

Strong influences of stand age and topography on post-fire understory recovery in a Chinese boreal forest

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ARTICLE INFO

Keywords:

Boreal forest
Composition
Diversity
Resource heterogeneity
Resource quantity
Understory recovery
Wildfire

ABSTRACT

Soil resource quantity and heterogeneity as well as overstory characteristics change along with stand age after fire disturbance, imposing strong influences on post-fire understory recovery. In this study, we aimed to assess how soil resource (nitrogen quantity and heterogeneity), topographic position (aspect), overstory characteristics (basal area), and stand age affected understory characteristics (cover, richness, evenness, and composition) during boreal forest succession after fire disturbance. We collected plant community and environmental data from 76 stands aged at 4 to 203 years post-fire in the boreal forest of Northeast China. We separately tested the effects of the considered factors on the characteristics of total understory, shrubs, and herbs. Total understory cover was higher at the south-facing slopes and flat locations than at north-facing slopes. Species richness of total understory, shrubs, and herbs was higher at the flat locations and south-facing slopes than at the north-facing slopes. The cover of total understory and shrubs showed increasing trends along with stand age, soil nitrogen quantity, and overstory basal area as well as decreasing trends along with soil nitrogen heterogeneity, while the cover of herbs showed reversed trends across all the three topographic positions. Understory richness showed decreasing trends along with soil nitrogen quantity as well as increasing trends along with soil nitrogen heterogeneity and overstory basal area. Total understory evenness showed flat trends along with soil nitrogen quantity, heterogeneity, and stand age as well as decreasing trends along with overstory basal area. Understory community composition was mainly affected by topographic position, stand age, and overstory basal area. During understory recovery, community composition shifted from shade-intolerant species to shade-tolerant species. Our results highlight the importance of topography and stand age in post-fire understory recovery in boreal forests of China, mediated through availability of light and soil nutrients.

1. Introduction

The increasing frequency of wildfire disturbances is causing widespread concerns about the degradation of boreal forest ecosystems, which are important habitats in maintaining global biodiversity and ecosystem function (Flannigan et al., 2009; Tchebakova et al., 2009). Wildfire creates spatial heterogeneity in resource availability and environmental conditions that can affect forest regeneration and recovery

(Krawchuk and Moritz, 2011; Dantas et al., 2016). Post-fire micro-habitat characteristics are expected to change along with successional changes in community composition and diversity. Therefore, understanding successional processes after a wildfire is imperative in boreal forest restoration (Krawchuk and Moritz, 2011; Palmer et al., 2016). In boreal forests, understory vegetation composes the majority of overall forest biodiversity, affects litter decomposition and carbon sequestration (Nilsson and Wardle, 2005; Jonathan et al., 2016). Understory

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<https://doi.org/10.1016/j.foreco.2020.118307>

Received 31 January 2020; Received in revised form 1 June 2020; Accepted 2 June 2020

Available online 27 June 2020

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recovery is considered to be a critical indicator of post-fire restoration success (Chen et al., 2018). Previous studies have examined patterns of understory cover, composition, and diversity in relation to stand development and overstory characteristics following fire disturbance (Ma et al., 2016; Kumar et al., 2017; Jean et al., 2019); however, the mechanisms driving post-fire recovery of understory cover, diversity, and community composition remain mostly speculative.

In boreal forests, plant diversity and growth are strongly limited by nitrogen deficiency due to slow rates of litter decomposition and nitrogen mineralization in the soil (Corbin et al., 2003; Allison et al., 2008; Näsholm et al., 2013). Therefore, two general hypotheses associated with soil nitrogen have been proposed to explain the patterns of species diversity and community composition in boreal forests. The soil nitrogen quantity hypothesis suggests that species diversity is mainly determined by the average supply of soil nitrogen (Strengbom et al., 2001). In contrast, the soil nitrogen heterogeneity hypothesis suggests that high species diversity is maintained by the spatial heterogeneity of soil nitrogen as co-occurring species have different demands for soil nitrogen through resource partitioning (Gundale et al., 2011). Understanding how the quantity or heterogeneity of soil nitrogen controls the patterns of understory cover, diversity, and community composition can potentially help to explain understory recovery during boreal forest succession after fire disturbance (Reich et al., 2012).

