturally regenerated forests (NR) and the reforested spruce forests (SP) on similar clear-cuts in the eastern Tibetan Plateau. Structure and species density of herbaceous layer were selected as dependent variables. Tree canopy and shrub cover were selected as explanation variables and stand as a random factor, with three plots nested in each stand, and nine quadrats nested in each plot. In both cases, Poisson error distributions with log-link function were selected in GLMMs.

Dependent Variable	Explanations Variable	NR			SP		
		Estimate	Z	Pr (>|z|)	Estimate	Z	Pr (>|z|)
Herbaceous cover	Tree canopy cover	−0.002	−0.747	0.455	−0.014	−7.203	<0.001
Herbaceous cover	Shrub cover	−0.001	−0.308	0.758	−0.011	−3.819	<0.001
Herbaceous average height	Tree canopy cover	−0.000	−0.177	0.86	−0.003	−2.436	0.015
Herbaceous average height	Shrub cover	−0.002	−1.309	0.299	−0.001	−0.749	0.454
Herbaceous shoot density	Tree canopy cover	−0.001	−0.747	0.455	−0.014	−6.746	<0.001
Herbaceous shoot density	Shrub cover	−0.002	−0.801	0.423	−0.011	−3.678	<0.001
Herbaceous species richness	Tree canopy cover	−0.001	−0.873	0.383	−0.004	−3.744	<0.001
Herbaceous species richness	Shrub cover	−0.002	−1.912	0.056	−0.001	−0.890	0.374
Fern shoot density	Tree canopy cover	0.002	0.679	0.497	−0.014	−6.746	<0.001
Fern shoot density	Shrub cover	0.001	0.131	0.896	−0.011	−3.678	<0.001
Forbs cover	Tree canopy cover	−0.003	−0.832	0.405	−0.013	−5.753	<0.001
Forbs cover	Shrub cover	−0.003	−0.603	0.546	−0.010	−2.955	0.003
Forbs average height	Tree canopy cover	0.001	0.440	0.66	−0.003	−2.276	0.023

Table 4. *Cont.*

Dependent Variable	Explanations Variable	NR			SP		
		Estimate	Z	Pr (>|z|)	Estimate	Z	Pr (>|z|)
Forbs average height	Shrub cover	−0.001	−0.461	0.645	−0.000	−0.121	0.904
Forbs shoot density	Tree canopy cover	−0.002	−0.980	0.327	−0.015	−6.546	<0.001
Forbs shoot density	Shrub cover	−0.002	−0.601	0.548	−0.012	−3.933	<0.001
Forbs species richness	Tree canopy cover	−0.001	−0.795	0.427	−0.003	−3.551	<0.001
Forbs species richness	Shrub cover	−0.001	−0.729	0.466	−0.003	−1.725	0.085
Graminoids cover	Tree canopy cover	−0.007	−1.077	0.282	−0.0108	−2.728	0.006
Graminoids cover	Shrub cover	−0.022	−2.111	0.035	−0.024	−3.494	<0.001
Gramindoids average height	Tree canopy cover	−0.001	−0.090	0.928	−0.006	−2.334	0.020
Gramindoids average height	Shrub cover	−0.016	−1.339	0.181	−0.008	−1.724	0.085
Gramindois shoot density	Tree canopy cover	−0.001	−0.151	0.880	−0.014	−3.551	<0.001
Graminoids shoot density	Shrub cover	−0.013	−1.566	0.117	−0.021	−3.316	0.001
Graminoids species richness	Tree canopy cover	−0.003	−0.888	0.375	−0.006	−2.334	0.020
Graminoids species richness	Shrub cover	−0.009	−1.729	0.084	−0.008	−1.724	0.085

4. Discussion

The present study highlighted the importance of the reasonable selection of forest regeneration strategies for the development of the understory vegetation structure and *in situ* conservation of vascular plant biodiversity. Our results clearly showed that implementation of two regeneration strategies on similar clear-cutting sites, the natural regeneration and spruce plantation, produced distinct stand structures of both overstory and understory (Table 1 and Figure 1) and inevitably led to different understory plant composition and diversity (Figures 2 and 3; Tables A2 and A3).

4.1. Understory Vascular Plant Species Diversity

We found a high ratio (63%, 212 species of total 334 species) of total vascular plant species co-occurring in two forests. Some important late-successional species, such as *Allium cyaneum* Regel, *Allium ovalifolium* Hand.-Mazz, and *Abies fabri* (Masters) Craib, which are possibly remnants of clear-cuts from the old-growth spruce-fir forests [24], could be preserved within the two forests (Tables A2 and A3). This suggests that forest regeneration, regardless of natural regeneration or conifer reforestation, can effectively promote and conserve some native plants on clear-cuts. This result supports the current insight that reforestation with indigenous trees may play an important role in biodiversity conservation [11,12,18].

The two forests (SP and NR) were both at the early successional stage [13,24] and included not only many pioneer species, but also some late-succession plant species in the understory (Tables A2 and A3), definitely contributing to relatively high species diversity. Thus, our results also support the previous assertion that the successional stage plays an important role in determining biodiversity and composition in the understory [12,16,25]. We further found that plant species composition was complicated and rich in the clear-cuts at the early developmental stage, containing not only many shade-intolerant and wind-dispersal species, such as annuals and ruderals, but also several remnant shade-intolerant or shade-tolerant species (Tables A2 and A3), as previously reported elsewhere [11,24,38]. Therefore, we confirmed that the initial species compositions and their attributes after clear-cutting are fundamental drivers of understory biodiversity and its response to different regeneration pathways.

However, our results underscored significantly different effects of spruce reforestation and natural regeneration in species composition and diversity. We found that in total the NR had 19 more vascular plant species in the understory than the SP (283 *vs.* 264), 20 woody plant species more than the SP (25 *vs.* 5), and only two herbaceous plant species less than the SP (Figure 3). The growth form species group analysis also showed that higher total species richness for tree seedlings (28 *vs.* 21), shrubs (54 *vs.* 41) and ferns (22 *vs.* 12), but less for forbs (159 *vs.* 167) and graminoids (20 *vs.* 23) were present in the NR than the SP (Table 2). The findings were also supported both by frequency distribution patterns of species density (Figure 2) and species group analysis (Figure 3). In conclusion, our results definitely indicated that the NR harbored more vascular plant species in the understory than the SP in similar site conditions with the same vegetation origination in the eastern Tibetan Plateau, mostly due to higher species richness of woody plants and ferns. This provided reliable support for the initial hypothesis that natural regeneration with deciduous tree mixture could improve the understory plant diversity preservation better than the spruce reforestation on clear-cuts, because natural regeneration could provide more suitable understory microhabitats to encourage plant settlement and regeneration than spruce reforestation. Our results also revealed the important insight that various growth forms in the understory could respond differently to the regeneration treatments, resulting in the naturally regenerated forests having higher species richness in ferns, shrubs and tree seedlings, but less in forbs and graminoids (Tables 1 and 2). The present result relating to tree seedling demography also supported previous speculations in the eastern Tibetan Plateau that traditional dense single tree reforestation can hinder settlement and natural regeneration of some indigenous pioneer deciduous trees [24].

