



Forest succession trajectories after fires in valleys and on slopes in the Greater Khingan Mountains, China

Chao Zhong¹ · Meng Guo¹ · Fenfen Zhou¹ · Jianuo Li¹ · Fangbing Yu¹ · Futao Guo² · Wenshan Li³

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Abstract Accurate assessment of postfire vegetation recovery is important for forest management and the conservation of species diversity. Topography is an important factor affecting vegetation recovery but whether species composition varies with different recovery stages and between valleys and slopes is unclear. Using field data and a space-for-time substitution method, we quantified species richness and diversity to obtain the successional trajectories of valleys and slopes. We surveyed the species of 10 burned areas from 1986 to 2010 in the Greater Khingan Mountains in northeastern China, and found that with increasing postfire recovery time, species richness in both valleys and slopes gradually decreased. However, species richness in valleys was relatively higher. Shrubs recovered rapidly in the valleys, and species diversity maximized approximately

11 years after fire. However, it maximized 17–18 years after fire on the slopes. Numerous shade-tolerant species were present in the valleys 11 years after fire but not until after 18 years on slopes. Larch appeared earlier than 11 years after fire and its recovery was slow in the valleys but appeared quickly on slopes and established dominance early. Our study provides some new insights into vegetation succession after fire at local scales. After fire, the vegetation recovery processes differ with topography and it affects the initial rate of recovery and species composition at different successional stages.

Keywords Vegetation recovery · Valleys and slopes · Space-for-time substitution · Species richness/diversity/composition · Greater Khingan Mountains

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✉ Meng Guo
guom521@nenu.edu.cn

¹ Key Laboratory of Geographical Processes and Ecological Security in Changbai Mountains, Ministry of Education, School of Geographical Sciences, Northeast Normal University, Changchun 130024, People's Republic of China

² College of Forestry, Fujian Agriculture and Forestry University, Fuzhou 350002, People's Republic of China

³ Huzhong Nature Reserve Administration of Heilongjiang Province, Huzhong 165033, People's Republic of China

Introduction

Wildfires are one of the most destructive natural disasters of forest ecosystems and hundreds of thousands occur annually around the world (Ubeda and Sarricolea 2016; Yue et al. 2020). They result in not only severe loss of resources but increase spatial heterogeneity of the forest environment, alter succession and composition, and reshape landscape diversity, changes that have an impact on vegetation regeneration and recovery (Wang et al. 2004; Xing et al. 2006; Boucher et al. 2020; Moradzadeh et al. 2020). Vegetation growth and recovery in burned forests are affected by solar radiation, hydrological conditions, soil nutrients, and other factors (Liu et al. 2017; Whitman et al. 2018a; Zhang et al. 2021a). Accurate evaluation of postfire vegetation recovery using species diversity indicators (Gonzalez-Tagle et al. 2008), especially under different topographic conditions, provides a scientific basis for forest decision-making and management

(Francos et al. 2020; Liu et al. 2020; Guo et al. 2021; Oettel and Lapin 2021).

In postfire vegetation recovery studies, field surveys, remote sensing, or a combination of both have been used to investigate species change and the direction of vegetation recovery at multiple scales (Kilgore and Dan 1979; Wang et al. 2004; Bright et al. 2019; Moya et al. 2020; Stinca et al. 2020; Smith-Ramirez et al. 2022). Smith-Ramirez et al. (2021) found that frequent fires made it difficult for vegetation to recover to its pre-fire state, even after more than 20 years. Fire severity and recovery time affect the distribution and composition of understory vegetation (Mathews and Kinoshita 2021; Weber et al. 2022). After low-severity fires, the vegetation becomes more homogeneous over time (Bataineh et al. 2006; Sun and Hu 2010; Shive et al. 2013; Harris and Taylor 2020), but high-intensity fires have a fundamental impact on vegetation composition and may change the direction of postfire succession (Han et al. 2015a, b; Meng et al. 2015; Moradzadeh et al. 2020). Moreover, climate is closely related to postfire vegetation recovery (Liu 2016; Hamberg et al. 2020; Guo et al. 2022). Bright et al. (2019) found a close relationship between postfire NBR (normalized burn ratio) and postfire precipitation and temperature. Prolonged drought can lead to the change of forest vegetation to open shrublands after fire (Baudena et al. 2020). Whitman et al. (2018a) found that climate and topography were the main factors in community change after fire in boreal coniferous forests. However, in postfire Siberian larch forests, Thuan et al. (2017) concluded that the main controlling factors for larch recovery were the extent of the fire and soil moisture content, and larch recovery rate was higher under a moderate fire. Smith-Ramirez et al. (2022) found that woody species richness could reach pre-fire levels after 20 years with no other intervention.

Remote sensing techniques have been used to produce vegetation indices, including NDVI (normalized differential vegetation index) and EVI (enhanced vegetation index), to represent the “greenness” of vegetation recovery at a large scale (Vasilakos et al. 2018; Shvetsov et al. 2019; Barm-poutis et al. 2020; Lacouture et al. 2020). Yang et al. (2017) found that NDVI recovery time would be longer than estimated by existing studies. However, there are limitations in using NDVI to monitor vegetation recovery, as it does not indicate species change and interspecific competition. Moreover, the index may reach “saturation” when vegetation cover density is high. For example, Guo et al. (2021) used sun-induced chlorophyll fluorescence (“SIF”) and EVI to compare dynamic vegetation recovery changes in postfire vegetation in northern China and found that 20 years after the fire was insufficient for vegetation recovery because SIF was still increasing. Compared to field investigations, Guo et al. (2021) found that EVI reached a pre-fire level but the vegetation was still recovering.

Postfire vegetation recovery is affected by topography, soil, and fire intensity (Näsholm et al. 2013; Han et al. 2015a, b; Kong et al. 2018; Whitman et al. 2018a, b), factors that influence the rate and direction of vegetation succession (Hart and Chen 2006; Liu et al. 2017; Gavito et al. 2021; Li et al. 2021). Changes in surface temperature and soil properties can affect seedling development (Bonan and Shugart 1989; Stefanski 2022; Vassilis et al. 2022). Furthermore, secondary succession can occur (Shvetsov et al. 2019; Stinca et al. 2020), and vegetation responsiveness influences recovery (Brooker et al. 2008; Gao et al. 2022). However, soil nutrients and moisture influence vegetation response (Veihmeyer and Hendrickson 1950; Adagbasa et al. 2020; Jiao et al. 2021); for example, they drive gully vegetation recovery processes (Zhang et al. 2021b; Zhu et al. 2021). However, topography and fire severity are the main drivers of postfire vegetation recovery (Ireland and Petropoulos 2015; Thuan et al. 2017; Whitman et al. 2018a). Topographic factors are important predictors of postfire forest patterns because they alter the hydrology conditions for vegetation growth and influence vegetation composition (Kong et al. 2003; Hart and Chen 2006; Cai et al. 2012; Liu et al. 2017; Moradi and Vacik 2018; Boag et al. 2020). Marler and del Moral (2018) found that slopes differed in light and water qualities, which changed species composition. Bassett et al. (2017) reported that topography caused regional vegetation structure differences. Shrub and fern cover in valleys was higher, and more complex than on slopes.

The Greater Khingan Mountains have ecological importance for China’s economic and social development (Zheng et al. 1986; Li 2004; Song et al. 2010). Wildfire is the most predominant natural disturbance and causes a serious loss of resources (Fang et al. 2021). To accurately assess boreal forest successional processes, studies have been carried out on vegetation composition and species diversity changes at community, ecosystem, and landscape scales (Huang et al. 2020b), monitoring dynamic changes in large-scale vegetation recovery, and exploring factors affecting them (Shu et al. 1999; Kong 2003; Yang et al. 2013; Han et al. 2015a, b; Wang et al. 2021). Additionally, researchers have found that vegetation recovery varies with fire intensity. Vegetation recovery is most pronounced following moderate fire disturbance (Sun and Hu 2010; Wei et al. 2016). However, there has been no quantitative research on species changes during vegetation recovery under the influence of topography in the Greater Khingan Mountains. This is also true for postfire succession comparisons between valleys and slopes. Essentially, it is unclear what, if any, are differences in species composition and population changes in postfire vegetation succession between slopes and valleys (Cai et al. 2018). Moreover, the diversity of understory vegetation plays an important role in maintaining ecosystem productivity. Differences in soil moisture and nutrients between valleys and

slopes affect vegetation diversity and understanding species composition and diversity differences between valleys and slopes can enrich forest management system science, important for species diversity conservation and improving ecosystem productivity (Yang et al. 2013).

