

Effect of Gaps on Species Diversity in the Naturally Regenerated Mixed Broadleaved-Korean Pine Forest of the Xiaoxing'an Mountains, China

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ABSTRACT: Recognizing the ecological importance of forest gap formation for forest community structure, we examined the differences in species diversity between forest gaps and closed canopy areas for trees and shrubs in three developmental stages (seedling, sapling I, and sapling II) in a typical mixed broadleaved-Korean pine forest. We randomly placed 100 sample plots (2×2 m for seedling and sapling I, and 5×5 m for sapling II) in forest gap and closed canopy areas of a 9 ha permanent sample plot for vegetation surveys of plants of each developmental stage in each habitat type. Even though the formation of forest gaps encouraged the occurrence of gap-dependent species and increased overall species diversity, there were no significant differences in species richness among the three developmental stages for both tree and shrub species ($p>0.05$). Comparing the two types of sites, statistical tests revealed no difference in species richness for trees, but highly significant differences ($p<0.01$) between forest types for shrubs for seedlings and sapling I, but not sapling II. Analysis of variance test indicated that there were no significant differences in species diversity among the three developmental stages of tree species ($p>0.05$) for both Simpson and Shannon indices. The variance for shrub seedlings was significantly different between forest gaps and closed canopy areas, but not for sapling I and sapling II. The analysis showed that the species diversity in forest gaps was significantly different from that of closed canopy areas for seedling and sapling I ($p<0.01$), but not for sapling II ($p>0.05$).

Key words: Forest gap, Mixed broadleaved-Korean pine forest, Species diversity

INTRODUCTION

The formation of forest gaps induces changes in microclimatic conditions such as light, temperature, and moisture (Canham et al. 1990, Ritter et al. 2004, Clarke and Kerrigan 2000). This ecological phenomenon permits the invasion, occurrence, and survival of light-demanding pioneer tree species which in turn provides both resources and competition for coexisting species in the gap (Connell 1978, Paine and Levin 1981). Gap formation leads to forests with patchily disturbed microhabitats due to staggered horizontal development patterns around former gaps, and this spatial dissimilarity is an important factor affecting the structure, dynamics, and biodiversity of the forest ecosystem (Kneeshaw and Bergeron 1998, Hubbell et al. 1999, Schnitzer and Carson 2001).

The species diversity in an area reflects the area's structural attributes and can provide useful information for understanding forest community ecology. Since forest communities composed of large numbers of species are constructed as a result of interactions among species, communities with high species diversity should be complex in many aspects of their ecology such as energy allocation

and flow, food chain structure, nutrient cycling, and niche composition. Species diversity may also be useful for measuring the stability and maturity of the communities (Kim 2002). As the forest gaps are formed in a staggered pattern, the species diversity in gaps should differ from that in nearby closed forest mainly due to the changed micro-environmental conditions produced by gap formation.

There is a substantial literature reporting research on various aspects of gap ecology in the mixed broadleaved-Korean pine forests such as the effect of gaps on natural regeneration (Wu 1998, Guo et al. 1998, Zang and Xu 1999, Zang et al. 1999a, Yu et al. 2001), the effect of gaps on species composition and stand structure (Zang et al. 1998), the effect of gap size on patterns of regeneration for major species (Zang et al. 1999b), and evaluation of the regeneration patterns of major species by developmental stages (Jin et al. 2007). Our study was designed to contribute of this body of knowledge by examining differences in species diversity between forest gap and closed canopy areas for plants of different developmental stages in a mixed broadleaved-Korean pine forest in the Liangshui National Reserve of the Xiaoxing'an Mountains, China.

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MATERIALS AND METHODS

Study Area

Mixed broadleaved-Korean pine forest is one of the major forest types in northeast region of China, having once being extensively distributed as a climax forest type. However, this forest type is presently restricted to the Changbai Mountains in Jilin Province; and the Wanda Mountains, Laoye Mountains, Zhangguangcai Mountains, and Xiaoxing'an Mountains of Heilongjiang Province, mainly as the result of the misuse of forest land and over-harvesting of timber (Wang 1995).

Our study was conducted in a mixed broadleaved-Korean pine forest in the Liangshui National Reserve of Xiaoxing'an Mountains (Fig. 1). The reserve is characterized by rolling mountainous terrain, ranging from 300 m asl to 707.4 m asl at its highest peak with an average slope gradient of 10~15°. The mean annual temperature is -0.3°C with a highest mean temperature of 7.5°C and lowest mean temperature of -6.6°C. Mean annual precipitation is 676 mm with 78% relative humidity (Jin et al. 2006).