4.2. Structure of Tree Canopy Cover and Understory Vegetation, and Their Correlations

We also found a significant difference in tree canopy cover and understory structure between the reforested spruce plantations and naturally regenerated stands. The SP had higher tree canopy covers than the NR, both in shrub quadrats and herb quadrats (Table 1). The results were further explained by the differences in frequency of size patterns of tree canopy cover, with higher a frequency present in Cover Class 6 (76%–100%) for the SP, but more frequently in Cover Classes 1 (<1%), 4 (26%–50%), and 5 (51%–75%) for the NR (Table 1; Figure 1a). It is clear that monospecific and high density reforestation can be more effective and rapid to establish dense canopy structure than naturally regeneration in the study area [24,33]. We further showed that the two forests presented significant differences in the understory vegetation structure (Table 1 and Figure 1). The SP had more undesirable shrub assembly structural features with less shrub cover, smaller stem density and shorter average height when compared to the NR (Table 1). This was also supported by the frequency distributions with more quadrats in shrub cover less than 5% (Cover Classes 1 and 2) in the SP and more quadrats in the cover between 6% and 75% (Cover Classes 3–5) in the NR (Figure 1b). Similarly, the SP also had more disadvantageous herbaceous community structures with less cover, shorter average shoot heights and slightly greater shoot density, in comparison with the NR (Table 1), which can be explained by different frequency distribution patterns with higher frequency in herbaceous cover at the lowest two classes (<5%) and the highest class (>75%) in the SP, and higher frequency at the medium cover class (6% - 50%) in the NR (Figure 1c). These results were also identical to the results of the growth form species group analysis (Table 2).

Our results further demonstrated that the important differences in understory vegetation structure between the NR and the SP may be ascribed to their distinct tree canopy cover (Tables 3 and 4). The tree canopy cover in the SP limited the structure of the shrub assembly and herbaceous community more seriously than the NR. Due to higher tree cover, the shrub cover only slightly hindered the cover and shoot density of graminoids (Table 4). Therefore, we identified our hypothesis (H2) that the tree canopy structure of the two forests disparately influences the structure and species diversity of the understory. Tree canopy closure for reforested spruce forests usually requires 8–14 years from time of cultivation [24], which is faster than the naturally regenerated deciduous forests with 18–20 years in the focal region of the eastern Tibetan Plateau [33], meaning that faster and stronger sunlight restriction in the SP hinders the understory plant growth and, accordingly, vegetation development more in this region than in the NR. Therefore, compared to the NR, the SP always had more quadrats with a shrub and herbaceous cover of less than 5% (Figure 1b,c) and a lower woody plant species richness (<four species per quadrat) (Figure 2a). Furthermore, the tree canopy cover still differed even after canopy closure (Table 1; Figure 1a), and it continued to hinder the understory community development and biodiversity at the early successional stage (Tables 3 and 4; Figure 2). Strong (2011) also found that poplar diameter or stem densities and spruce size in the forest canopy layer could explain three-fourths of the variation in understory species abundance in the boreal forests [25]. This finding further illustrated that the dense tree canopy more significantly limited the organizational structure of the understory vegetation in the SP stands in comparison with the NR natural sites (Tables 1, 3 and 4), which inevitably influenced the understory plant composition and biodiversity [18,39]. Therefore, reducing the tree canopy cover in the dense spruce plantation by earlier thinning can be a reasonable management choice to promote understory development and *in-situ* plant diversity conservation.

It should be noted that the disturbance regime during reforestation has long been considered to influence plant settlement and development in the early stages [4,40,41]. Reforestation practice comprises a series of activities, including site preparation, pit digging, seedling planting, initial weeding, and subsequent seedling tending and trampling, which can also directly influence the remnant understory vegetation community [24,39] Natural regeneration, on the other hand, has no further anthropogenic disturbance after clear-cutting. Moreover, the reforestation management activities expose the soil surface by reducing ground vegetation [41]. The engineering activities during reforestation on clear-cuts also destroy habitat and transform the microclimate, so that its conditions are less favorable for the establishment and growth of remnant shade-tolerant plants. Consequently, many reforested microhabitats were altered into "more hostile environments" for some shade-tolerant species (e.g., orchids), while settling opportunities for pioneers and disturbance species were enhanced [39]. In the initial years, the weeding and tending measures also continued to restrain population growth and the reproduction of high shrubs and large herbs, and indirectly drove some shade-tolerant plants into decline or led them to disappear, such as *Kingdonia uniflora* I. B. Balfour & W. W. Smith, the red-list protection herb endemic to China, *Paris polyphylla* Smith, orchids (*Listera puberula* var. *maculata*

S.C. Chen & Y. B. Luo and *Platanthera chlorantha* F. Maekawa), and so on (Table A3). Therefore, because of human-made activities on clear-cuts, the spruce reforestation severely restricted the shrub community development and obviously increased invasions by pioneer annuals and ruderals. Meanwhile, however, it was harmful to those remnant species populations sensitive to habitat alteration [3,12]. Thus we suggestthat to reduce the initial planting density of target trees during reforestation design was also a fundamental measure to decrease damage to initial ground vegetation and to allow the combination of reforestation and natural regeneration.