Because of hydrothermal differences due to topography, it is assumed that vegetation recovery to a pre-fire state will be faster in valleys than on slopes. For this study, 10 burned and 2 unburned areas (reference samples) from 1986 to 2010 were selected in the Greater Khingan Mountains. Based on a space-for-time substitution method, it was hypothesized that all burned and unburned areas had similar site conditions (including altitude, slope, vegetation cover, and in the case of burned areas, fire intensity), and formed a chronosequence to study species composition and diversity trends in valleys and on slopes. The study aims to: (1) quantify and compare changes in species diversity during vegetation recovery after fire in valleys and on slopes of the Greater Khingan Mountains; and (2) analyze changes in species composition in succession and determine vegetation recovery time to a pre-fire state.

Materials and methods

Study region

The study region is in the Greater Khingan Mountains of northeastern China (48.56°–51.45° N, 121.34°–123.41° E) across Inner Mongolia and Heilongjiang Province (Fig. 1). The area is a coniferous forest region and is the southern extension of the Eurasian coniferous zone. It has a cold temperate continental climate, with long, dry winters and short, humid summers. The average annual temperature is $-2.8\text{ }^{\circ}\text{C}$, and average annual precipitation 460 mm (Wen et al. 2021b). Zonal vegetation is mixed coniferous and broad-leaved forest dominated by larch and birch. Understory shrubs are mainly *Rhododendron dauricum* L., *Vaccinium uliginosum* L. *Betula fruticosa* Pallas, *Vaccinium vitis-idaea* L., and *Rosa davurica* Pallas (Wu 1982; Han et al. 2015a, b; Wang 2016a).

Precipitation is relatively low and vegetation burns readily; thus, wildfires are the main natural disturbance in the region (Guo et al. 2021). The annual average

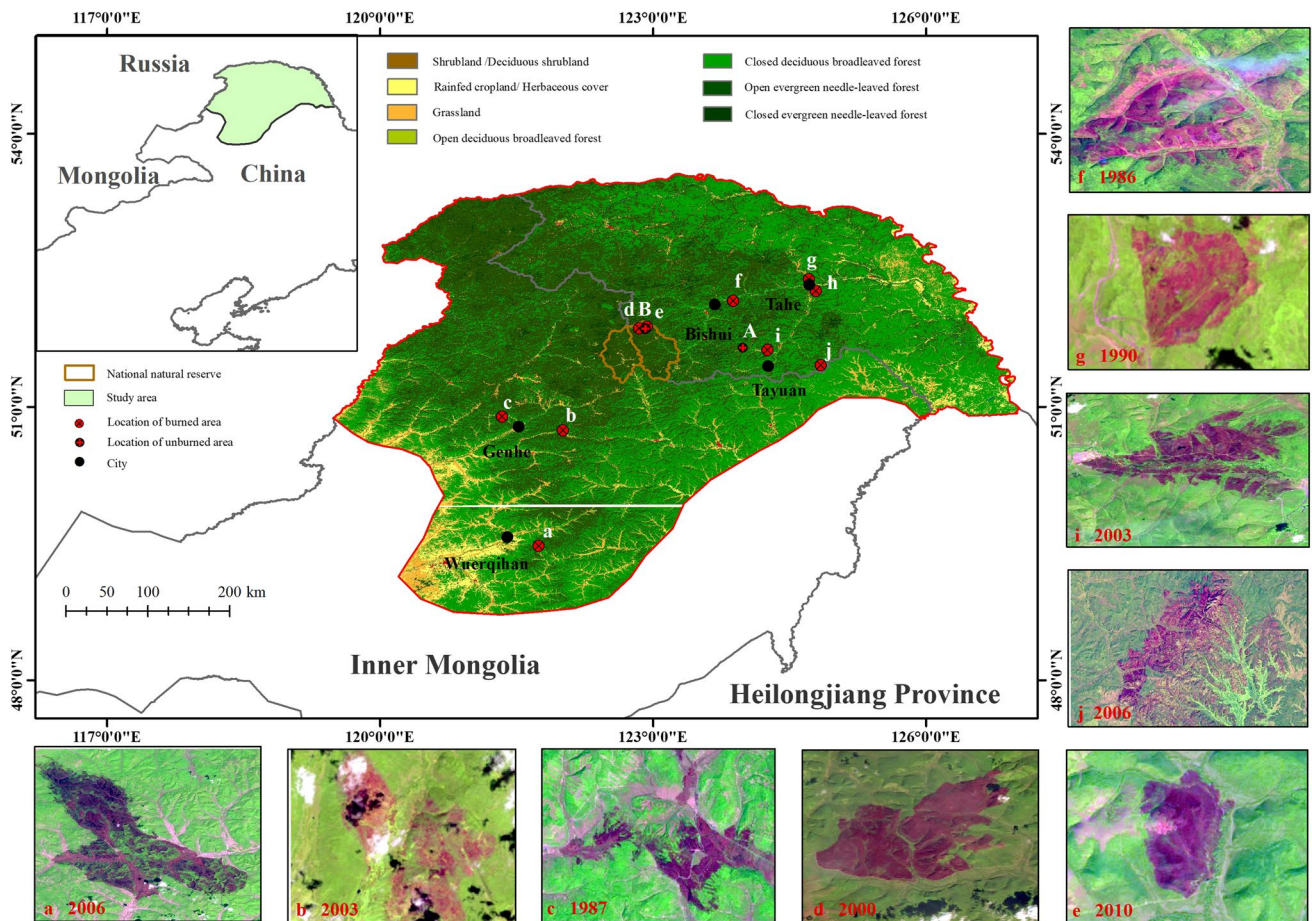


Fig. 1 Study area and selected burn locations surrounding the Landsat images (the same year or 1 year after the fire) of each burn scar; the Landsat image of burned area *h* is not shown because it was very close to *g*

number of fires exceeds 35, and the average area burnt is 76,600 ha, usually by predominantly moderately intense fires, with few fires of low and high intensity. Topography, climate, and vegetation types tend to cause spatial heterogeneity of fire intensity (Liu 2011; Huang et al. 2020a; Yuan 2020). Due to the relatively simple vegetation composition, the area is ideal for studying postfire vegetation recovery processes. We selected 10 different-aged burned areas (1986–2010) in the Greater Khingan Mountains. The locations of burned sites, fire dates, and postfire Landsat images are shown in Fig. 1.

Field survey data

In the summers of 2020 and 2021, the 10 burned and 2 unburned areas were surveyed (detailed information in Supplementary Table S1, and fire intensities of the 10 burned areas shown in Fig. 2). Since the vegetation types in the area are dominated by larch and birch and habitats basically similar, two controls were selected and tree ages between 80 to 120 years determined. It was assumed that the control sites were a fire-origin site 100 years after a fire in the valley or slope (Sun and Hu 2010).

