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Plant and insect diversity along an experimental gradient of larch-birch mixtures in Chinese boreal forests

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Abstract: Maintaining and increasing biodiversity level especially in pure plantations is one important way to improve the resistance of forests to pests in Chinese boreal forests. The present study tested the hypothesis that the increased degree of tree species mixture (quantified by the stem proportion of *Betula platyphylla* Suk. and *Larix gmelinii* (Rupr.) Rupr.) can affect the species richness and diversity of understory and insects. Twenty-one plots, ranging from pure larch stand to pure birch stand, were sampled in several thinned forests in a Chinese boreal forest area. Data of environmental factors, understory plant species and insect assemblage were collected from the field and connected with historical records, and analyzed using, e.g., multivariate methods and de-trended canonical correspondence analysis (DCCA). The results showed that the variation of plant and insect species was mainly influenced by birch mixture and light conditions in the forest. Species richness and diversity of plants and insects increased with the increasing mixture of birch, and finally declined after passing the peak point in 30% or 50% of birch mixture. The study gives tools to improve the integrated pest management (IPM) especially in man-made pure plantations of boreal forests in China.

Key words: *Betula platyphylla*, boreal forest, diversity, insect, *Larix gmelinii*, plant

Introduction

Conservation of biodiversity in managed forests is a crucial issue and a major challenge in sustainable forest management because of its key role in human welfare, economy and ecosystem services (Hooper et al. 2005; Stephens and Wagner 2007; Wang and Chen 2010). Jactel et al. (2005) indicated that the forest stands deviated from their natural conditions were susceptible to insect outbreaks. Therefore, the transformation of man-made pure stands by various management practices is widely conducted with an expected increase of biodiversity and the stability of forest stands (Parrotta et al. 1997; Matthes and Ammer 2000).

Forest management has various effects on plants and arthropods in term of species diversity (Lindenmayer et al. 2000; Nagaike et al. 2003; Jobidon et al. 2004; Maleque et al. 2009; Taki et al. 2010). As the most widely conducted management practice, thinning has multiple effects on plants and arthropods since it changes canopy structure, thus affecting understory composition (Zeide 2001, 2004; Wilson and Puettmann 2007). Studies on thinning have demonstrated positive (Homyack et al. 2005;

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Ishii et al. 2008), negative (Nagai and Yoshida 2006), or no (Sullivan et al. 2002; Lei et al. 2007) effects on understory diversity. Controversies exist because the effects vary with stand conditions, observation period and thinning intensity (Nagaike 2002; Lei et al. 2007). Investigation of understory and insect communities within the forests following thinning will provide new information on biodiversity issues (Lindgren et al. 2006; Sullivan et al. 2009).

Dodson et al. (2008) concluded that thinning altered the canopy structure, which affected the microclimate, light conditions, soil moisture, and nutrient availability in the understory layer, and so it may have positive or negative effects on understory diversity (Barbier et al. 2008). Berger and Puettmann (2000) studied aspen, aspen-conifer, and aspen-hardwoods stands and indicated that herbaceous diversity had significant positive, negative, and no relations with the basal area of different tree species. Furthermore, thinning and its consequences play a major role in the abundance and diversity of arthropods, including insects, but very few reports exist in this field (Taki et al. 2010).

In northern China, extensive thinning practices on larches have been conducted in semi-natural Dahurian larch, *Larix gmelinii* (Rupr.) Rupr., stands mixed with Asian white birch, *Betula platyphylla* Suk. These thinning practices have resulted in a gradient of larch-birch mixtures. The gradient ranged from pure Dahurian larch cover to pure Asian white birch cover with various mixture proportions. No other tree species grow in our study sites.

The objective of the present study was to examine the effects of tree species mixture gradient on the plant and insect diversity. We hypothesized that the tree species mixture can affect the species composition, distribution, richness and diversity of understory vascular plants and insects in forests. We also hypothesized that there could be a certain larch-birch mixture where the diversity would be the highest. We conducted a direct gradient analysis using the plant species occurrence and several environmental factors. The diversity of understory and insects in the forests along the larch-birch mixture gradient was sampled and analyzed. On the basis of the results obtained, thinning and other forest management practices can accordingly be developed in Chinese boreal forests.