5. Conclusions and Implications

Regeneration strategies are critical for consequent forest succession, biodiversity conservation, and timber production on clear-cuts. However, their effects in deciding the understory vegetation and biodiversity are continually controversial and currently not well-known [11,12,14]. We implemented the current study to compare the understory structure and vascular plant diversity between the naturally regenerated deciduous forest and the reforested spruce plantation with similar age, following the same clear-cut logging of old-growth spruce-fir forests in the eastern Tibetan Plateau. We tried to explore the effects of two regeneration strategies on the understory structure and plant diversity, natural regeneration, and spruce reforestation. We found that the naturally regenerated forest harbored richer vascular plant species, featuring more species of tree seedlings, shrubs and ferns, but similar forbs and graminoids in comparison to the reforested spruce forest. Furthermore, the naturally regenerated deciduous stands had less tree cover, but more desirable understory vegetation structure than the reforested spruce stands. Comparatively, the tree canopy cover more seriously hindered the understory structure development in the spruce plantation than in the naturally regenerated deciduous forest. Our findings comprehensively suggest that forest regeneration alternatives have distinct effects on the understory plant community and biodiversity, mostly due to initial disturbances and subsequent tree canopy attributes. It is implied that, relative to the coniferous reforestation, natural regeneration is better for the preservation of indigenous plant diversity and the understory vegetation at the early forest succession stage (20–40-years of age). The present study highlights the importance of regeneration strategy selection in biodiversity preservation, which has been neglected during in forest restoration on large areas of degraded forestlands worldwide. Given that conifer plantations are increasing in China and other biomes [11,14], it is urgent to modify the current reforestation management prescription for the promotion of the stand structure, the understory vegetation, and biodiversity preservation. Therefore, we recommend choosing the natural regeneration strategy on clear-cuts in the eastern Tibetan Plateau to better improve indigenous plant diversity conservation in the early successional forests, because this region with high elevation environmental fragility and importance in ecological and biodiversity conservation has been acknowledged as a key area aiming at ecological preservation and biodiversity conservation in the China National Region Development Strategy. However, due to the greater stand productivity in the spruce plantation [13], if we aim at striking a balance between biodiversity conservation and timber productivity, integrating natural regeneration and artificial reforestation into the local regeneration prescription would be a better choice. Such a mixed approach should greatly decrease the initial spruce seedling planting density for reducing reforestation disturbances and improving the proportion of mixed deciduous tree canopy by natural regeneration on clear-cuts. Furthermore, for current large areas of dense spruce plantation forests, we propose the timely implementation of reasonable selective thinning or the creation of artificial gaps to maintain the heterogeneous crown structure and to improve understory development and biodiversity conservation.

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Author Contributions

Designing the investigation work: Weikai Bao; implementing field investigation and data collection: Zhiqiang Fang, Xiaoli Yan and Weikai Bao; data processing, and statistical analysis: Zhiqiang Fang and Xin Liu; article writing and revising: Zhiqiang Fang and Weikai Bao.

Conflicts of Interest

The authors declare no conflict of interest.

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Appendix

Table A1. Characteristic of naturally regenerated (NR) and reforested spruce plantations (SP) stands originating from similar clear-cuts in the eastern Tibetan Plateau. Differences between NR and SP plots were tested by independent *t*-test.

Forest Type	NR (n = 12)	SP (n = 12)	p-value
Altitude (m)	3094 ± 73	3219 ± 64	$p = 0.073$
Aspect class	3.1 ± 0.81	4.0 ± 0.7	$p = 0.347$
Slope inclination (°)	39.3 ± 1.5	30.6 ± 1.0	$p = 0.419$
Time since clear-cutting	31.9 ± 2.9	32.4 ± 2.6	$p = 0.438$

Table A2. Woody plant species composition of the naturally regenerated forests (NR) and the artificial reforested spruce plantation (SP) originating from similar clear-cuts in the eastern Tibetan Plateau. The difference of frequency between the NR and the SP was tested by generalized linear mixed-effects models (GLMMs). Treatment (NR *vs.* SP) was introduced as fixed factor and stands (12 *vs.* 12) as random factor, three plots nested in each stand, and nine quadrats nested in each plot. In each case, binomial error distribution with logit-ling function for presence (1) and absence (0) was selected in GLMMs. Frequency tendency distribution (FTD): natural regeneration species (NRS), species only present or more frequent in naturally regeneration forests relative to reforested spruce plantations; reforestation species (RES), species only or more frequent in reforested spruce plantations species relative to natural stands; GES, generalist species. Growth-form: S, shrub; T, tree seedlings.

Species Name	Frequency		Estimate	Z	Pr (>|z|)	FTD	Growth Form
	NR	SP					
Present only in Naturally Regenerated Forests							
Berberis polyantha Hemsl.	8	0	-	-	-	NRS	S
Caragana boisi Lam.	2	0	-	-	-	NRS	S
Caragana tangutica Maxim.ex Kom.	16	0	-	-	-	NRS	S
Euonymus sanguineus Loes.	5	0	-	-	-	NRS	S
Helwingia sp.	1	0	-	-	-	NRS	S
Hydrangea bretschneideri Dipp.	2	0	-	-	-	NRS	T
Isodon dawoensis Hand.-Mazz.	4	0	-	-	-	NRS	S
Litsea chunii W.C. Cheng	4	0	-	-	-	NRS	T
Lonicera rupicola J.D. Hook. & Thomson	1	0	-	-	-	NRS	S
Maddenia hypoxantha Koehne	10	0	-	-	-	NRS	T
Malus hupehensis (Pamp.) Rehd.	7	0	-	-	-	NRS	T
Picea likiangensis var. *rubescens* Rehd. & E.H.Wilson	11	0	-	-	-	NRS	T
Pinus densata Masters	16	0	-	-	-	NRS	T
Populus adenopoda Maxim.	3	0	-	-	-	NRS	T
Rhododendron sp.	3	0	-	-	-	NRS	S