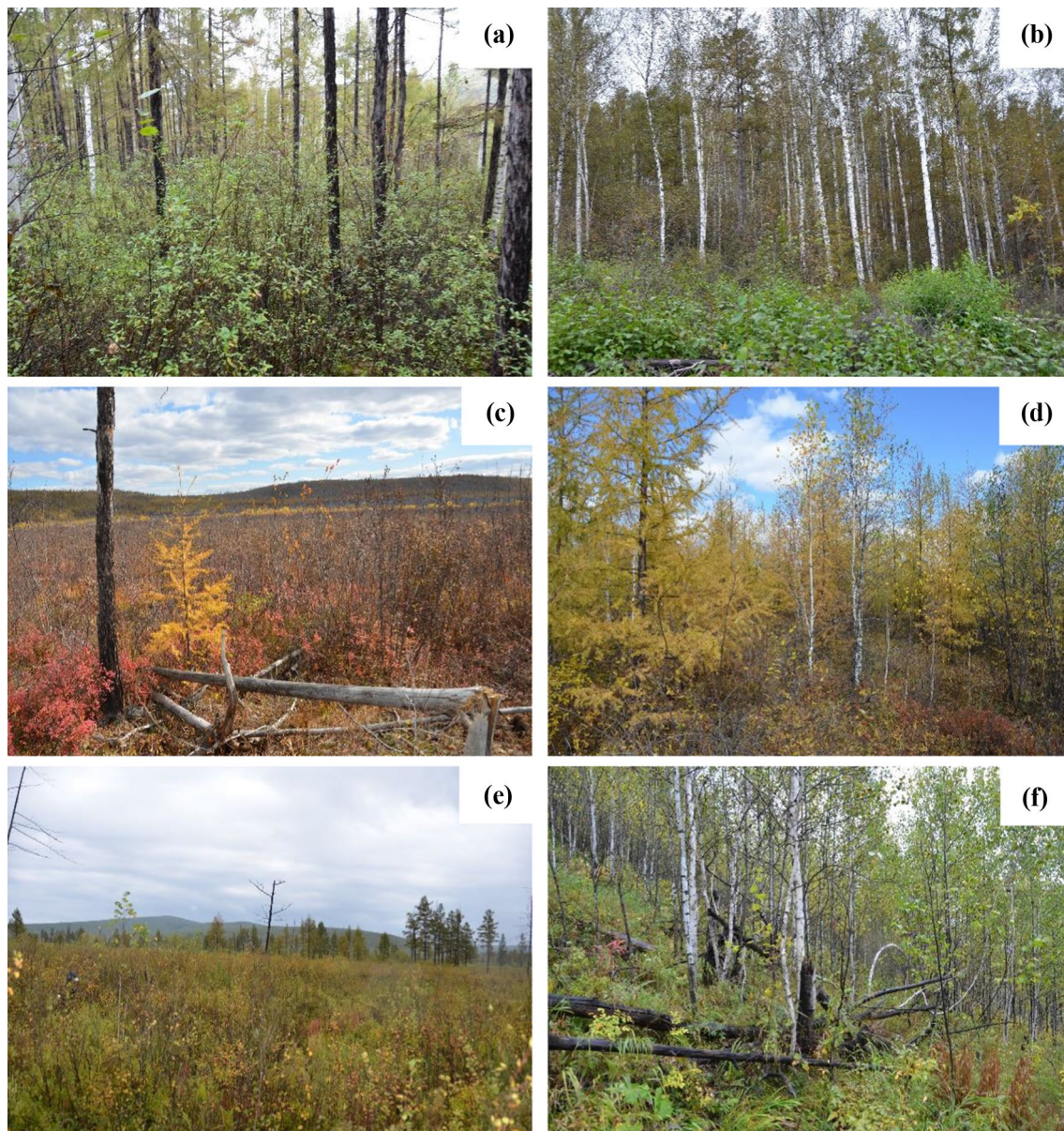


Fig. 2 Spatial distribution of fire intensity in 10 burned areas. Sample point locations were obtained with photos taken by GPS cameras during the sampling process

Vegetation recovers rapidly and grows well after moderate fires and burn patches are ideal areas to study postfire vegetation recovery (Roberts 2004; Sun and Hu 2010; Yang et al. 2013). In each burned area, three 20 m × 20 m tree quadrats and six 5 m × 5 m shrub quadrats were established in moderate fire patches in valleys and on slopes according to the composite burn index (Wang et al. 2013). Species

number, plant number, plant DBH (diameter at breast height) and plant crown width were recorded. Typical field survey sites of forests/shrublands in valleys and on slopes are shown in Fig. 3.

In addition, the differential normalized burn ratio (“dNBR”) was calculated, and three fire intensities set (Fig. 3) using the TOA (top-of-atmosphere reflectance) threshold method (Fang

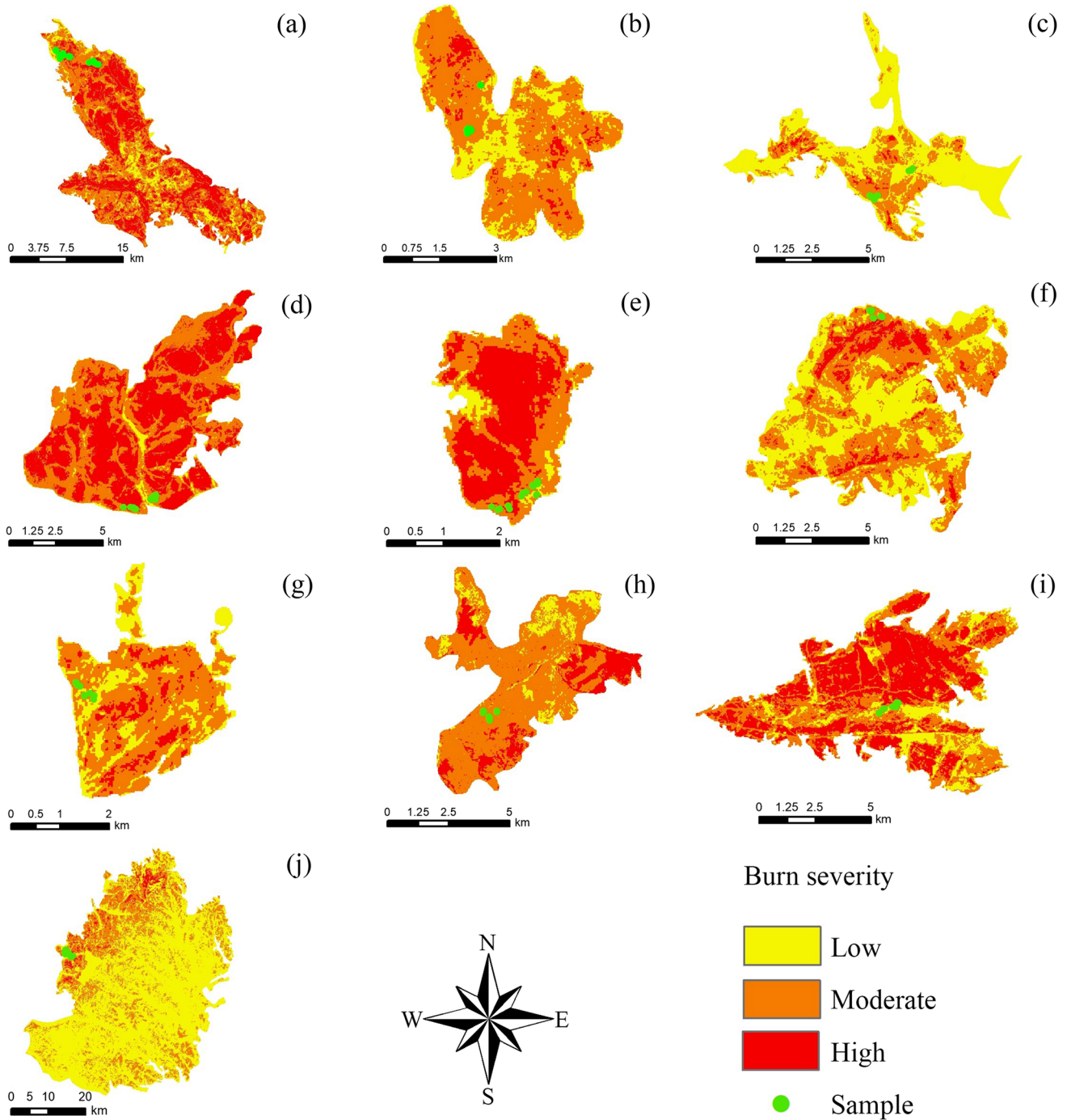


Fig. 3 Photos of areas burned in 1986 (a valley, b slope; photo taken in 2021), 2003 (c valley, d slope; photo taken in 2020) and 2006 (e valley, f slope, photo taken in 2021)

2014). In subsequent data processing, we excluded sample point data at other fire intensities.

Ecological indices

Five indices were selected for analysis (Zhang 2004, 2007; Wang et al. 2015). The equations for the indices (1–5) and ecological significance (Table 1) are as follows:

$$Y = a + b + c \quad (1)$$

where Y is the importance value, a is the relative abundance, b is the relative frequency, and c is the relative significance.

Shannon–Wiener diversity index (H):

$$H = - \sum_{i=1}^s P_i \ln P_i \quad (2)$$

where $P_i = n_i/N$, represents the relative abundance of the i th species; n_i is the number of individuals of species i ; N is the total number of individuals of all species in the community.