Materials and methods

Study site and design

The study was carried out in the Aershan Forestry Region, located in Inner Mongolia autonomous region in northeastern China (47°07′-47°55′N, 119°51′-120°57′E). Man-made forests cover 20% of this area. The dominant tree species is the Dahurian larch, *L. gmelinii*. Semi-natural forests have Asian white birch, *B. platyphylla*, as an admixed deciduous tree species. The study area has a cold, temperate climate (Wang 2005; Yuan et al. 2010) with an average elevation of 1105 m above sea level. Mean annual precipitation and temperature is 445.3 mm and –3.1 °C, respectively. Mean monthly minimum and maximum temperatures range between –25.6 and 16.6 °C.

Stands investigated in the present study included natural pure larch forests (average age 45 years), semi-natural mixed forests by larches (45 years old) and birches (40 years old), various mixed forests created by thinning, and natural pure birch forests (50 years old). Thinning practices was conducted in 1990. As planned, the thinning practices posed a gradient of larch-birch mixtures from pure larch stands to pure birch stands. Consequently, the proportion of birch within the canopy layer ranged from close to 0% to close to 100% in a scale of at least 0.7 ha.

In 2009, pure larch forests, pure birch forests, and 5 forest sites with different larch-birch mixtures were chosen as our study sites. The 7 forest types were identified according to the relative stem ratio of larches (L) and birches (B) as follows: L10B0 (birch mixture is 0%), L9B1, L7B3, L5B5, L3B7, L1B9, and L0B10 (Table 1). Three experimental plots were established in each forest site as replicates. Mean area of the plots was 1.6 ha (0.7-4.6 ha) with a distance of at least 3 km between each other. To avoid the problems from pseudo-replicates, 3 plots of each type were all chosen from different stands with similar soil type, topography, stand condition, etc.

Field investigation

Investigation on the understory was carried out in July and August 2009. Square plots (20 × 20 m) were set up in the center of each stand. Basic survey on altitude, slope, aspect, basal area, forest light condition (quantified by canopy closure), and stand soil organic matter was first done. Five quadrats (5 ×5 m), 1 in the center and 4 in the corners of each plot, were placed for the shrub layers analysis. Each quadrat was similarly divided into 5 sub-quadrats (1 × 1 m). Understory vascular plants were recorded by species names, individual numbers, dominant heights, and covers. Most species were identified in situ, while the unknown ones were sampled or photographed for further identification.

Insect sampling was conducted during the same period as plants in 2009 with window traps in the day time and light traps at night. The crossed windows were made of 29.5 ×19.0 × 0.2 cm polymethyl methacrylate with a 23.0 × 17.3 cm oval collecting container. Three window traps, tied to three 1.3 m wooden sticks, were hung 50 m apart in a row in each forest. The resulting design was 63 traps in the 21 forest stands. A water, soap, and salt mixture was used as a preservative. All traps were checked weekly from May to August. Three black light lamp traps were fixed to tree trunks at 1.5 m, 100 m apart in each forest stand type. Each light lamp was a 20 W UV light bulb (Jiaduo, Hebi, China) with a battery as power and a white cloth-screen as a collector. The operation of the light traps within the investigated forest stands took place synchronously to avoid confounding factors such as temperature and humidity (Steinbauer 2003). Captured insects were collected synchronously once per week from May to August in situ and the trapped moths were killed with ethyl ether. The insects were identified to morphospecies. Voucher specimens were retained at both the Aershan Forestry Bureau and the Lab of Forest Silviculture and Conservation at the Beijing Forestry University.

Canopy digital images taken by fish-eye lenses were analyzed by Adobe Photoshop software (Qi et al. 2009) to measure the canopy closure to quantize the light condition within the stands. Canopy layers of each plot above 3 measure points, chosen along the stand diagonal lines, were photographed and transformed into gray and duotone images in Photoshop. Afterwards, the pixel values of canopy layer (A) and the gaps (a) were obtained, and so the canopy closure (ε) was calculated with the formula: $\varepsilon = 1 - a\,A^{-1}$.

Soil organic matter (%) was determined with the wet oxidation method of Walkley and Black (1934). Titration following the classic procedures was conducted until the endpoint came, when the normality of the ferrous ammonium sulphate could be calculated as (mL of dichromate × 1.0 N) mL^{-1} of ferrous ammonium sulphate. Furthermore, the OM (%) was calculated as (Blank–Sample titration in mL) × $N_{\text{Fe solution}}$ × 1.36, based on the assumption that organic matter is 58% carbon.