The effects of soil nitrogen quantity or heterogeneity on understory cover, diversity, and community composition is predicted to vary in stands of different ages and frequencies of intermediate disturbance (Bartels and Chen, 2010; De Grandpré et al., 2011; Kumar et al., 2017). As reviewed by Bartels and Chen (2010), resource quantity determines understory species diversity in both young and mature stands, whereas resource heterogeneity strongly impacts understory species diversity in old-growth stands. Furthermore, resource quantity played an important role in determining understory diversity in both disturbed and undisturbed forests, but resource heterogeneity played an important role in determining understory diversity in disturbed forests (Bartels and Chen, 2010). A subsequent study supports the hypothesis that resource heterogeneity resulting from disturbances contributes to the maintenance of understory diversity by allowing the coexistence of early-successional species with late-successional ones (De Grandpré et al., 2011). Recently, an eight-year nitrogen addition experiment conducted in a Chinese boreal forest has shown that nitrogen addition had no significant effect on species richness of understory vascular plants but changed the community composition (Xing et al., 2019). Therefore, how soil nitrogen quantity and heterogeneity will affect understory diversity maybe highly dependent on environmental context.

Besides soil nitrogen, understory vegetation is expected to be strongly influenced by light transmission to forest floor which is controlled by the overstory characteristics, such as tree basal area (Kumar et al., 2017). Overstory can reduce light availability in the forest understory through the absorption and reflection of solar radiation (Lieffers et al., 1999), leading to low light availability for understory growth (Kumar et al., 2017). At the early successional stage following fire, abundant growing space and high light availability generally lead to rapid colonization and increases in the cover and species richness of shade-intolerant and nutrient-demanding understory vegetation (Hart and Chen, 2006). Along with stand development, overstory canopy generally becomes closed and reduces the light availability to understory, which leads to the decrease in the cover and richness of understory species that established during the early successional stage (Hart and Chen, 2008; Zhang et al., 2017). The decrease in light availability is fast after closure of the initial post-fire cohort of shade-intolerant deciduous trees, and commonly continues as shade-tolerant conifers become increasingly dominant in the overstory at late successional stages (Kumar et al., 2017).

Topographic variables also affect understory vegetation by means of creating spatial variation in levels of soil nitrogen (Chipman and Johnson, 2002; Seibert et al., 2007), sometimes at small spatial scales

(Seibert et al., 2007; Griffiths et al., 2009). In boreal forest, soil nitrogen quantity at the burned site was significantly greater on the south-facing slope than on the north-facing slope, though this pattern was reversed at the unburned site (Kong et al., 2015; Kong et al., 2019). Topography can also significantly control light availability under the tree canopy and in turn, affects understory composition and diversity (Takashima et al., 2006).

The relationships between individual environmental factors and understory vegetation have been examined in boreal forests, but few studies have considered these factors together. To provide complementary information on the mechanisms of post-fire understory recovery, we aimed to assess how the multiple factors of soil nitrogen quantity and heterogeneity, stand age, topographic position, and overstory basal area affected understory characteristics (cover, richness, evenness, and composition) during boreal forest succession. We separately tested the effects of environmental factors on understory characteristics of total understory, shrubs, and herbs. We hypothesized that during forest succession after fire (1) understory cover, richness, and evenness increase along with increasing soil nitrogen quantity and heterogeneity and conversely decrease along with increasing stand age and overstory basal area (2) all of the environmental variables would have significant effects on understory composition.