Simpson diversity index (D):

$$D = 1 - \sum_{i=1}^s \frac{N_i N_i - 1}{NN - 1} \quad (3)$$

where N_i is the number of species i and N the number of individuals of all species in the community.

Pielou evenness index (J):

$$J = H/\ln S \quad (4)$$

where S is the number of species in the sample and H is the Shannon–Wiener diversity index.

Margalef richness index:

$$D_{mg} = (S - 1)/\ln N \quad (5)$$

where N is the number of individuals of all species in the community and S the number of species.

Space-for-time substitution method

This method is primarily used to study slow/long-term ecological processes, and widely used in ecology and geomorphology using spatial data to replace different stages of the process (Ma et al. 2017; Damgaard 2019; Huang et al. 2020a).

Normally areas at different successional stages in regions with similar environments are selected. The terrain in the Greater Khingan Mountains is less undulating (Han et al. 2015a, b) with mainly brown coniferous forest soil, which is distributed on slopes dominated by larch, and swampy soil distributed in the valley lowlands where there is more birch and less larch (Zhao 2009; Chen et al. 2012). However, in general the regional vegetation types are similar (Guo et al. 2020). In this study, we selected several moderately burned areas from different fire years for sampling. As noted previously, the study areas had similar elevations, slopes, and aspects and it was assumed that moderate fire scars on valleys and slopes were homogeneous. Field sampling data in different years constituted the valley and slope vegetation recovery sequences.

Data analysis

All analyses were conducted using Microsoft Excel 2016 and RStudio (the “vegan” package). One hundred and eight 108 shrubs and 54 tree quadrats were surveyed within 18 sample plots in the 10 burned areas and two unburned areas. Mean species number, vegetation canopy width and tree DBH for each quadrat were recorded to represent vegetation recovery information (Wang et al. 2004). The species diversity index of each sample plot was calculated using RStudio (Weinhold et al. 2021). Quadrat species importance values were determined using methods described above. Species richness and species diversity of the 10 valleys and eight slope plots were calculated, and species compositional changes for valleys and slopes at six recovery stages were analyzed.

Table 1 Selected indices and their ecological meaning

Index name	Ecological meaning
<i>Importance value</i>	
Species importance value	Indicates the relative importance of a species in the community, and a greater value means a greater importance and dominance of the species
<i>Alpha diversity</i>	
Shannon–Wiener diversity index	Estimates the degree of species within the community
Simpson diversity index	Estimates community dominance, and a larger value means an uneven distribution of different species and that the dominant species is prominent
Pielou evenness index	Describes the evenness distribution of individual species
Margalef richness index	Describes the species richness of the community, and a greater value means a greater species richness

Results

Species richness changes

Shrub and tree species numbers changed over time in valleys and on slopes (Figs. 4 and 5). With increasing recovery time, there was a decrease in the total number of species in the community and the total number of shrub species. Tree species richness did not change drastically; the most common species were *Larix gmelinii* and *Betula platyphylla*. The maximum number of total species and shrub species in both valleys and slopes occurred 14-year postfire, and there were no significant differences between valleys and slopes. The minimum number of total species and shrub species in valleys occurred 100-year postfire, and 15-year

postfire on slopes. For the slopes, this was mainly due to the large, burned areas affecting species migration and to the vegetation having not fully recovered after the previous fire disturbance. It appears that species moved into the burned slope areas before the peak years, followed by competition until species populations stabilized.

Species diversity index changes

To further understand the characteristics of community change in burned areas by recovery years, the species diversity index of the valleys and slopes in different recovery years were calculated (Fig. 6).

With increasing recovery time in valleys, the Shannon–Wiener diversity, Simpson diversity, and Pielou

Fig. 4 Variation in species richness over time in postfire valleys

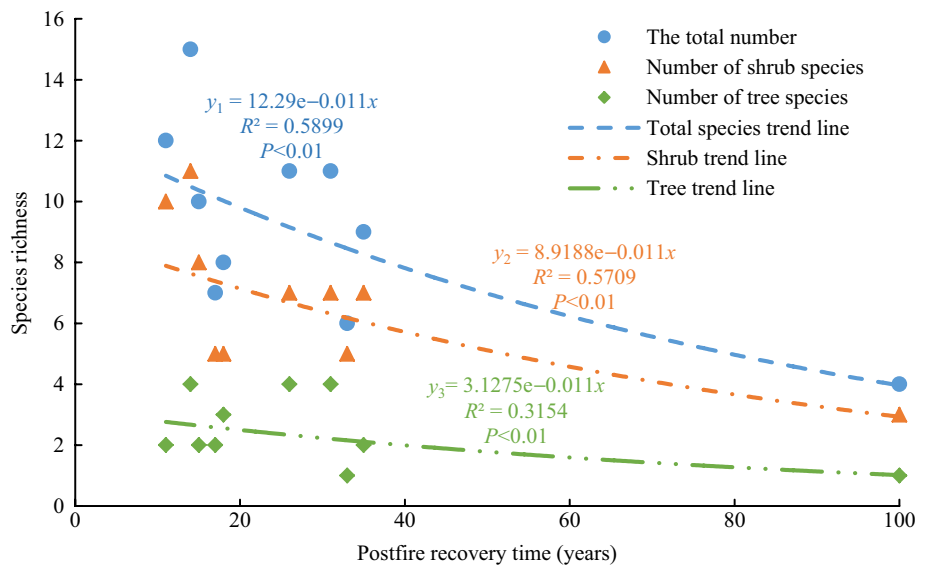
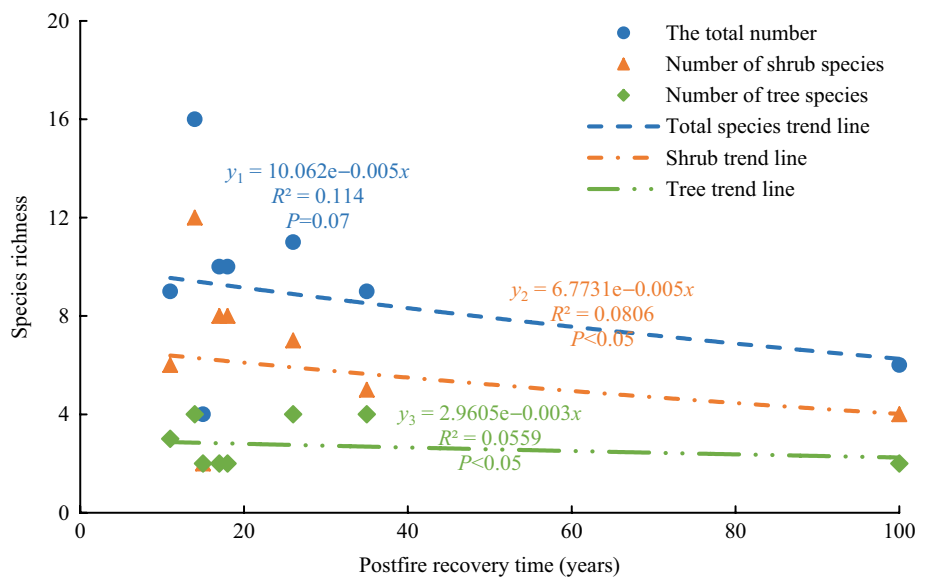