The Liangshui National Reserve covers 12,133 ha of total land area with about 1.7 million m³ of growing stock and 98% of canopy coverage. The Reserve contains one of the most concentrated and well-conserved secondary broadleaved-Korean pine patches after major disturbances from over-harvesting around the region. The forest vegetation is primarily composed of *Pinus koraiensis*, *Picea koraiensis*, *Abies nephrolepis*, *T. amurensis*, *T. mandshurica*, *Acer mono*, *Fraxinus mandshurica*, *Ulmus laciniata*, *Betula costata*, *B. platyphylla*, *Quercus mongolica*, *Larix gmelini*, *Juglans mandshurica*, *A. ukurunduense*, and *A. tegmentosum* (Jin et al. 2006).

Data Collection

We established a permanent 300×300 m experimental plot in

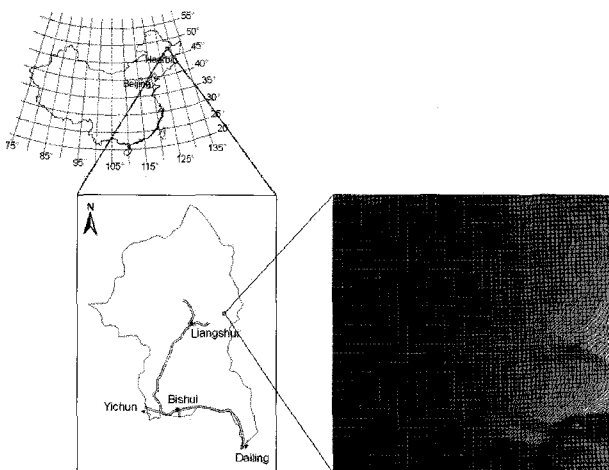


Fig. 1. Location of the study area and map of the 9 ha permanent plot.

the typical mixed broadleaved-Korean pine forest in 2005. We then divided the plot into 900 10×10 m sub-plots and planted stakes in the corners of each sub-plots to mark their position. Every woody plant of greater than 2 cm diameter was marked with a numbered aluminum tag and mapped on a coordinate grid, and its DBH, height, crown width, and bole height were measured.

The 10×10 m sub-plots were then subdivided further into 3600 5×5 m grids. We regarded a 5×5 m grid as a forest gap if the crown projection area for trees of total height of >10 m was less than 30% (Miura et al. 2001). The 5×5 m grid was the basic unit of area for measurement of gaps. One specific gap could be composed of several adjacent grids (Jin et al. 2007) (Fig. 2).

Regenerating woody plants were classified as seedling (height of <1 m), sapling I (height of >1 m, DBH of <2 cm), or sapling II (2 cm<DBH<5 cm). One hundred randomly placed sample plots (2×2 m for seedlings and sapling I, and 5×5 m for sapling II) for vegetation surveys were established for each developmental stage in each type of area (forest gap and closed canopy). For every regenerating trees or shrubs, we identified the species, measured the height, mapped its coordinates, and marked the plants with a numbered aluminum tag.

Data Analysis

We calculated species richness and the Simpson index (which gives more weight to the common species) and the Shannon index (which gives more weight to the rare species) for every developmental stage (seedling, sapling I, and sapling II) (Magurran 1988, Krebs 1999).

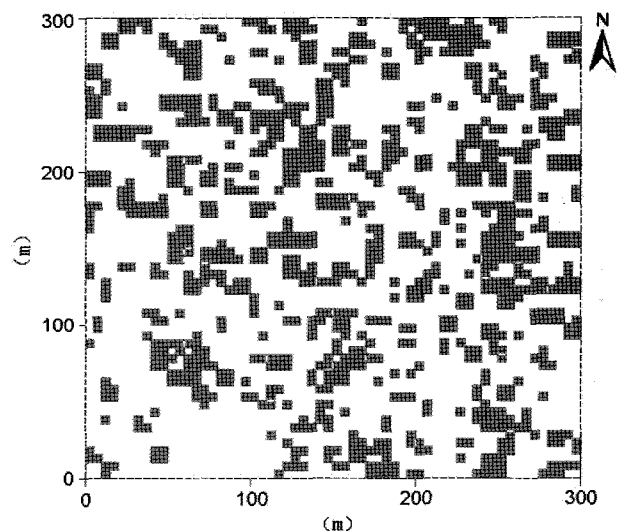


Fig. 2. Map of the 9 ha permanent plot in the broadleaved-Korean pine mixed forest. White and grey areas represent closed canopy and canopy gaps, respectively.