Data analysis

α diversity of understory vegetation and insects were measured. Species richness was defined as the number

Table 1. Information of the study stands. Here, the L10B0 to L0B10 refer to the stand along the gradient, ranging from pure Dahurian larch stand (L10B0) to pure Asian white birch stand (L0B10).

Forest Type	Sample plots	Pre-thinning stands	Altitude (m)	Basal area ($\mathrm{m^2\,ha^{-1}}$)	Mixing ratio (larch:birch)	Birch mixture in canopy layer (%)
L10B0	1-3	Pure larch	1070	30.16	10:0	0
L9B1	4-6	Mixed stands	1109	27.52	9:1	10
L7B3	7-9	Mixed stands	1104	24.87	7:3	30
L5B5	10-12	Mixed stands	1112	29.23	5:5	50
L3B7	13-15	Mixed stands	1116	27.88	3:7	70
L1B9	16-18	Mixed stands	1087	25.80	1:9	90
L0B10	19-21	Pure birch	1135	25.44	0:10	100

of species. The species diversity was quantified using the Shannon-Wiener index (H´) (Magurran 2004).

Species composition of plants and insects among forest types was compared by de-trended canonical correspondence analysis (DCCA) performed with CONOCO 4.5 (Microcomputer Power, Ithaca NY, USA, 2002), using the data on the occurrence status (present or absent) of species in the 21 plots. The explaining environmental factors within forest stands included birch mixture % (BM), canopy closure (CC), stand slope (SS), and soil organic matter (OM).

ANOVA followed by Tukey's HSD method was performed to test the effect of mixing gradient on the diversity of understory vegetation and insects. A P-value of 0.05 or less was defined as statistically significant. All computations and statistical operations were performed in MS Excel 2007 and SPSS 16.0 for Windows.

Results

Ordination of understory vegetation

DCCA ordination of the 88 plants on the basis of species occurrence is presented in Figure 1. DCCA axis 1 accounted for 33.3% ($P = 0.006$) of the variation in species- environment relations while axis 2 explained 19.6%. Axis 1 had a significantly negative relation with the birch mixture (BM) ($r = –0.947$, $P < 0.001$) and a positive relation with the canopy closure (CC) ($r = 0.800$, $P< 0.001$). The distribution of the plots supported this result by the fact that the sequence of the plots in the environmental axes from L10B0 (Plot 1, 2, 3) to L0B10 (Plot 19, 20, 21) corresponded to their BM values, as well as canopy closure. Stand slope (SS) had a significantly positive relation with axis 2 ($r = 0.448$, $P < 0.05$). However, soil organic matter (OM) did not show any obvious relation to axis 1 or 2. The stands were well separated from each other by axis 1 and axis 2, even though no clear separation between L10B0 and L9B1 (Plot 3 and 4) was observed in axis 2. A significant relation ($r = –0.828$, $P < 0.001$) was found between BM and CC, indicating that CC changed negatively with BM. A positive relation ($r = 0.497$, $P < 0.05$) was recorded between SS and CC.

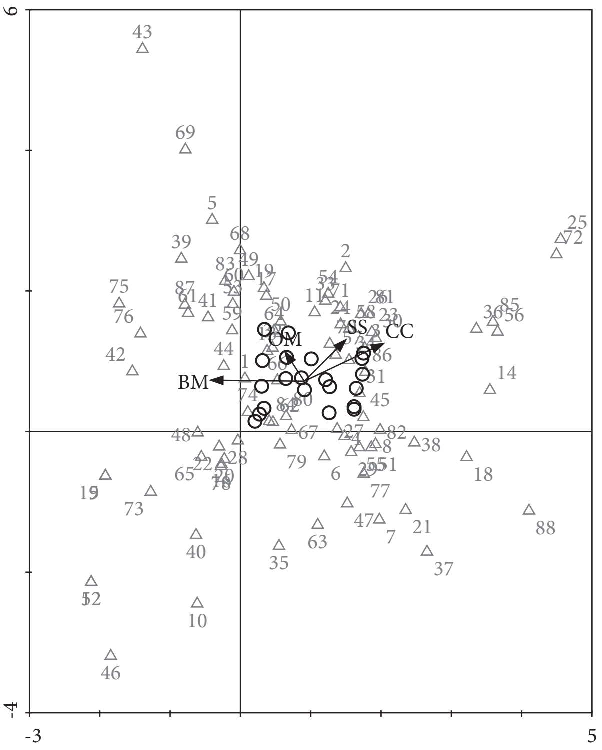

Figure 1. Ordination of 88 plant species on the first 2 axes by DCCA. Here, 1-88 stand for the plant species while BM, OM, SS, and CC are birch mixture, soil organic matter, stand slope, and canopy closure, respectively. Twenty-one sample plots are presented by the circles in the figure.