Fig. 5 Variation in species richness over time on postfire slopes



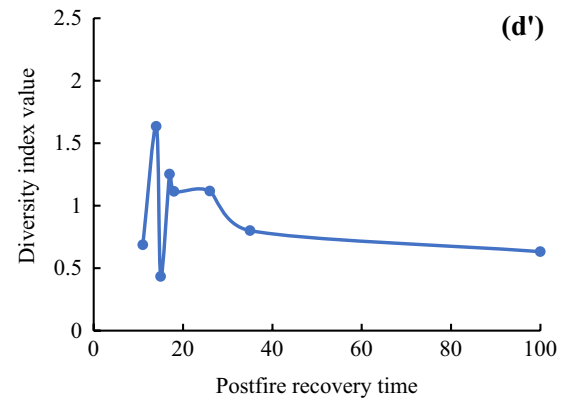
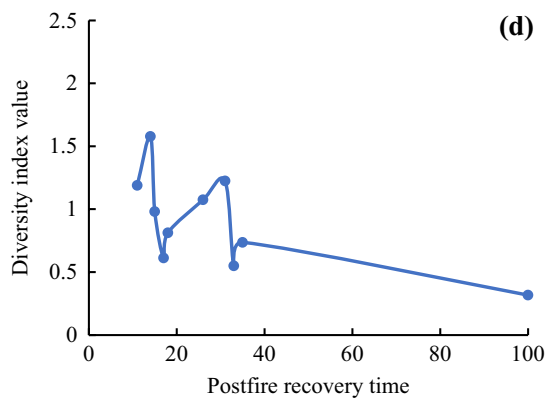
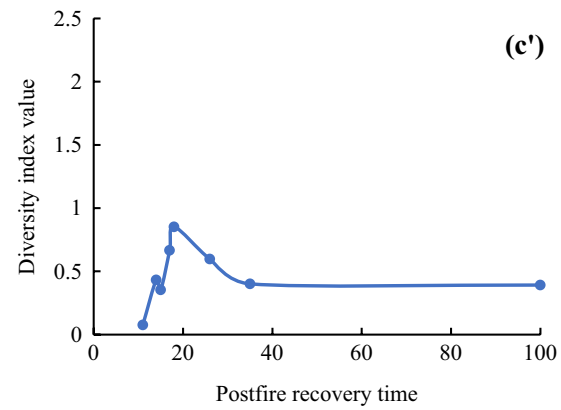
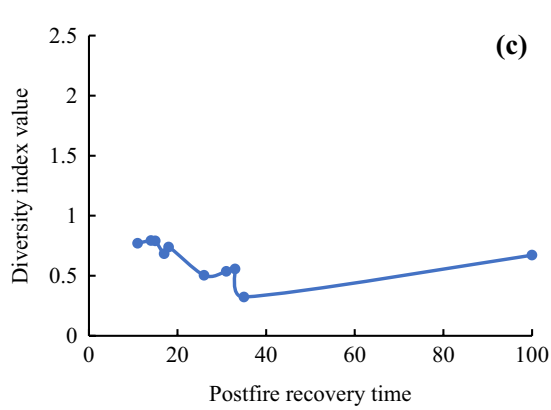
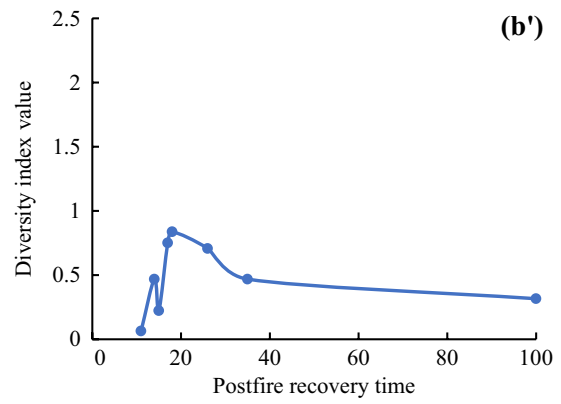
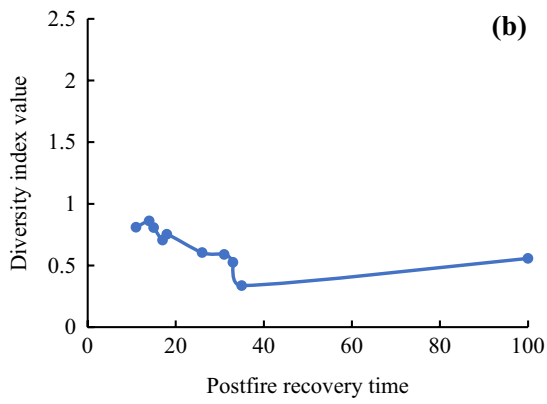
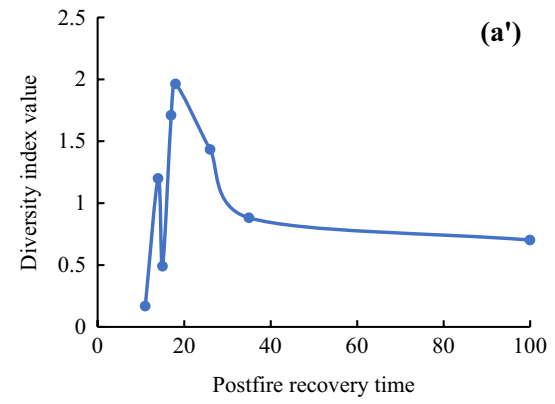
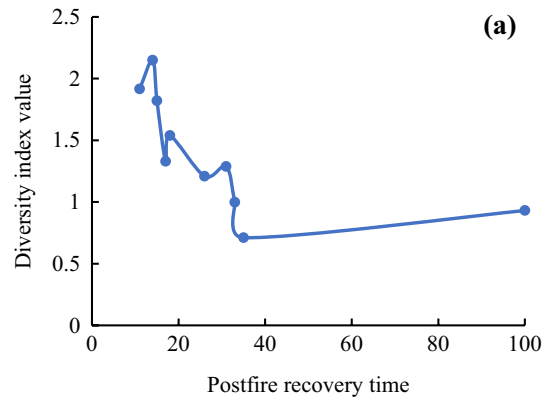


Fig. 6 Changes in species diversity over time in postfire valleys and slopes: **a, a'** Shannon–Wiener diversity index; **b, b'** Simpson diversity index; **c, c'** Pielou evenness index; and **d, d'** Margalef richness index

evenness indices all showed a decrease (Fig. 6a–c), indicating that the degree of species diversity declined, and species distribution was uneven. However, the Margalef richness index increased initially, then decreased and followed the same pattern with increasing recovery time, indicating marked fluctuations in the number of species over time.

In contrast, with increasing recovery time on slopes, the four indices showed an overall trend of initially increasing and then decreasing (although some individual years did not match the overall trend) (Fig. 6a'–d'), indicating marked initial increases in community species richness and diversity and then a decline. However, as discussed in the previous section, species change at 15-year postfire was unique, which led to a difference in the Margalef richness index from the other indices.

Overall, community diversity reached its maximum at approximately 11–14-year postfire in valleys and gradually decreased with recovery time, while it was 17 or 18 years after the fire on slopes.

Species importance value changes

To quantify the dynamic change in species vegetation at different recovery times in the valleys, the importance value of recovered species was calculated (Table 2). From 11- to 35-year postfire, shade-tolerant shrubs such as *Vaccinium vitis-idaea*, *V. uliginosum*, *Salix rosmarinifolia*, and *Betula fruticosa* were continuously present and increased. Light-demanding shrubs such as *Rhododendron dauricum* and *Rosa davurica* gradually decreased or disappeared entirely. The transition from light-demanding to shade-tolerant shrubs indicates an increase in canopy density and a gradual recovery of the tree layer (Wang et al. 2004).

In the initial stage of postfire vegetation recovery, shrubs rapidly appeared and became abundant (Table 2). At the same time, tree recovery was slow. Larch began to dominate 30-year postfire while shrubs were relatively few.

The importance values of species vegetation at different recovery times on slopes were calculated (Table 3). From 11- to 35-year postfire, shade-tolerant shrub species such as *Ledum palustre*, *Spiraea salicifolia*, *Vaccinium vitis-idaea* and *V. uliginosum* appeared and became dominant. However, light-demanding species with low importance values such as *Rosa davurica* were less dominant.

From 11- to 35-year postfire, larch and *B. platyphylla* were early abundant species and larch was dominant in the middle and late recovery stages. Generally, larch and *B. platyphylla* were abundant 11-year postfire, accompanied by a small

amount of *Populus davidiana*. With increasing recovery time, larch increasingly dominated the canopy layer accompanied by some *B. platyphylla* and *Pinus sylvestris*. Unlike in the valleys, trees on the slopes such as larch and *B. platyphylla* dominated in the early stages of postfire recovery, while shrub species were relatively scarce.