$$D = 1 - \sum_{i=1}^s P_i^2$$

D : Simpson index

P_i : Proportion of species i in the sample plot

s : Number of species

$$H' = - \sum_{i=1}^s (P_i)(\log P_i)$$

H' : Shannon index

P_i : Proportion of species i in the sample plot

s : Number of species

After comparing species richness, Simpson index and Shannon index between habitat types for the three developmental stages using ANOVA, we conducted t -tests to compare the indices between forest gap and closed canopy areas for each developmental stage (Rosner 2005).

RESULTS AND DISCUSSION

Regeneration in Forest Gap and Closed Canopy Area

Numbers of regenerating individuals in forest gap and closed canopy areas in the studied mixed broadleaved-Korean pine forest are presented in Table 1. Relatively abundant species included *Syringa reticulata* var. *mandshurica*, *Fraxinus mandshurica*, *Acer mono*, *A. tegmentosum*, *A. ukurunduense*, and *Tilia amurensis*. Among the 24 tree species recorded, *Quercus mongolica* was found regenerating only in closed canopy areas, whereas *Maackia amurensis*, *Populus ussuriensis*, *Phellodendron amurense*, *Salix integra*, and *Rhamnus diamantica* grew only in forest gaps, which suggests that these species depend upon the formation of gaps to make minimum regeneration.

Shrub species found at high density included *Deutzia glabata*, *Lonicera maackii*, *Philadelphus schrenkii*, *Corylus mandshurica*, *Euonymus pauciflorus*, *Acanthopanax senticosus*, *Sorbaria sorbifolia*, and *Ribes mandshuricum*. *Spiraea salicifolia* was recorded only in closed canopy areas, and no shrub species occurred only in forest gap areas.

Thousand of seedlings were regenerating per hectare in both forest gap and closed canopy areas. However, as the forest developed and seedlings grew into bigger trees, the number of individuals tended to decrease perhaps as an adjustment to stand and site conditions. This phenomenon could be interpreted as directional development of the regenerating forest toward a specific species composition, because trees occurring primarily in the understory must be shade tolerant and only a limited number of such species survive in both forest gap and closed canopy areas.

The Difference in Species Richness between Forest Gap and Closed Canopy Areas

To examine the difference in species richness between forest gap

and closed canopy areas for the three developmental stages, we conducted both F -tests for the equality of the variance of species richness and t -tests for comparison between forest areas. The F -test did not detect significant differences in species richness among the three developmental stages for both tree and shrub species at the 95% probability level (Table 2). This suggests that although the number of individuals decreases as the trees got older, the species richness does not change. In comparisons between the two types of forest areas, the t -test again showed no difference in species richness for trees of any developmental stage, or shrub in sapling II between areas, but detected a highly significant differences ($p < 0.01$) for shrubs for seedling and sapling I (Table 2).

Zang et al. (1998) reported that the species richness in forest gaps was higher than in closed canopy areas for tree and shrub species in the mixed broadleaved-Korean pine forest of Changbai Mountain Natural Reserve. Wang et al. (2003) also noted higher species richness within forest gaps in a subtropical broadleaved forest. Bianba et al. (2004) suggested that the species richness in forest gaps was much higher than in closed canopy areas in primitive subalpine fir forest of Tibet because gap formation improved micro- environmental conditions creating opportunities for invasion by shade intolerant species. However, the sampling methods used in previous studies differed from ours and they did not combine data from all of their plot for statistical analysis

The Difference in Species Diversity between Forest Gap and Closed Canopy Areas

To detect differences in species diversity between forest gap and closed canopy areas for each developmental stage, we conducted F -tests for the equality of the variance of species diversity indices for each developmental stage and then conducted t -tests for comparisons between forest areas. The results are presented in Tables 3 and 4 for the Simpson index and the Shannon index, respectively. The analysis of variance detected no significant differences in species diversity among the three developmental stages at the 95% probability level for both the Simpson index and the Shannon index for tree species. On the other hand, for shrubs the variance in the Simpson index for seedlings were significantly different between forest gap and closed canopy, but the variances of the sapling I and sapling II stages were not different between two sites. The t -test showed that the indices of species diversity for forest gaps were significantly different from those for closed canopy areas for seedlings and saplings I at the 99% probability level, but were not significantly different for sapling II at the 95% probability level (Table 3 and 4).