Table A2. *Cont.*

Species Name	Frequency		Estimate	Z	Pr (>|z|)	FTD	Growth Form
	NR	SP					
Rubus parvifolius L.	13	0	-	-	-	NRS	S
Salix luctuosa H. Léveillé	19	0	-	-	-	NRS	S
Salix paraplesia C.K. Schneider	3	0	-	-	-	NRS	S
Schisandra sphenanthera Rehd.& E.H. Wilson	5	0	-	-	-	NRS	S
Sorbaria arborea C.K. Schneider	1	0	-	-	-	NRS	S
Spiraea japonica L.	4	0	-	-	-	NRS	S
Spiraea schneideriana Rehd.	13	0	-	-	-	NRS	S
Stachyurus chinensis Franchet	1	0	-	-	-	NRS	S
Tilia chinensis Maxim.	5	0	-	-	-	NRS	T
Tsuga chinensis (Franchet) E. Pritzel	10	0	-	-	-	NRS	T
Present only in reforested spruce plantations							
Cotinus coggygria Scopoli	0	1	-	-	-	RES	S
Lonicera ferdinandii Franchet	0	2	-	-	-	RES	S
Picea asperata Masters	0	18	-	-	-	RES	T
Cotoneaster silvestrii Pamp.	0	20	-	-	-	RES	S
Sorbus setschwanensis (C.K. Schneid.) Koehne	0	20	-	-	-	RES	T
Ubiquitous							
Abies fabri (Masters) Craib	5	1	−1.8	−1.498	0.134	GES	T
Abies fargesii var.*faxoniana* (Rehd. & E.H. Wilson) Tang S. Liu	8	4	−0.728	−1.052	0.293	GES	T
Abies sp.	42	34	−0.263	−1.028	0.304	GES	T
Acer davidii subsp. *grosseri* (Pax) P.C. de Jong	3	1	−1.196	−0.985	0.325	GES	T
Actinidia leptophylla C.Y. Wu	64	60	−0.091	−0.434	0.664	GES	S
Berberis aggregate C.K. Schneider	26	27	0.042	0.142	0.887	GES	S
Berberis dasystachya Maxim.	2	2	−0.002	-0.001	0.999	GES	S
Betula albo-sinensis Burk.	48	43	−0.138	−0.596	0.551	GES	T
Cerasus trichostoma (Koehne) T.T. Yu & C.L. Li	46	39	−0.211	−0.874	0.382	GES	T
Cotoneaster adpressus Bois	3	2	−0.463	−0.409	0.682	GES	S
Cotoneaster ambiguous Rehd. & E.H. Wilson	4	2	−0.706	−0.749	0.454	GES	S
Cotoneaster apiculatus Rehd. & E.H. Wilson	2	1	−0.745	−0.577	0.564	GES	S
Daphne tangutica Maxim.	11	9	−0.223	−0.459	0.646	GES	S
Detuzia sp.	3	4	0.304	0.352	0.725	GES	S
Hippophae rhamnoides L.	5	1	−1.772	−1.422	0.155	GES	S
Lonicera hispida Pallas ex Schultes	6	1	−1.819	−1.463	0.144	GES	S
Lonicera tangutica Maxim.	42	58	0.396	1.764	0.078	GES	S
Lonicera trichosantha Bureau & Franchet	12	12	−0.000	-0.001	0.999	GES	S
Lonicera webbiana Wallich ex Candolle	7	10	0.380	0.718	0.473	GES	S
Ribes maximowiczianum Komarov	18	20	0.131	0.361	0.718	GES	S
Rosa graciliflora Rehd. & E.H. Wilson	32	43	0.355	1.385	0.166	GES	S
Rosa omeiensis Rolfe	32	30	−0.088	−0.316	0.752	GES	S

Table A2. *Cont.*

Species Name	Frequency		Estimate	Z	Pr (>|z|)	FTD	Growth Form
	NR	SP					
Rubus pileatus Focke	2	1	−0.699	−0.570	0.569	GES	S
Rubus xanthocarpus Bureau & Franche	11	5	−1.09	−1.699	0.089	GES	S
Salix rehderiana C.K. Schneider	4	6	0.422	0.569	0.569	GES	T
Salix wallichiana Andersson	8	8	−0.002	−0.003	0.997	GES	T
Sibiraea angustata (Rehder) Hand.-Mazz.	4	6	0.456	0.662	0.508	GES	S
Sorbus hupehensis C.K. Schneider	2	7	1.412	1.649	0.099	GES	T
Spiraea cantoniensis Loureiro	12	11	−0.099	−0.215	0.83	GES	S
Spiraea myrtilloides Rehder	7	13	0.702	1.228	0.219	GES	S
Viburnum sp.	9	17	0.739	1.635	0.102	GES	S
More frequent in naturally regenerated forest stands relative to reforested spruce plantations							
Acer maximowiczii Pax	61	10	−2.487	−6.308	<0.001	NRS	T
Acer pictum subsp. *mono* (Maxim.) H. Ohashi	25	5	−1.946	−3.610	<0.001	NRS	T
Arundinaria faberi Rendle	131	80	−1.427	−5.822	<0.001	NRS	S
Berchemia floribunda (Wallich) Brongniart	12	2	−1.902	−2.232	0.026	NRS	S
Betula platyphylla Sukaczev	12	3	−1.487	−2.151	0.032	NRS	T
Cornus hemsleyi C.K. Schneider & Wangerin	63	6	−3.615	−6.552	<0.001	NRS	T
Cotoneaster acuminatus Lindley	44	1	−4.22	−3.962	<0.001	NRS	S
Cotoneaster glabratus Rehd. & E.H. Wilson	13	1	−3.045	−2.631	0.009	NRS	S
Eleutherococcus giraldii (Harms) Nakai	81	38	−1.173	−4.874	<0.001	NRS	S
Euonymus porphyreus Loes.	60	41	−0.517	−2.210	0.027	NRS	S
Euonymus sp.	125	100	−0.427	−2.342	0.019	NRS	S
Hydrangea xanthoneura Diels	19	3	−2.052	−3,040	0.002	NRS	T
Malus kansuensis (Batalin) C.K. Schneider	10	1	−2.430	−2.017	0.044	NRS	T
Padus obtusata (Koehne) T.T. Yu & T.C. Ku	14	2	−2.060	−2.504	0.012	NRS	T
Ribes glaciale Wallich	17	4	−1.581	−2.618	0.009	NRS	S
Ribes tenue Janczewski	30	8	−1.489	−3.528	<0.001	NRS	S
Rubus pungens Cambessèdes	126	68	−1.020	−5.385	<0.001	NRS	S
Smilax menispermoidea A. de Candolle	66	24	−1.356	−4.989	<0.001	NRS	S
Smilax stans Maxim.	91	63	−0.563	−2.820	0.005	NRS	S
Sorbus rehderiana Koehne	76	53	−0.523	−2.445	0.0145	NRS	T
More frequent in reforested spruce plantation stands relative to naturally regenerated forests							
Cotoneaster acutifolius Turczaninow	5	43	2.639	4.980	<0.001	RES	S
Philadelphus purpurascens (Koehne) Rehder	1	11	2.562	2.266	0.024	RES	S
Picea sp.	10	42	1.661	4.391	<0.001	RES	T
Quercus aquifolioides Rehd. & E.H. Wilson	8	27	1.660	3.532	<0.001	RES	T
Ribes himalense Royle ex Decaisne	11	27	1.155	2.858	0.004	RES	S
Rubus phoenicolasius Maxim.	1	14	3.200	2.790	0.005	RES	S

Table A3. Herbaceous plant species composition of the naturally regenerated forests (NR) and the artificial reforested spruce plantation (SP) originating from similar clear-cuts in the eastern Tibetan Plateau. The difference of frequency between the NR and the SP was tested by generalized linear mixed-effects models (GLMMs). Treatment (NR *vs.* SP) was introduced as fixed factor and stands (12 *vs.* 12) as random factor, three plots nested in each stand, and nine quadrats nested in each plot. In each case, binomial error distribution with logit-ling function for presence (1) and absence (0) was selected in GLMMs. Frequency tendency distribution (FTD): NRS, species only present or more frequent in naturally regeneration forests relative to reforested spruce plantations; RES, species only or more frequent in reforested spruce plantations species relative to natural stands; GES, generalist species. Growth-form: FB, forbs; FN, fern; GM, graminoids.