Ordination of forest insects

Figure 2 shows the ordination of insects; 33.8% ($P < 0.05$) and 12.9% of the variations in species–environment relations were explained by axis 1 and 2, respectively. Significant relations were also found between BM ($r = –0.938$, $P < 0.001$), CC ($r = 0.861$, $P < 0.001$), and axis 1. Moreover, soil OM was not well explained by axis 1 or 2. The figure also indicated that our forest stands were well separated by the 2 axes. The correlation coefficients of environmental factors showed that significant positive or negative relations were found between BM ($r = –0.830$, $P < 0.001$), SS ($r = 0.496$, $P < 0.05$), and CC.

Relations between diversity and tree species mixture

Totally, 88 vascular plant species of 58 genera and 28 families were recorded in our study sites. The dominant populations were *Carex chingannensis* Litw., *Lolium perenne* L., *Fragaria orientalis* Lozinsk.,

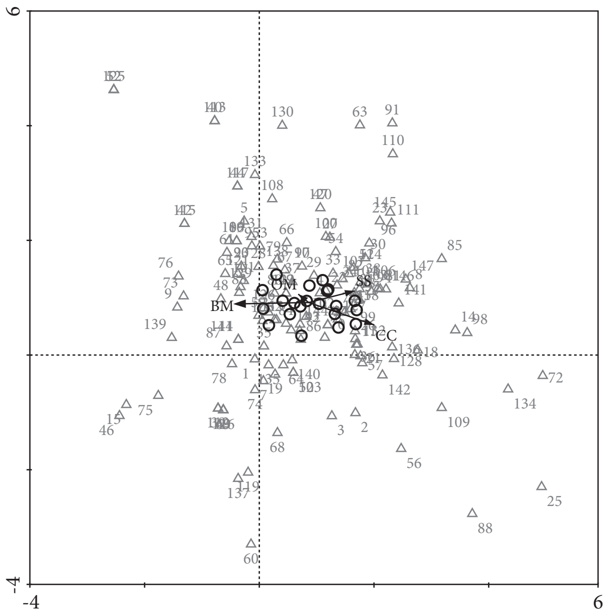

Figure 2. Ordination of 147 insect species on the first 2 axes by DCCA. Here, 1-147 stand for the insect species while BM, OM, SS, and CC are birch mixture, soil organic matter, stand slope, and canopy closure, respectively. Twenty-one sample plots are presented by the circles in the figure.

Equisetum palustre L., *Geranium dahuricum* DC., and *Galium boreale* L., which were distributed in most of the forest types. The fitted models describing the relations between the diversity and tree species mixture corresponded well to the results of the diversity pattern. The birch mixture (BM) explained 88.6% ($P < 0.001$) of the variation found in the plant species richness, which significantly peaked in the areas where the proportion of birch was 30% (L7B3) (Tables 2 and 3). The plant richness was much lower in the areas where the proportion of birch was either 0% (L10B0) or 100% (L0B10) (Table 2). Of the variation in plant species diversity 53.2% ($P = 0.001$) was explained by BM (Table 3).

In total, 147 insect species representing 78 families and 13 orders were sampled across all the 21 sample plots. Among all the species, *Loxostege sticticalis* (Linnaeus), *Chilo suppressalis* (Walker), *Lymantria dispar* (Linnaeus), *Evodinus interrogationis* (L.), *Monochamus sutor* (L.), unknown species in Culicidae, and unknown species in Ichneumonidae were found as the dominant populations in our study sites. Of the variations in insect species richness 49.5% ($P < 0.001$)

Table 2. Patterns of the species richness and diversity of plants and insects. Here, the L10B0 to L0B10 stand for the stand along the gradient, ranging from pure Dahurian larch stand (L10B0) to pure Asian white birch stand (L0B10).