2. Materials and methods

2.1. Study area

This study was conducted in the Great Xing'an Mountains of Northeast China, located in the southern margin of the Eurasian boreal forest (51°56'31" to 51°17'42"N; 122°42'14" to 123°18'05"E; 239 to 1488 m a.s.l.). The regional climate is characterized by annual monsoons and prolonged and severe winters. The mean annual temperature of the study region is -4.7°C (range: -2.7°C to -5.3°C), and the mean annual precipitation is 500 mm (range: 400 mm to 600 mm) (Chang et al., 2007). The topography is undulating, dominated by sloping uplands and large areas of flat lowlands. Wildfire is the predominant natural disturbance in this region and fire-return intervals vary between 120 and 150 years (Chang et al., 2007). Temperate coniferous forest dominated by larch (*Larix gmelinii* (Rupr.) Kuzen.) is the typical habitat type (Zhou, 1991). Other tree species, such as birch (*Betula platyphylla* Suk.), pine (*Pinus sylvestris* L. var. *mongolica* Litv.), spruce (*Picea koraiensis* Nakai), aspen (*Populus davidiana* Dode, *Populus suaveolens* Fisch.), and willow (*Chosenia arbutifolia* (Pall.) A. Skv.) grow within the larch forests. The dominant understory vegetation includes *Betula fruticosa* Pall., *Ledum palustre*, *Rhododendron dauricum* L., *Vaccinium uliginosum* L., and *Chamerion angustifolium* (Liu et al., 2017).

2.2. Sampling design

A total of 76 forest stands from six different post-fire age classes (4, 14, 27, 76, 98 and 203 years) were chosen for this study (Table 1). These stands represent different successional phases, namely the stand initiation phase (4-year-old), early stem exclusion phase (14-year-old), late stem exclusion phase (27-year-old), early canopy transition phase (76-year-old), late canopy transition phase (98-year-old), and gap dynamics phase (203-year-old) (Chen and Popadiouk, 2002). There were at least four replicates of study plots in each of three topographic positions (south-facing slope, north-facing slope, and flat locations) to control for differences in microclimate and understory vegetation.

The ages of forest stands were determined by analyzing tree cores for older stands (> 50 years) or by recent fire history for younger stands (≤ 50 years) (Liu et al., 2012). For younger stands, detailed fire records kept since 1965 were obtained from local forest fire prevention bureaus. For older stands, we confirmed fire to be the primary disturbance factor based on the black carbon in soil and the burned stump and used the ages of the dominant tree species, larch, as a proxy for

Table 1

Characteristics of 76 stands that were sampled in the boreal forests of the Great Xing'an Mountains. Values are means with SE in parentheses for density and basal area. For the 4- and 203-year age classes, seedling basal area were not reported because tree heights were < 1.3 m.

Age class (year)	n	Tree density	Tree basal area (m ² /ha)	Seedling and sapling density combined	Sapling basal area (m ² /ha)
4	16	0	0	5146 (1761)	0
14	12	0	0	4889 (1859)	3.70 (2.04)
27	12	2976 (343)	15.56 (1.26)	2202 (546)	2.05 (0.47)
76	12	3065 (147)	26.61 (1.47)	575 (179)	0.54 (0.20)
98	12	1743 (117)	19.03 (1.16)	1041 (526)	0.71 (0.16)
203	12	1272 (159)	31.94 (3.65)	0	0

stand age (Hart and Chen, 2008). We took a core sample at breast height (1.3 m above the root collar) from three to five larch trees in each stand. These cores were stored and transported in plastic straws before being mounted on grooved, wooden core strips and sanded to make the rings visible in the laboratory. Subsequently, the same observer counted tree rings with a hand-held magnifier until an identical number was obtained in three successive instances. Tree ages were corrected to stand age by adding eight years to the ring counts made at breast height to account for the time taken to reach the breast height (Vasilaiuskas and Chen, 2002; Hart and Chen, 2008).

Selected stands were geographically interspersed across the study area, and they were located within walking distance (50 to 2000 m) from the nearest road. Stands were comparable in terms of slopes (range: 5° to 35°), stem density, and overstory composition (i.e., all dominated by larch). All selected stands were on well-drained brown coniferous forest soil, which is the dominant soil type in this study area (Gong, 2001).