Species Name	Frequency		Estimate	Z	Pr (>|z|)	FTD	Growth Form
	NR	SP					
Present only in naturally regenerated forests							
Aceratorchis tschiliensis Schltr.	1	0	-	-	-	NRS	FB
Aconitum brunneum Hand.-Mazz.	1	0	-	-	-	NRS	FB
Adenophora stricta subsp. *aurita* (Franchet) D.Y. Hong & S. Ge	6	0	-	-	-	NRS	FB
Adiantum flabellulatum L.	1	0	-	-	-	NRS	FN
Ajuga sp.	1	0	-	-	-	NRS	FB
Artemisia princeps Pamp.	12	0	-	-	-	NRS	FB
Athyrium dentigerum (Wallich ex C.B. Clarke) Mehra & Bir	1	0	-	-	-	NRS	FN
Carex chinensis Retzius	6	0	-	-	-	NRS	GM
Chamaesium paradoxum H. Wolff	12	0	-	-	-	NRS	FB
Clinopodium polycephalum (Vaniot) C.Y. Wu & Hsuan ex P.S. Hsu	1	0	-	-	-	NRS	FB
Clintonia udensis Trautvetter & C.A. Meyer	9	0	-	-	-	NRS	FB
Corydalis impatiens (Pallas) Fischer	7	0	-	-	-	NRS	FB
Corydalis sp.	2	0	-	-	-	NRS	FB
Cyrtomium sp.	2	0	-	-	-	NRS	FN
Cystopteris montana (Lamarck) Bernhardi ex Desvaux	8	0	-	-	-	NRS	FN
Delphinium tongolense Franchet,	1	0	-	-	-	NRS	FB
Elymus tangutorum (Nevski) Hand.-Mazz.	2	0	-	-	-	NRS	GM
Equisetum arvense L.	1	0	-	-	-	NRS	FN
Foeniculum vulgare (L.) Miller	2	0	-	-	-	NRS	FB
Goodyera yunnanensis Schlechte	1	0	-	-	-	GES	FB
Isodon flabelliformis (C.Y. Wu) H. Hara	4	0	-	-	-	NRS	FB
Kingdonia uniflora I.B. Balfour & W.W. Smith	2	0	-	-	-	NRS	FB
Lepisorus contortus (Christ) Ching	1	0	-	-	-	NRS	FN
Lepisorus pseudonudus Ching	1	0	-	-	-	NRS	FN

Table A3. *Cont.*

Species Name	Frequency		Estimate	Z	Pr (>|z|)	FTD	Growth Form
	NR	SP					
Lilium nepalense D. Don	14	0	-	-	-	NRS	FB
Listera puberula var. *maculate* (T. Tang et F.T. Wang) S.C. Chen et Y.B. Luo	1	0	-	-	-	NRS	FB
Lunathyrium sp.	3	0	-	-	-	NRS	FN
Morina nepalensis var.*alba* (Hand.-Mazz.) Y.C. Tang	1	0	-	-	-	NRS	FB
Ophiopogon intermedius D. Don	9	0	-	-	-	NRS	FB
Osmorhiza aristata (Thunberg) Rydberg	3	0	-	-	-	NRS	FB
Panax pseudo-ginseng Wall.	1	0	-	-	-	NRS	FB
Paris polyphylla Smith	5	0	-	-	-	NRS	FB
Phymatopteris shensiensis (Christ) Pic.	3	0	-	-	-	NRS	FN
Platanthera chlorantha (Custer) Reichenbach	1	0	-	-	-	NRS	FB
Polemonium coeruleum L.	1	0	-	-	-	NRS	FB
Polystichum herbaceum Ching & Z.Y. Liu	1	0	-	-	-	NRS	FN
Primula fasciculate I.B. Balfour & Kingdon-Ward	4	0	-	-	-	NRS	FB
Pteris sp.	3	0	-	-	-	NRS	FN
Rodgersia podophylla A. Gray	40	0	-	-	-	NRS	FB
Saxifraga sp.	1	0	-	-	-	NRS	FB
Sedum angustum Maxim.	1	0	-	-	-	NRS	FB
Spodiopogon ramosus Keng	1	0	-	-	-	NRS	GM
Thalictrum javanicum Blume	5	0	-	-	-	NRS	FB
Tiarella polyphylla D. Don	2	0	-	-	-	NRS	FB
Tipularia szechuanica Schlechter	1	0	-	-	-	NRS	FB
Present only in reforested spruce plantations							
Actaea asiatica Wallich	0	1	-	-	-	RES	FB
Adenophora liliifolioides Pax & K. Hoffmann	0	8	-	-	-	RES	FB
Agrimonia pilosa Ledebour	0	6	-	-	-	RES	FB
Allium sp.	0	2	-	-	-	RES	FB
Anaphalis sp.	0	3	-	-	-	RES	FB
Anemone demissa J.D. Hooker & Thomson	0	2	-	-	-	RES	FB
Artemisia lancea Vaniot	0	2	-	-	-	RES	FB
Aster diplostephioides (Candolle) Bentham ex C.B. Clarke	0	10	-	-	-	RES	FB
Astragalus mahoschanicus Hand.-Mazz.	0	5	-	-	-	RES	FB
Bupleurum longicaule de Candolle	0	3	-	-	-	RES	FB
Carex breviculmis R. Brown	0	3	-	-	-	RES	GM
Carex dimorpholepis Steudel	0	1	-	-	-	RES	GM
Carex ovatispiculata F.T. Wang & Y.L. Chang ex S. Yun Liang	0	6	-	-	-	RES	GM