To more vividly and intuitively understand species succession in valleys and on slopes, conceptual figures based on our results, analyses and field surveys were drawn (Figs. 7 and 8). Probable years for different successional stages were evaluated. In the early stages of valley vegetation succession, tall shrubs dominated. With increasing recovery time, they were gradually replaced by larch and birch, accompanied by a small number of low shrubs. However, in the early stage of slope vegetation succession, larch and birch existed in large numbers. With increasing recovery time, other tall shrubs began to appear and gradually decreased. Finally, a mixed forest of larch and birch formed accompanied by some low shrubs.

Effect of slope on postfire vegetation recovery

Slope changes light, soil moisture, and nutrient conditions (Hart and Chen 2006; Han et al. 2015a, b; Liu et al. 2017), which affects vegetation growth. For the same burned area, there were significant vegetation recovery differences between slopes and valleys. Therefore, we selected six burned scars with both slopes and valleys and compared species richness and diversity (Fig. 9).

The 17-year postfire was the cutoff point in species richness changes in valleys and slopes from Fig. 9a. Initially, species richness in the valleys was higher than on slopes, but 17-year postfire it was the opposite. Species diversity (as measured by the four indices) in the valleys was higher than on slopes to 17 years, but after 17 years, this pattern was reversed. Since species richness determines community richness, slope richness was higher than in the valleys 17-year postfire.

Figure 9 shows that slope affects the rate of vegetation succession. In the initial stage, shrubs rapidly established on the scar of the burn in valleys. Both species richness and diversity were significantly higher than in burns on slopes. However, with increasing time, species richness gradually increased on slopes. In the middle and later stages of vegetation recovery, species richness and diversity of valleys and slopes were similar, or marginally higher on slopes.

Discussion

Characteristics of postfire vegetation succession

After fire, the forest community re-established from shrubs and grass to trees, although the recovery pattern varied with

Table 2 Changes in species importance values in postfire valleys over time

Canopy structure	Species	11-year postfire	15-year postfire	18-year postfire	26-year postfire	31-year postfire	35-year postfire
Shrub layer	<i>Ledum palustre</i>	0.241	0.272	–	0.430	0.095	0.340
	<i>Betula fruticose</i>	0.121	1.026	1.169	0.696	–	0.398
	<i>Vaccinium vitis-idaea</i>	0.435	0.130	–	0.077	–	1.039
	<i>Betula middendorffii</i>	0.344	–	0.327	–	–	0.194
	<i>Vaccinium uliginosum</i>	0.501	0.478	0.612	1.168	0.495	0.536
	<i>Potentilla fruticose</i>	0.181	0.152	–	–	–	–
	<i>Salix rosmarinifolia</i>	0.547	0.496	0.242	0.071	0.082	0.124
	<i>Salix pentandra</i>	–	0.129	–	–	–	–
	<i>Chamaedaphne calyculata</i>	–	–	–	–	1.553	–
	<i>Salix hsinganica</i>	0.080	–	–	0.131	–	–
	<i>Alnus mandshurica</i>	–	–	–	–	0.066	–
	<i>Rhododendron dauricum</i>	0.176	0.267	0.525	–	–	0.121
	<i>Rosa davurica</i>	0.078	–	–	–	0.225	–
	<i>Flueggea suffruticosa</i>	–	–	0.125	–	–	–
	<i>Spiraea salicifolia</i>	–	–	–	0.074	0.314	–
Tree layer	<i>Rosa acicularis</i>	–	–	–	–	–	–
	<i>Populus davidiana</i>	–	–	–	0.156	0.707	–
	<i>Larix gmelinii</i>	–	0.862	1.212	0.439	0.349	2.609
	<i>Betula platyphylla</i>	–	2.138	1.788	1.301	1.543	0.391
	<i>Quercus mongolica</i>	–	–	–	1.451	0.401	–

the terrain. Quantifying the different patterns of vegetation recovery at different successional stages is important for understanding the recovery process.

Several researchers have found that postfire, species richness initially increases, then decreases and stabilizes over time (Wang et al. 2004; Han et al. 2015a, b). Moreover, species composition transitions from light-demanding to shade-tolerant shrubs (Song et al. 2010; Yang et al. 2013; Liu et al. 2017). Shrub and herb recovery is rapid but tree recovery is slow (Wang et al. 2004; Han et al. 2015a, b). Our results confirm these patterns. However, we further considered the impact of topographical factors on vegetation recovery and arrived at some new findings. Species such as larch recovered faster than shrubs on slopes. Conversely, shrub species flourished in valleys where moisture conditions were more favorable (Zhao 2009; Wang 2016b). Previous studies of postfire vegetation succession have generally focused on regional or landscape scales (Vasilakos et al. 2018; Lacouture et al. 2020; Guo et al. 2021), while neglecting the local scale which can more accurately reflect succession patterns.

The speed and direction of vegetation succession after fire disturbance depend on the degree and duration of environmental factors affecting vegetation growth (Cai et al. 2012; Zong and Tian 2022). Light, water, and soil fertility are

necessary for vegetation growth and important determinants of species composition, soil nutritional status, mobilization of elements and organic matter turnover and can change soil fertility and thus affect vegetation growth and development (Mao and Zhu 2006; Zhu et al. 2021). Fire disturbances can consume soil organic matter, improve soil structure and composition (Kong et al. 2018), and increase nutrient return rate (Yang et al. 2013). Conversely, fires burn large areas of vegetation (Wang et al. 2004; Yue et al. 2020), which reduce canopy density and improve light transmittance (Hart and Chen 2006; Cai et al. 2012; Yang et al. 2013).

At the initial stage of postfire recovery, many understory species rapidly colonized and thrived due to sufficient light and rich soil nutrients. Biomass turnover was high, thus favoring stable and durable light-demanding shrubs (Liu et al. 2017). However, the fundamental condition for vegetation growth is a supply of sufficient seed and subsequent seed germination (Liu et al. 1995). Studies have shown that a moderate fire has little effect on seeds (Sun and Hu 2010). Also, larch seed supply is sufficient (Zhou 1988; Shan 1996). However, a larger burnt area may cause a shortage of seed sources. Suitable temperature and humidity are required for seed germination (Ibáñez et al. 2022). In valleys with deep organic layers (Bassett et al.

Table 3 Changes in species importance values on postfire slopes over time

Canopy structure	Species	11-year postfire	15-year postfire	18-year postfire	21-year postfire	26-year postfire	35-year postfire
Shrub layer	<i>Ledum palustre</i>	1.668	–	0.294	0.249	0.355	0.385
	<i>Betula fruticose</i>	0.079	–	–	0.084	–	–
	<i>Vaccinium vitis-idaea</i>	0.212	–	–	0.775	0.619	0.940
	<i>Betula middendorffii</i>	0.134	–	–	0.289	–	–
	<i>Vaccinium uliginosum</i>	–	–	0.307	0.325	0.477	0.151
	<i>Potentilla fruticose</i>	–	–	–	0.048	–	–
	<i>Salix rosmarinifolia</i>	0.084	–	0.186	0.143	0.042	–
	<i>Juniperus davurica</i>	–	–	0.186	–	–	–
	<i>Chamaedaphne calyculata</i>	–	–	0.783	–	0.789	0.911
	<i>Salix floderusii</i>	–	–	0.168	–	–	–
	<i>Salix pyrolifolia</i>	–	–	–	0.047	–	–
	<i>Salix hsinganica</i>	–	–	–	0.042	–	–
	<i>Rhododendron dauricum</i>	–	–	–	0.078	–	–
	<i>Rosa davurica</i>	–	0.218	0.055	0.091	–	–
	<i>Rosa acicularis</i>	0.059	–	–	–	–	–
Tree layer	<i>Spiraea salicifolia</i>	–	2.782	0.810	–	0.051	0.073
	<i>Quercus mongolica</i>	–	–	–	–	0.476	0.000
	<i>Populus davidiana</i>	0.196	1.625	2.239	–	–	0.279
	<i>Larix gmelinii</i>	1.548	–	0.761	2.441	1.529	2.073
	<i>Betula platyphylla</i>	1.256	1.375	0.000	0.559	0.627	0.354
	<i>Pinus sylvestris</i>	–	–	–	–	0.367	0.294