In Zang et al.'s (1998) study in the mixed broadleaved-Korean pine forest of Changbai Mountain Natural Reserve, the Shannon

Table 1. The number of individuals per hectare by developmental stage for each species in forest gap and closed canopy areas in broad-leaved-Korean pine forest

	Species	Forest gap			Closed canopy		
		Seedling	Sapling I	Sapling II	Seedling	Sapling I	Sapling II
Tree species	<i>Syringa reticulata</i> var. <i>mandshurica</i>	1,900	225	32	1,450	75	72
	<i>Fraxinus mandshurica</i>	1,125	125	8	2,050	75	8
	<i>Ulmus laciniata</i>	550	475	48	200	0	96
	<i>Acer mono</i>	500	250	60	1,025	450	52
	<i>Acer tegmentosum</i>	450	250	68	1,425	175	32
	<i>Acer ukurunduense</i>	225	200	112	300	250	96
	<i>Tilia amurensis</i>	275	200	36	525	125	40
	<i>Abies nephrolepis</i>	425	25	16	150	25	4
	<i>Ulmus japonica</i>	200	200	24	25	200	0
	<i>Betulla costata</i>	125	125	40	125	125	12
	<i>Maackia amurensis</i>	50	175	0	0	0	0
	<i>Prunus padus</i>	75	100	44	50	50	40
	<i>Picea koraiensis</i>	150	50	4	25	0	4
	<i>Pinus koraiensis</i>	50	0	16	200	75	12
	<i>Rhamnus davurica</i>	50	0	0	0	0	0
	<i>Populus ussuriensis</i>	0	0	32	0	0	0
	<i>Phellodendron amurense</i>	0	0	8	0	0	0
	<i>Tilia mandshurica</i>	0	0	8	25	25	8
	<i>Salix integra</i>	0	0	8	0	0	0
	<i>Alnus sibirica</i>	0	0	8	0	0	4
	<i>Sorbus pohuashanensis</i>	0	0	4	0	0	4
	<i>Rhamnus diamantica</i>	0	0	4	0	0	0
	<i>Prunus maackii</i>	0	0	4	0	0	4
<i>Quercus mongolica</i>	0	0	0	0	0	4	
	Total	6,150	2,400	584	7,575	1,650	492
Shrub species	<i>Deutzia glabata</i>	5,325	2,050	0	7,175	2,750	4
	<i>Lonicera maackii</i>	4,025	600	12	6,500	700	0
	<i>Philadelphus schrenkii</i>	2,025	1,000	24	2,100	950	12
	<i>Corylus mandshurica</i>	975	1,675	384	1,675	2,500	288
	<i>Euonymus pauciflorus</i>	2,200	700	28	4,650	925	20
	<i>Acanthopanax senticosus</i>	700	1,525	0	1,650	1,450	16
	<i>Sorbaria sorbifolia</i>	975	250	0	400	250	0
	<i>Ribes manshuricum</i>	425	250	0	1,025	500	0
	<i>Aralia mandshurica</i>	475	50	24	50	25	16
	<i>Viburnum burejaeticum</i>	225	100	0	125	275	0
	<i>Ribes burejense</i>	150	25	0	575	0	0
	<i>Berberis amurensis</i>	125	50	0	300	150	0
	<i>Spiraea elegans</i>	125	50	0	250	200	0
	<i>Viburnum sargentii</i>	100	50	0	75	75	0
	<i>Rosa koreana</i>	100	0	0	200	50	0
	<i>Lonicera caerulea</i>	0	50	0	25	75	0
	<i>Spiraea salicifolia</i>	0	0	0	75	0	0
	Total	17,950	8,425	472	26,850	10,875	356

Table 2. *F*-test for equality of variation and *t*-test for means of species richness in comparisons between forest gap and closed canopy areas by developmental stage