Table A3. *Cont.*

Species Name	Frequency		Estimate	Z	Pr (>|z|)	FTD	Growth Form
	NR	SP					
Carpesium sp.	0	3	-	-	-	RES	FB
Comastoma cyananthiflorum (Franchet) Holub	0	12	-	-	-	RES	FB
Silene baccifera (L.) Roth	0	1	-	-	-	RES	FB
Elymus strictus (Keng) S.L. Chen	0	3	-	-	-	RES	GM
Euphorbia sp.	0	12	-	-	-	RES	FB
Euphrasia pectinata Tenore	0	2	-	-	-	RES	FB
Gueldenstaedtia verna (Georgi) Borissova	0	4	-	-	-	NRS	FB
Gymnadenia orchidis Lindle	0	1	-	-	-	RES	FB
Inula japonica Thunberg	0	12	-	-	-	RES	FB
Leontopodium haplophylloides Hand.-Mazz.	0	1	-	-	-	RES	FB
Ligularia virgaurea (Maxim.) Mattfeld ex Rehder & Kobuski	0	3	-	-	-	RES	FB
Lotus corniculatus L.	0	11	-	-	-	RES	FB
Medicago lupulina L.	0	3	-	-	-	RES	FB
Melica przewalskyi Roshevitz	0	5	-	-	-	RES	GM
Pedicularis chenocephala Diels	0	16	-	-	-	RES	FB
Pedicularis superba Franchet ex Maxim.	0	2	-	-	-	RES	FB
Pleione sp.	0	1	-	-	-	RES	FB
Polygonatum franchetii Hua	0	2	-	-	-	RES	FB
Potentilla lineata Treviranus	0	19	-	-	-	RES	FB
Primula sp.	0	2	-	-	-	RES	FB
Rumex nepalensis Sprengel	0	22	-	-	-	RES	FB
Sanicula elata Buchanan-Hamilton ex D. Don	0	2	-	-	-	RES	FB
Saussurea epilobioides Maxim.	0	20	-	-	-	RES	FB
Saussurea nigrescens Maxim.	0	4	-	-	-	RES	FB
Saussurea polycephala Hand.-Mazz.	0	2	-	-	-	RES	FB
Silene himalayensis (Rohrbach) Majumdar	0	5	-	-	-	RES	FB
Stellera chamaejasme L.	0	1	-	-	-	RES	FB
Stipa penicillata Hand.-Mazz.	0	1	-	-	-	RES	GM
Tibetia himalaica (Baker) H.P. Tsui	0	2	-	-	-	RES	FB
Trollius ranunculoides Hemsley	0	5	-	-	-	RES	FB
Veronica szechuanica Batalin	0	3	-	-	-	RES	FB
Vicia pseudorobus Fisch. et C.A. Mey	0	14	-	-	-	RES	FB
Viola yunnanfuensis W. Becker	0	6	-	-	-	RES	FB
Woodsia andersonii (Beddome) Christ	0	1	-	-	-	RES	FN
Ubiquitous							
Aconitum scaposum Franchet	7	1	−2.082	−1.783	0.075	GES	FB

Table A3. *Cont.*

Species Name	Frequency		Estimate	Z	Pr (>|z|)	FTD	Growth Form
	NR	SP					
Aconitum sinomontanum Nakai	2	3	0.462	0.455	0.649	GES	FB
Aconitum sp.	10	14	0.415	0.883	0.377	GES	FB
Acronema tenerum (de Candolle) Edgeworth	6	3	−0.704	−0.923	0.356	GES	FB
Adenophora potaninii Korshinsky	3	8	1.166	1.613	0.107	GES	FB
Adoxa moschatellina L.	7	14	1.003	1.848	0.065	GES	FB
Agrostis clavata Trinius	20	23	0.172	0.510	0.610	GES	GM
Ainsliaea henryi Diels	8	17	0.918	1.948	0.051	GES	FB
Aletris glabra Bureau & Franchet	1	1	0.003	0.002	0.998	GES	FB
Allium cyaneum Regel	1	1	0.003	0.002	0.998	GES	FB
Allium ovalifolium Hand.-Mazz.	4	8	1.031	1.445	0.149	GES	FB
Anaphalis margaritacea (L.) Bentham & J.D. Hooker	1	6	1.926	1.464	0.143	GES	FB
Anemone rivularis Buchanan-Hamilton ex de Candolle	60	63	0.086	0.387	0.699	GES	FB
Aquilegia ecalcarata Maxim.	23	14	−0.547	−1.484	0.138	GES	FB
Artemisia sp.	1	3	1.165	0.889	0.374	GES	FB
Aster ageratoides	24	19	−0.340	−0.921	0.357	GES	FB
Aster smithianus Hand.-Mazz.	15	22	0.633	1.527	0.127	GES	FB
Botrychium lunaria (L.) Swartz	1	1	0.003	0.002	0.998	GES	FN
Brachypodium sylvaticum (Hudson) P. Beauvois	14	15	0.079	0.200	0.842	GES	GM
Caltha palustris L.	3	1	−1.110	−0.849	0.396	GES	FB
Carex asperifructus Kükenthal	15	10	−0.475	−1.058	0.290	GES	GM
Carex doniana Sprengel	17	25	0.441	1.308	0.191	GES	GM
Chamerion angustifolium (L.) Holub	3	8	1.150	1.519	0.129	GES	FB
Cimicifuga foetida L.	19	18	−0.062	−0.173	0.863	GES	FB
Circaea alpina L.	73	75	0.053	0.262	0.793	GES	FB
Clematis montana Buchanan-Hamilton ex de Candolle	73	70	−0.081	−0.373	0.709	GES	FB
Clematis sp.	2	1	−0.705	−0.483	0.629	GES	FB
Clinopodium gracile (Bentham) Matsumura	10	10	0.002	0.004	0.997	GES	FB
Corydalis curviflora Maxim.	5	6	0.199	0.287	0.774	GES	FB
Daucus carota L.	1	2	0.699	0.570	0.569	GES	FB
Delphinium caeruleum Jacquemont	4	2	−0.772	−0.784	0.433	GES	FB
Dendranthema indicum (L.) Des Moul.	10	14	0.384	0.853	0.394	GES	FB
Diphylleia sinensis H.L. Li	2	1	−0.705	−0.483	0.629	GES	FB
Disporum bodinieri (H. Léveillé & Vaniot) F.T. Wang & T. Tang	12	7	−0.675	−1.234	0.217	GES	FB
Epipactis mairei Schlechter	1	2	0.710	0.485	0.628	GES	FB
Festuca elata Keng ex E.B. Alexeev	45	50	0.190	0.756	0.450	GES	GM