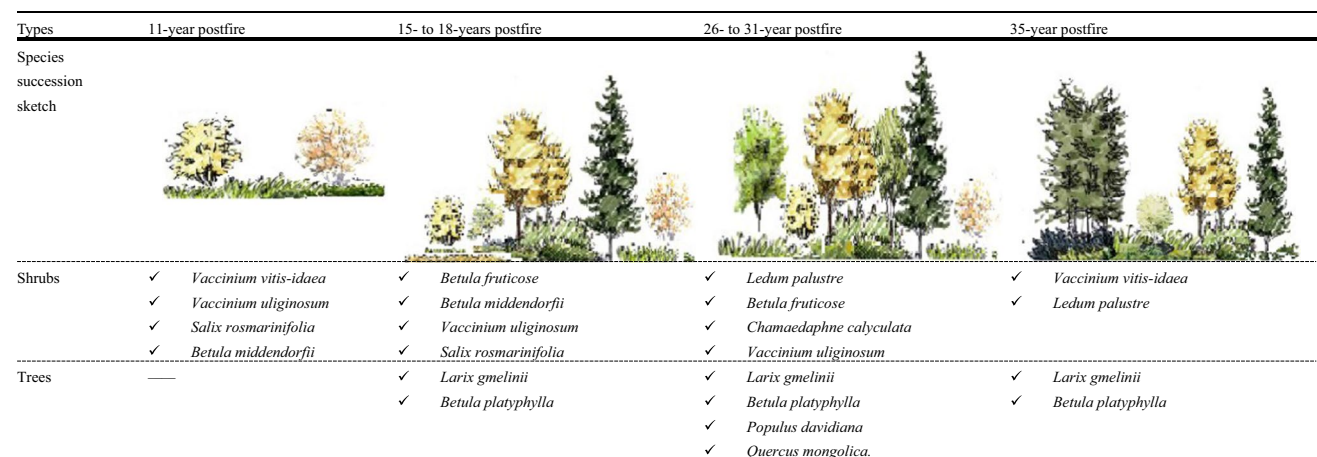


Fig. 7 Species succession in valleys

2017), there is sufficient moisture but a thick moss layer on the surface (shown through field investigation), making it difficult for larch and birch seeds to germinate (Bonan and Shugart 1989; Ibáñez et al. 2022; Kilpeläinen et al. 2022). Therefore, in the initial stage of vegetation recovery after fire, shrubs dominate (Wang 2016a). As recovery

time increased, tree species gradually established (Wang et al. 2004), canopy density increased as trees occupied a dominant position, and shrub species began to decline, leading to a gradual decline in overall species richness (Zhao 2009; Han et al. 2015a, b).





Types	11-year postfire	15- to 18-years postfire	26- to 31-year postfire	35-year postfire
Species succession sketch				
Shrubs	<ul style="list-style-type: none"> ✓ <i>Ledum palustre</i> ✓ <i>Vaccinium vitis-idaea</i> 	<ul style="list-style-type: none"> ✓ <i>Spiraea salicifolia</i> ✓ <i>Rosa davurica</i> ✓ <i>Chamaedaphne calyculata</i> ✓ <i>Vaccinium uliginosum</i> ✓ <i>Ledum palustre</i> ✓ <i>Salix floderusii</i> 	<ul style="list-style-type: none"> ✓ <i>Vaccinium vitis-idaea</i> ✓ <i>Betula middendorfi</i> ✓ <i>Vaccinium uliginosum</i> ✓ <i>Ledum palustre</i> ✓ <i>Chamaedaphne calyculata</i> 	<ul style="list-style-type: none"> ✓ <i>Ledum palustre</i> ✓ <i>Vaccinium vitis-idaea</i> ✓ <i>Chamaedaphne calyculata</i>
Trees	<ul style="list-style-type: none"> ✓ <i>Populus davidiana</i> ✓ <i>Larix gmelinii</i> ✓ <i>Betula platyphylla</i> 	<ul style="list-style-type: none"> ✓ <i>Populus davidiana</i> ✓ <i>Larix gmelinii</i> ✓ <i>Betula platyphylla</i> 	<ul style="list-style-type: none"> ✓ <i>Larix gmelinii</i> ✓ <i>Betula platyphylla</i> 	<ul style="list-style-type: none"> ✓ <i>Larix gmelinii</i> ✓ <i>Betula platyphylla</i>

Fig. 8 Species succession on slopes

Slope affects soil moisture and nutrients and changes the conditions for growth, which leads to differences in vegetation recovery between valleys and slopes (Luo 2002; Liu et al. 2017). Shrubs thrive when moisture is abundant and the soil rich in nutrients (Bassett et al. 2017), while larch is adaptable and can grow well where soil moisture and nutrient conditions are poor, even in permafrost (Qu et al. 2022). Shrubs and *B. platyphylla* are pioneer species in the early stages of vegetation recovery (Wang 2016a). *B. platyphylla* has adequate seed production, long-distance seed dispersal, and good sexual reproduction (Shi et al. 2014). Larch however, produces fewer seeds and grows slowly when young (Wang et al. 2004). Therefore, it was expected that shrub establishment and growth in the valleys to be rapid, *B. platyphylla* to be present and larch to be absent. However, in the survey, birch as a pioneer species in moist valleys was rare, and most were shrubs such as bush-birch. The possible reason for this is that the thickness of the active permafrost layer in the Greater Khingan Mountains is shallow and impedes nutrient absorption by *B. platyphylla* roots, thereby hindering growth (Wen et al. 2021a). In the field survey, we also found that in some low elevation valleys, there was no *B. platyphylla* stage, succession went from shrub to larch directly because of abundant permafrost. On slopes, water and soil nutrients are lower, shrub growth is limited, and *B. platyphylla* and larch quickly establish (Yang et al. 2013; Liu et al. 2020). On slopes, forests dominated by larch developed more quickly, although the change in shrub species was relatively slow (Fig. 10).

Topography generally led to an unsynchronized process of vegetation succession, but species composition of valleys and slopes was similar in the later stages as both were dominated by larch and birch.

Diversity characteristics of vegetation succession

The recovery of species richness and diversity is an important factor and indicator of ecosystem recovery and development (Wang et al. 2021). With increasing species diversity, community stability and productivity increased (Wang et al. 2015) and forest ecosystems gradually recovered. Researchers have found that species diversity is dynamic in postfire vegetation recovery (Wang et al. 2004, 2015; Han et al. 2015a, b). Generally, as recovery time increases, species diversity initially increases, decreases, and then stabilizes (Song et al. 2010). Wang (2016a) found that the community diversity index maximized 20-year postfire. In this study, species diversity indices of burned areas on slopes initially increased and then declined, a similar trend to that of previous studies (Li and Shao 2004; Yang 2019); however, the time to attain maximum species diversity was different. Our results indicate that valleys reach their maximum approximately 11- and 17-year post-fire for slopes.

Dynamic changes in species diversity during postfire vegetation recovery were closely related to the growth environment. Initially, after fire, light, water, and soil nutrients were sufficient (Wang et al. 2004, 2015; Yang et al. 2013); thus, shrubs rapidly colonized (Song et al. 2010; Liu et al. 2017). With increasing time, light, soil nutrients, and moisture became limited (Zong and Tian 2022). At this point, vegetation growth and development were hindered and interspecific competition became the limiting factor affecting community diversity (Chu et al. 2021). Interspecific competition can generate new niches to increase species diversity. Subject to the limits of the environment, in mid-late vegetation recovery, interspecific competition and intraspecific competition are intense, and vegetation enters a self-thinning