Variables		L10B0	L9B1	L7B3	L5B5	L3B7	L1B9	L0B10
Plant	Species richness	48 (2.91) bc	56 (1.45) ab	64 (0.88) a	59 (1.76) a	55 (2.00) ab	44 (1.76) c	32 (2.85) d
	Species diversity	2.70 (0.35) b	2.73 (0.13) b	3.91 (0.12) a	3.85 (0.16) a	3.54 (0.16) a	3.50 (0.22) a	3.52 (0.10) a
Insect	Species richness	53 (3.79) bc	53 (2.08) bc	84 (5.51) a	65 (5.86) b	60 (2.08) bc	56 (3.21) bc	44 (2.65) c
	Species diversity	1.93 (0.03) b	2.18 (0.04) a	2.35 (0.02) a	2.19 (0.06) a	1.99 (0.04) b	1.96 (0.01) b	1.92 (0.02) b

Values in parentheses are standard errors. Different letters indicate significant differences among different forest types at $P < 0.05$.

Table 3. Regression models describing the relationship between plant species richness (PSR), plant species diversity (PSD), insect species richness (ISR), insect species diversity (ISD), and birch mixture (BM).

Model	n	r^2 (adjusted)	P
$PSR = 35.714 + 15.008\ (BM) - 2.23\ (BM)^2$	21	0.886	< 0.001
$PSD = 1.925 + 0.762\ (BM) - 0.079\ (BM)^2$	21	0.532	< 0.001
$ISR = 36.381 + 18\ (BM) - 2.452\ (BM)^2$	21	0.495	= 0.001
$ISD = 1.830 + 0.213\ (BM) - 0.03\ (BM)^2$	21	0.492	= 0.001

were attributed to BM. The quadratic model indicated that insect species richness significantly peaked ($P < 0.05$) in L7B3 (Tables 2 and 3), and then decreased to the both ends of the birch mixture gradient. Also the insect species diversity was significantly associated with BM ($r^2 = 0.492$, $P < 0.001$). The peak value of insect species diversity appeared in L7B3, followed by L5B5 and L9B1, and its minimum value was found in L0B10 (Table 3).

Discussion

Ter Braak (1986) indicated that the distribution of species along an environmental gradient could be analyzed using De-trended Canonical Correspondence Analysis (DCCA). In the present study, significant relationships between DCCA axis 1 and birch mixture (BM) as well as canopy closure (CC) (Figure 1) indicated that the composition of the tree crown and forest light conditions are important determinants of the composition and distribution of understory plants in boreal areas. Interestingly, we found a significant relationship between CC and BM, indicating that the proportion of birch was a significant factor in shaping the gradient of light conditions within the understory layer. In addition, stand slope (SS) also played a role in changing the light conditions in the forest. Many studies have reported that light conditions are crucial in the plant diversity patterns within forests (Kobe 1999; Chávez and Macdonald 2010). Barbier et al. (2008) indicated that the light was critical for forest vegetation, and it was controlled by canopy structure. Our study was consistent with these previous conclusions, and this might be also one of the reasons why the birch mixture affected the understory. However, in some cases only small or indirect effects of light on the plant species have been found, mainly because of the higher light intensity in the uniform canopy layer (Ito et al. 2004) or because the classification of plots could not well separate the light environment (Nagaike 2002).

Thinning was hypothesized to have various effects on understory in terms of species richness and diversity in our study. However, Sagar et al. (2003) claimed that the species richness would show a cumulative response in the forests under disturbance; moreover, Jobidon et al. (2004) concluded that the understory layer covered most of the floral diversity in a boreal forest, and so it could be indicative for plant diversity of the whole forest. In the present study, α diversity, as measured by 2 indices, species richness and Shannon-Wiener index, was significantly affected by the proportion of larch and birch, light conditions (Tables 2 and 3). Species diversity peaked in the areas with intermediate birch mixture (L7B3, L5B5, and L3B7) while the lower values were observed in the pure or close-to-pure forests (Table 2). The values first increased and then decreased, showing a hump-shape pattern with the increased proportion of birch. Our results provided a new example of the advantage of mixed forests over pure forests in maintaining plant diversity, which had been speculated but rarely been confirmed (Barbier et al. 2008). Previous studies found positive (Ewald 2000), negative (Hicks 1980), or no (Williams et al. 1999) linear effects of canopy mixing on understory richness and diversity. Our results indicated that this relation was well described by a curved model rather than a linear one (Table 3). Furthermore, the optimal proportions of birch for the species richness and diversity of understory in mixed forests was found to be 30% and 50%, respectively. Similar results were obtained in a study on the spruce *Picea mariana* (Mill.) B.S.P. forest along a gradient of northern hardwoods abundance. In that study, Jobidon et al. (2004) found that a 50% mixture of *P. mariana* and hardwoods (basal area proportion) was most favorable for understory species richness and diversity. With a purpose of enhancing stand volume, Chinese studies on the mixture of *Cunninghamia lanceolata* (Lamb.) Hook and *Ormosia hosiei* Hemsl. et Wils. (Weng 2008), *Castanopsis hystrix* A. DC. (Huang 2008), *Liriodendron chinese* × *L. tulipifera* (Chen 2008) concluded that the optimal mixing ratio should be 7:3, 7:3, and 8:2, respectively. Therefore, the effect of mixing proportion varied with tree species according to Thomas et al. (1999) and Barbier et al. (2008).