Table A3. *Cont.*

Species Name	Frequency		Estimate	Z	Pr (>|z|)	FTD	Growth Form
	NR	SP					
Geranium platyanthum Duthie	61	55	−0.213	−0.845	0.398	GES	FB
Geranium pseudo-farreri Z.M. Tan	3	6	0.903	1.110	0.267	GES	FB
Geum aleppicum Jacquin	2	6	1.446	1.535	0.125	GES	FB
Heracleum scabridum Franchet	5	6	0.207	0.297	0.767	GES	FB
Lactuca graciliflora de Candolle	22	12	−0.722	−1.816	0.069	GES	FB
Laportea bulbifera (Siebold & Zuccarini) Weddell	15	7	−0.888	−1.771	0.077	GES	FB
Ligularia sagitta (Maxim.) Mattfeld ex Rehder & Kobuski	3	2	−0.471	−0.457	0.648	GES	FB
Lunathyrium shennongense Ching	8	7	−0.119	−0.214	0.830	GES	FN
Luzula effusa Buchenau	8	3	−1.047	−1.349	0.177	GES	GM
Lysimachia sp.	7	4	−0.629	−0.879	0.379	GES	FB
Maianthemum henryi (Baker) LaFrankie	14	9	−0.577	−1.141	0.254	GES	FB
Notopterygium incisum C.C. Ting ex H.T. Chang	31	32	0.063	0.221	0.825	GES	FB
Oenanthe sp.	8	11	0.372	0.720	0.472	GES	FB
Paeonia anomala subsp. *veitchii* (Lynch) D.Y. Hong & K.Y. Pan	6	4	−0.436	−0.557	0.577	GES	FB
Panax pseudoginseng var. *bipinnatifidus* (Seem.) Li	11	11	−0.004	−0.008	0.994	GES	FB
Parasenecio roborowskii (Maxim.) Y.L. Chen	37	24	−0.555	−1.870	0.062	GES	FB
Parnassia delavayi Franchet,	2	4	0.843	0.867	0.386	GES	FB
Pedicularis kansuensis Maxim.	2	1	−0.782	−0.575	0.565	GES	FB
Pedicularis rudis Maxim.	2	2	0.002	0.002	0.998	GES	FB
Pedicularis sp.	9	2	−1.671	−1.902	0.057	GES	FB
Phlomis megalantha Diels	14	9	−0.580	−1.150	0.250	GES	FB
Picris hieracioides L.	26	20	−0.340	−0.952	0.341	GES	FB
Poa chalarantha Keng ex L. Liu	6	7	0.194	0.310	0.757	GES	GM
Poa lithophila Keng ex L. Liu	1	1	0.003	0.002	0.998	GES	GM
Poa nubigena Keng ex L. Liu	5	6	0.197	0.296	0.767	GES	GM
Polygonum cyanandrum Diels	13	10	−0.352	−0.728	0.467	GES	FB
Polygonum macrophyllum D. Don	10	10	0.003	0.005	0.996	GES	FB
Polystichum brachypterum (Kuntze) Ching	2	1	−0.676	−0.463	0.644	GES	FN
Primula kialensis Franchet	2	4	0.991	1.049	0.294	GES	FB
Primula moupinensis Franchet	2	3	0.416	0.425	0.671	GES	FB
Primula odontocalyx (Franchet) Pax	2	4	0.744	0.769	0.442	GES	FB
Pteridium revolutum (Blume) Nakai	5	13	0.997	1.781	0.075	GES	FN
Pternopetalum heterophyllum Hand.-Mazz.	31	29	−0.083	−0.291	0.771	GES	FB

Table A3. *Cont.*

Species Name	Frequency		Estimate	Z	Pr (>|z|)	FTD	Growth Form
	NR	SP					
Rorippa elata (J.D. Hooker & Thomson) Hand-Mazz.	16	13	−0.235	−0.541	0.589	GES	FB
Rumex acetosa L.	2	2	0.002	0.001	0.999	GES	FB
Salvia cynica Dunn	34	37	0.120	0.450	0.653	GES	FB
Salvia maximowicziana Hemsley	26	17	−0.700	−1.713	0.087	GES	FB
Salvia przewalskii Maxim.	7	11	0.487	0.933	0.351	GES	FB
Sambucus adnata Wallich ex Candolle	15	16	0.071	0.183	0.855	GES	FB
Saussurea retroserrata Y.L. Chen & S. Yun Liang	8	4	−0.726	−1.101	0.271	GES	FB
Scutellaria hypericifolia H. Léveillé	5	2	−1.053	−1.116	0.265	GES	FB
Sedum tatarinowii	6	3	−0.868	−1.095	0.274	GES	FB
Sinopodophyllum hexandrum (Royle) T.S. Ying	12	18	0.468	1.141	0.254	GES	FB
Stellaria chinensis Regel	19	19	−0.001	−0.003	0.997	GES	FB
Stellaria sp.	10	18	0.665	1.538	0.124	GES	FB
Thalictrum finetii B. Boivin	1	3	1.979	0.744	0.457	GES	FB
Thalictrum oligandrum Maxim.	14	24	0.642	1.741	0.082	GES	FB
Triosteum himalayanum Wallic	4	10	1.073	1.276	0.202	GES	FB
Valeriana officinalis L.	16	27	0.643	1.844	0.065	GES	FB
Valeriana tangutica Batalin	1	5	1.771	1.422	0.155	GES	FB
Vicia cracca L.	1	7	2.245	1.882	0.060	GES	FB
More frequent in naturally regenerated forest stands relative to reforested spruce plantations							
Adiantum davidii Franchet	52	32	−0.696	−2.584	0.010	NRS	FN
Adiantum pedatum L.	16	1	−3.814	−3.239	0.001	NRS	FN
Allium ovalifolium var. *cordifolium* (J.M. Xu) J.M. Xu	47	6	−2.589	−5.393	<0.001	NRS	FB
Aruncus sylvester Kosteletzky ex Maxim.	30	6	−1.814	−3.817	<0.001	NRS	FB
Asplenium pekinense Hance	9	2	−1.696	−1.986	0.047	NRS	FN
Bromus plurinodes Keng ex Keng f.	33	20	−0.667	−2.061	0.039	NRS	GM
Cardamine impartiens L.	9	1	−2.289	−2.013	0.044	NRS	FB
Carex huolushanensis P.C. Li	12	2	−1.881	−2.162	0.031	NRS	GM
Carex lehmanii Drejer	18	3	−2.916	−3.274	0.001	NRS	GM
Carex sp.	54	29	−0.838	−3.125	0.002	NRS	GM
Carpesium divaricatum Siebold & Zuccarini	86	54	−0.715	−3.358	0.001	NRS	FB
Cystopteris moupinensis Franchet	122	90	−0.774	−3.501	<0.001	NRS	FN
Deyeuxia scabrescens (Grisebach) Munro ex Duthie	9	1	−2.397	−1.962	0.049	NRS	GM
Dryopteris rosthornii (Diels) C. Christensen	43	8	−1.924	−4.701	<0.001	NRS	FN
*Dryopteris sinofibrillos*a Ching	43	16	−1.176	−3.676	<0.001	NRS	FN
Galium paradoxum Maxim.	52	33	−0.569	−2.276	0.023	NRS	FB