Stage	Forest gap (<i>n</i> =100)		Closed canopy (<i>n</i> =100)		<i>F</i> ^a	<i>P</i> (<i>t</i> -test)	
	Mean	Variation	Mean	Variation			
Tree	Seedling	1.180	2.331	1.140	1.697	0.728 ^{ns}	0.842 ^{ns}
	Sapling I	0.570	0.773	0.440	0.714	0.923 ^{ns}	0.288 ^{ns}
	Sapling II	0.880	1.137	0.800	0.828	0.729 ^{ns}	0.569 ^{ns}
Shrub	Seedling	2.330	3.072	3.250	2.694	0.877 ^{ns}	0.000 ^{**}
	Sapling I	1.490	1.545	1.940	1.431	0.926 ^{ns}	0.010 ^{**}
	Sapling II	0.420	0.367	0.390	0.362	0.984 ^{ns}	0.726 ^{ns}

^a : $p \leq 0.05$ ($F_{99,99, 0.025}=0.673$, $F_{99,99, 0.975}=1.486$).

^{**} : Highly significantly different ($p < 0.01$).

Table 3. *F*-test for equality of variation and *t*-test for means of Simpson indices in comparisons between forest gap and closed canopy areas by developmental stage

Stage	Forest gap (<i>n</i> =100)		Closed canopy (<i>n</i> =100)		<i>F</i> ^a	<i>P</i> (<i>t</i> -test)	
	Mean	Variation	Mean	Variation			
Tree	Seedling	0.162	0.070	0.169	0.064	0.912 ^{ns}	0.853 ^{ns}
	Sapling I	0.054	0.028	0.039	0.021	0.776 ^{ns}	0.511 ^{ns}
	Sapling II	0.118	0.049	0.106	0.042	0.856 ^{ns}	0.694 ^{ns}
Shrub	Seedling	0.350	0.098	0.492	0.054	0.556 [*]	0.000 ^{**}
	Sapling I	0.225	0.070	0.332	0.072	1.019 ^{ns}	0.005 ^{**}
	Sapling II	0.026	0.011	0.025	0.010	0.953 ^{ns}	0.969 ^{ns}

^a : $p \leq 0.05$ ($F_{99,99, 0.025}=0.673$, $F_{99,99, 0.975}=1.486$).

^{*} : Significantly different ($0.05 < p < 0.01$).

^{**} : Highly significantly different ($p < 0.01$).

Table 4. *F*-test for equality of variation and *t*-test for means of Shannon indices in comparison between forest gap and closed canopy areas by developmental stage

Stage	Forest gap (<i>n</i> =100)		Closed canopy (<i>n</i> =100)		<i>F</i> ^a	<i>P</i> (<i>t</i> -test)	
	Mean	Variation	Mean	Variation			
Tree	Seedling	0.275	0.223	0.277	0.185	0.830 ^{ns}	0.980 ^{ns}
	Sapling I	0.086	0.075	0.064	0.063	0.829 ^{ns}	0.543 ^{ns}
	Sapling II	0.186	0.129	0.156	0.094	0.731 ^{ns}	0.531 ^{ns}
Shrub	Seedling	0.623	0.342	0.881	0.214	0.625 ^{ns}	0.001 ^{**}
	Sapling I	0.365	0.201	0.534	0.207	1.033 ^{ns}	0.009 ^{**}
	Sapling II	0.037	0.022	0.037	0.022	0.968 ^{ns}	0.979 ^{ns}

^a : $p \leq 0.05$ ($F_{99,99, 0.025}=0.673$, $F_{99,99, 0.975}=1.486$).

^{**} : Highly significantly different ($p < 0.01$).

species diversity index in forest gap areas was greater than that in closed canopy areas for both trees and shrubs. Zang et al. (1998) argue that the formation of forest gaps improves propagation and growth of trees by improving light conditions, augmenting their ability to utilize resources, allowing invasion by shade intolerant species, and providing space for lottery competition among large numbers of species, producing a relatively uniform distribution of species in the forest and resulted in higher species diversity.

In this study, however, even though the formation of forest gaps encouraged the occurrence of such tree species as *Maackia amurensis*, *Populus ussuriensis*, *Phellodendron amurense*, *Salix integra*, and *Rhamnus diamantica* and increased overall species diversity, we did not find a significant difference in species diversity indices among developmental stages for the sample plots. However, the indices of diversity for shrub seedlings and stage I saplings were lower in the forest gap areas, perhaps because they suffered from higher competition with herbaceous plants for growing resources in the forest gaps (Jin et al. 2007). Additional scientific work will be required to clarify the causes of variation in species diversity indices across forest types in different forest habitats.

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