Gripenberg and Roslin (2007) claimed that the distribution of insects in a forest depended on the availability and quality of resources, including food, light, and water. By altering the microclimate such as temperature and humidity (Weng et al. 2007; Seiwa et al. 2009), thinning could be expected to change the insect communities in the forests (Niemelä et al.

2007). This prediction was supported by the present study: the insect species richness had a similar sensitivity to thinning to plants. The highest values were recorded in areas with 30% birch mixture and the lowest values in areas in pure birch forest. Species diversity was not as sensitive. High values appeared in pure larch forest and several mixed forests (L9B1, L7B3, and L5B5). The pattern of insect richness and diversity might be affected by crown structure since the thinning has caused forest gaps, providing a better spatial environment for the insect community. Taki et al. (2010) also indicated that this pattern might also be affected by the alteration of understory vegetation. Our study supported this view, since the pattern of insect corresponded very well to that of plant communities. Previous studies on the effects of thinning on arthropods have focused on one or more specific groups such as litter-dwelling arthropods (Yi and Moldenke 2005) or leaf beetles and weevils (Ohsawa 2005) and concluded that the effects varied depending on animal groups (Sullivan et al. 2005). Our results have shown the pattern of the whole insect community in the forests after thinning. However, more detailed information on specific insect groups in relation to thinning and tree species mixtures is needed.

Mixed forests were considered to be more stable against pests than pure forests on the basis of the resource-concentration hypothesis (Root 1973), enemy hypothesis (Humphrey et al. 1999), or associational resistance hypothesis (Hambáck et al. 2000) integrating the 2 former hypotheses. An example supporting these hypotheses is the Siberian moth (*Dendrolimus superans* Butler), which occurred as a pest only in pure man-made larch forests during its latest outbreak in Aershan, Inner Mongolia, since 2001 (Zhang and Hao 2002). However, the optimal proportions of tree species mixtures enhancing the forest resistance are not well known. The present study provided a testable conclusion on this issue, and the following quantified thinning practices should benefit from the present results. In addition, future studies should not ignore discriminating the polyphagous pests from monophagous ones since the mixed forests will not always be so stable when confronted with highly polyphagous pests. These pests are not so sensitive to their specific hosts and they can also be developed when several other hosts are present (Heiermann and Schütz 2008).

Chinese forestry policy has been targeted the ecological service rather than timber production alone. Dahurian larch, as one of the most broadly planted tree species in northern China, is fast growing and high yielding. However, large areas of larch plantations in this region incurred a high risk of pests, such as the Siberian moth (Zhang and Hao 2002). Various practices of forest management aiming at transforming the pure forests into more diverse ones are necessary and a higher diversity level, both in plants and animals, is expected (Malcolm et al. 2001). It is important to figure out the response of larch stands to various management practices. Our study has been a pioneering exploration in northeast China. In the present study, thinning practices resulted in the change of canopy when mixing 2 dominant tree species. We proposed the optimal mixing proportion favoring species richness and diversity of plants and insects, thus promoting understory development and allowing other arbor species to share the canopy layer (Lei et al. 2007). Our results have demonstrated the importance of thinning and proposed a good way to conduct quantified thinning practice. It should be emphasized that our study has provided a specific example for boreal forests in northeast China. A question in forestry is how to balance the conservation of regional biodiversity and the requirement of timber production (Battles et al. 2001). Our study has conducted a prospective probe, but further studies are still needed. The final suggestion is that a win-win status for biodiversity and wood production can be obtained only if we take ecology into consideration.

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