Table A3. *Cont.*

Species Name	Frequency		Estimate	Z	Pr (>|z|)	FTD	Growth Form
	NR	SP					
Geranium pylzowianum Maxim.	33	8	−1.834	−4.123	<0.001	NRS	FB
Hackelia brachytuba (Diels) I.M. Johnston	74	20	−2.022	−6.406	<0.001	NRS	FB
Impatiens delavayi Franchet,	15	2	−2.292	−2.717	0.007	NRS	FB
Impatiens dicentra Franchet ex J.D. Hooker	73	14	−2.180	−6.547	<0.001	NRS	FB
Ligularia przewalskii (Maxim.) Diels	19	2	−2.662	−3.152	0.002	NRS	FB
Maianthemum tatsienense (Franchet) LaFrankie	23	10	−0.929	−2.289	0.022	NRS	FB
Notoseris gracilipes Shih	28	4	−2.374	−3.946	<0.001	NRS	FB
Ophiopogon bodinieri H. Léveillé	60	7	−3.154	−6.584	<0.001	NRS	FB
Oxalis acetosella L.	25	7	−1.513	−3.237	0.001	NRS	FB
Parasenecio deltophyllus (Maxim.) Y.L. Chen	36	20	−0.710	−2.307	0.021	NRS	FB
Parasenecio forrestii W.W. Smith & J. Small	31	18	−0.703	−2.125	0.034	NRS	FB
Pseudocystopteris subtriangularis (Hook.) Ching	213	125	−1.430	−7.616	<0.001	NRS	FN
Pyrola calliantha Andres	11	2	−1.949	−2.339	0.019	NRS	FB
Rubia cordifolia L.	133	103	−0.458	−2.617	0.009	NRS	FB
Streptopus obtusatus Fassett	110	52	−1.311	−5.894	<0.001	NRS	FB
Thalictrum petaloideum L.	11	3	−1.605	−2.258	0.024	NRS	FB
More frequent in reforested spruce plantation stands relative to naturally regenerated forests							
Anaphalis lacteal Maxim.	39	71	0.920	3.767	<0.001	RES	FB
Angelica biserrata (R.H. Shan & C.Q. Yuan) C.Q. Yuan & R.H. Shan	2	10	1.909	2.204	0.028	RES	FB
Artemisia annua L.	3	27	2.525	3.909	<0.001	RES	FB
Artemisia tangutica Pamp.	2	20	2.540	3.232	0.001	RES	FB
Cardamine hirsute L.	10	31	1.463	3.543	<0.001	RES	FB
Cardamine tangutorum O.E. Schulz	56	112	1.898	6.438	<0.001	RES	FB
Carex capilliformis Franchet	11	39	1.706	4.376	<0.001	RES	GM
Carpesium cernuum L.	9	65	2.856	6.695	<0.001	RES	FB
Chrysosplenium griffithii J.D. Hooker & Thomson	4	14	1.567	2.498	0.013	RES	FB
Clematis pogonandra Maxim.	29	53	1.018	3.439	0.001	RES	FB
Deyeuxia pyramidalis (Host) Veldkam	3	21	2.916	3.997	<0.001	RES	GM
Epilobium fangii C.J. Chen	5	33	2.251	4.314	<0.001	RES	FB
Epilobium fastigiatoramosum Nakai,	11	37	1.434	3.858	<0.001	RES	FB
Epilobium tibetanum Haussknecht	27	44	0.592	2.214	0.027	RES	FB
Epipactis helloborine (L.) Crantz.	1	10	2.467	2.096	0.036	RES	FB
Fragaria vesca L.	66	123	1.133	5.565	<0.001	RES	FB
Galium trifidum L.	15	41	1.263	3.774	<0.001	RES	FB

Table A3. *Cont.*

Species Name	Frequency		Estimate	Z	Pr (>|z|)	FTD	Growth Form
	NR	SP					
Geranium nepalense Sweet	7	38	2.180	4.67	<0.001	RES	FB
Halenia elliptica D. Don	13	30	0.961	2.712	0.007	RES	FB
Impatiens apsotis J.D. Hooke	5	18	1.346	2.501	0.012	RES	FB
Lobelia nummularia Lamarck	3	16	1.941	2.768	0.006	RES	FB
Pedicularis labordei Vaniot ex Bonati	2	10	1.808	2.156	0.031	RES	FB
Phlomis umbrosa Turczaninow	3	13	1.723	2.473	0.013	RES	FB
Plantago depressa Willdenow	2	23	3.411	3.909	<0.001	RES	FB
Poa annua L.	4	25	2.681	4.138	<0.001	RES	GM
Polygonatum verticillatum (L.) Allioni	12	41	1.686	4.394	<0.001	RES	FB
Polygonum viviparum L.	90	122	0.576	3.092	0.002	RES	FB
Primula palmate Hand.-Mazz.	28	45	2.274	4.016	<0.001	RES	FB
Ranunculus japonicas Thunberg	2	23	3.243	3.914	<0.001	RES	FB
Ranunculus tanguticus (Maxim.) Ovczinnikov	2	32	3.585	4.432	<0.001	RES	FB
Sanicula hacquetioides Franchet	2	48	4.395	5.247	<0.001	RES	FB
Stellaria vestita Kurz	12	40	1.436	4.032	<0.001	RES	FB
Trigonotis tibetica (C.B. Clarke) I.M. Johnston	8	24	1.291	2.909	0.004	RES	FB
Veronica vandellioides Maxim.	10	27	1.120	2.835	0.005	RES	FB
Vicia unijuga A. Braun	4	22	1.979	3.345	0.001	RES	FB
Viola biflora L.	47	74	1.019	3.646	<0.001	RES	FB