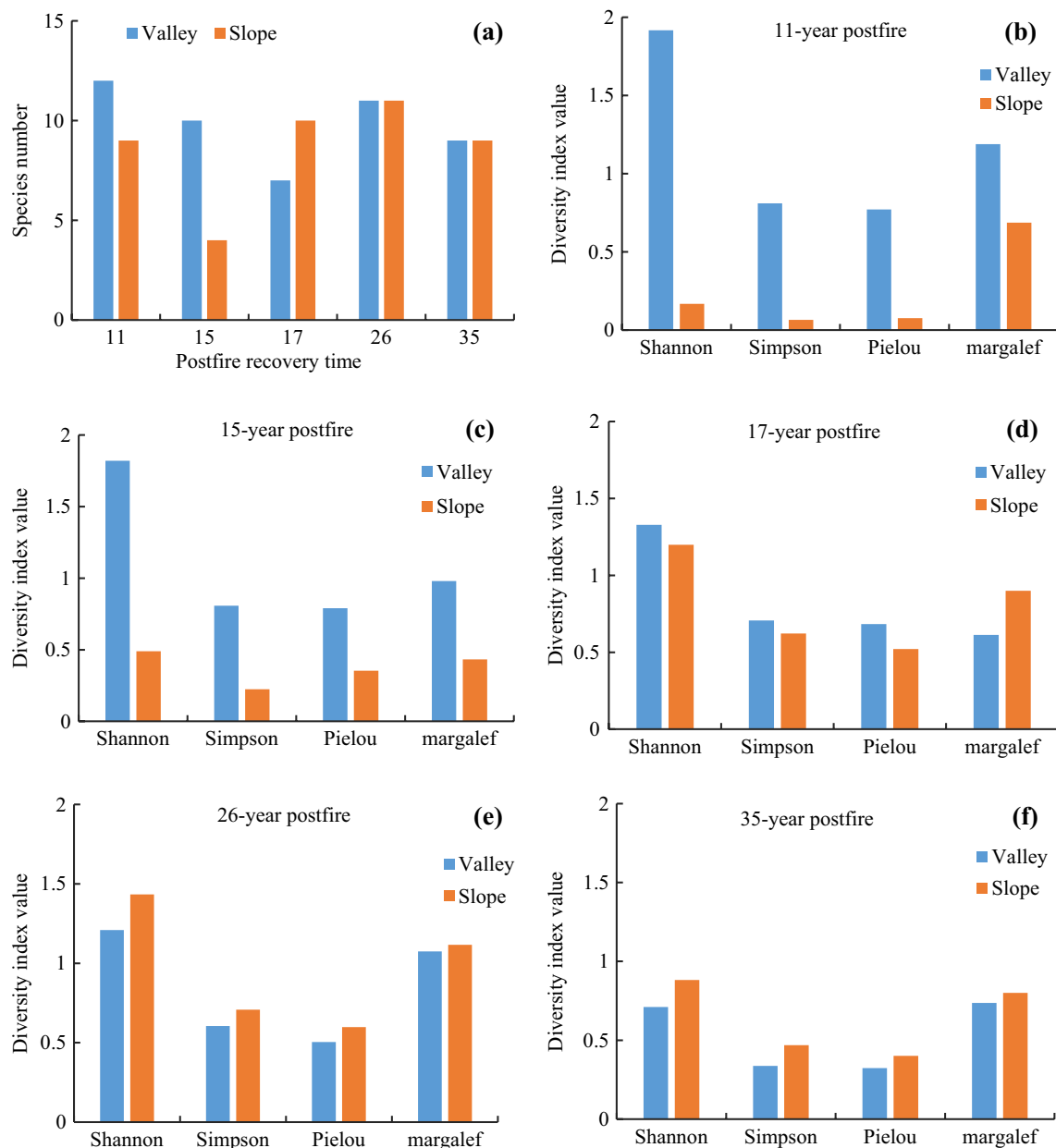


Fig. 9 Changes in species richness and diversity postfire in valleys and slopes in the same burn

stage (Bolnick et al. 2010; Jensen and Lof 2017), and community species diversity decreases.

Important value characteristics of vegetation succession

Species importance values reveal dominant changes at different successional stages and dynamic changes during vegetation recovery (Wang 2016a). Species changes depend on differences in environmental conditions for growth (Kong et al. 2003; Mao and Zhu 2006). Because of the different adaptabilities of vegetation to the environment, different dominant species appear in different

successional stages after fire (Song et al. 2010). Research has shown that light-demanding species dominate the initial stages of vegetation recovery and shade-tolerant species (*Vaccinium vitis-idaea*, *Salix floderusii*, *Betula fruticosa*, appear and gradually dominate 8–9-year post-fire (Wang et al. 2004; Mao and Zhu 2006; Sun 2011). Additionally, Wang et al. (2015) found that shade-tolerant species may appear or increase after fire for 20 years. However, these studies did not distinguish different topographies. In this study, light-demanding species gradually disappeared in both valleys and on slopes, while shade-tolerant species initially increased and then declined.

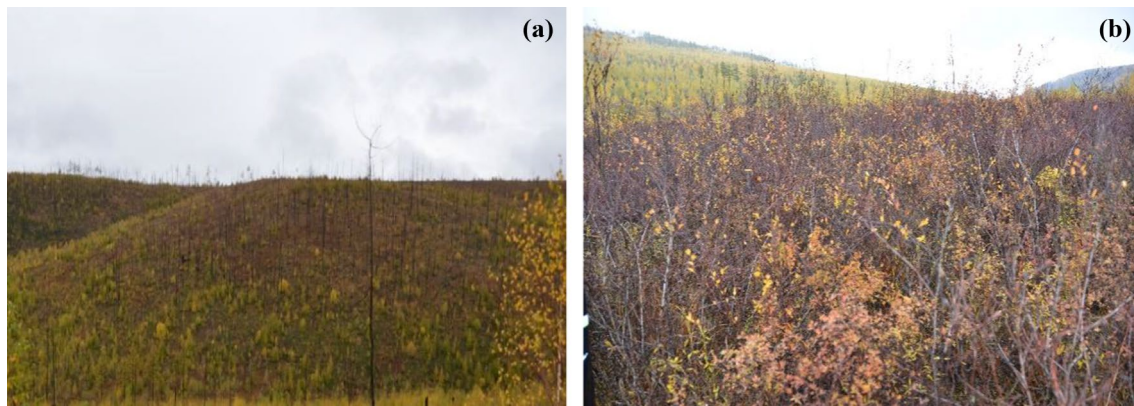


Fig. 10 **a** abundant larch seedlings on a burnt slope in 2006; **b** abundant *Betula middendorfii* and *B. fruticosa* in a burnt valley in 2006. Photos taken in 2021

The difference between valleys and slopes is that shade-tolerant species predominated 11- and 18-year postfire, respectively.

Vegetation recovery of burned areas is a long and gradual process (Kong et al. 2003) whereby shrub and grass communities gradually give way to communities dominated by larch (Zhao et al. 2013). Some researchers consider that larch only appears 16-year postfire, while others consider that it can recover as early as five years after fire, depending on the growth environment (Wang et al. 2004; Yang 2019). We documented the presence of larch and birch in valleys and slopes 11-year postfire. Larch recovered quickly and became dominant on the slopes in far greater numbers than in valleys. Water and soil nutrient conditions on slopes are unsuitable for the growth of many shrubs (Luo 2002; Liu et al. 2020) and thus provide an ecological niche for the growth of larch (Qu et al. 2022). The thin organic layer creates ideal conditions for the germination of larch seeds. *B. platyphylla* is a pioneer species that has small seeds, strong germination and is conducive to spreading. The sparse structure of *B. platyphylla* stands also creates conditions for larch regeneration (Han et al. 2015a, b; Sun 2011). In the early stages of vegetation recovery, larch and birch mixed forests readily appear, which are more obvious on slopes, while shrubs dominate in valleys.

Limitations

Vegetation succession after fire is a long-term process that requires many of years. We selected the longest recovery time as 35 years but did not find recovery steps. This may lead to errors in the recovery stage division and may not allow the appearance of some species.

Secondly, we only distinguished vegetation recovery between slopes and valleys and did not distinguish slope

angles. Therefore, differences in vegetation recovery on different slope angles could not be determined.

Finally, we did not survey areas only lightly or severely burned, and only sampled moderately burned areas. Therefore, only general insights into vegetation recovery of burned areas can be provided.

In a subsequent study, vegetation recovery over a longer period will be examined and under different slope angles and burn intensities.

Conclusion

A chronosequence of 10 burned areas and two unburned areas from 1986 to 2010 in the Greater Khingan Mountains was established to study post-fire vegetation recovery in valleys and on slopes. Topography played an important role in successional processes, and although it did not change their direction, it did affect the initial rate of recovery and species composition at different successional stages. Species diversity in valleys and slopes initially increased and then decreased, with species diversity peaking earlier in valleys than on slopes. In the middle and late successional periods (35-year postfire), a stable community of larch and birch with a small number of low shrubs formed in both valleys and slopes. This study could enrich boreal forest management plans. However, due to the short and inconsistent intervals of the time series constructed, there may be differences in the time of vegetation recovery to different stages.

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