2.3. Field survey

We conducted a vegetation survey between July and August of 2013 during the period of peak vegetation cover. In each stand ($N = 76$), a 20×20 m plot was established in a random location to measure overstory vegetation. In each plot, we counted the amounts of seedlings, saplings, and trees to calculate stem density. We measured the diameters at breast height (DBH) for saplings ($0 \text{ cm} < \text{DBH} < 4 \text{ cm}$) and trees ($\text{DBH} \geq 4 \text{ cm}$) around 1.3 m above the root collar to calculate overstory basal area (Elledge and Barlow, 2010). For stands in the 4-year age class, the seedling basal area was not reported because seedlings were < 1.3 m in height. For understory vegetation, we followed the protocol of Hart and Chen (2008) and randomly positioned four 1×1 m quadrats in each of 76 stands. We divided the plot into four quadrants and set a quadrat in each quadrant at random distances from the plot center. In each quadrat, all shrub and herb species were identified up to the species level, and their covers were visually estimated in the field by the same observer (Brundrett et al., 2019). Specimens were collected and verified with the Herbarium of Northeast China and Flora of China (<http://www.iplant.cn/frps>). Plant nomenclature follows the International Code of Nomenclature for algae, fungi, and plants (Turland et al., 2018).

Total soil nitrogen exhibits a positive correlation with available soil nitrogen in various ecosystems (Vlassak, 1970; Guinto and Catto, 2016); thus, we used total nitrogen (TN, g/kg) from each quadrat in our analyses. We sampled ~ 250 g of mineral soil at a depth of 0 to 15 cm from the center of each quadrat with a shovel. Fresh soil samples were placed in sealed plastic bags, marked with plot information, and transported to the laboratory after field survey. We took part of the fresh soil from each soil sample to dry at 105 °C for 48 h to measure soil moisture. The left fresh soil for each soil sample was air dried and ground in order to pass through a 2-mm sieve. Total soil nitrogen (TN) was measured using a wet Kjeldahl digestion method (Bremner, 1996). All analyses were conducted according to the Standard Methods for Observation and Analysis in Chinese Ecosystem Research Network (Liu, 1996).

2.4. Data preparation and statistical analyses

2.4.1. Data preparation

All vegetative (understory cover and diversity) and soil nutrient data were averaged across quadrats to reduce noise and generate a stand-level mean (Biswas et al., 2017). Understory species richness and evenness were used to describe understory diversity. We calculated understory species richness as the total number of species present at each stand and evenness as the relative proportion members of each plant species comprised within the community by following (Pielou, 1980):

$$\text{Evenness} = \frac{-\sum p_i \log p_i}{\ln(\text{Richness})} \quad (1)$$

where p_i is the proportion of species i percent cover to total vegetation cover. Considering that shrubs and herbs may respond differently to soil nitrogen, stand age, overstory basal area, and topographic position, we calculated these metrics separately for total understory species, shrubs, and herbs.

Total soil nitrogen from the four quadrats were averaged to derive a stand-level mean (N_m), which approximates the stand-level nitrogen quantity. The standard deviation of total nitrogen in the four quadrats for each stand (N_{sd}) was calculated to represent the stand-level nitrogen heterogeneity.

2.4.2. Statistical analyses

All analyses were performed in the statistical program R 3.4.1 (R Development Core Team, 2017). We used generalized linear models (GLM) to examine the impacts of soil nitrogen quantity (N_m), soil nitrogen heterogeneity (N_{sd}), overstory basal area (BA), topographic position (TP), and stand age (SA) on understory cover, richness, and evenness. We used GLM separately for total understory species, shrubs only, and herbs only (total nine models). Initially, we fitted the model with all terms and all-way interactions. Then, we performed stepwise regression and compared the performance of AICs to select the most parsimonious models. The final model for the richness of the total understory, shrubs, and herbs took the form:

$$Y = \mu + N_m + N_{sd} + TP + BA + SA + SA \times TP + \varepsilon \quad (2)$$

and the final model for the cover and evenness of the total understory, shrubs, and herbs took the form :

$$Y = \mu + N_m + N_{sd} + TP + BA + SA + \varepsilon \quad (3)$$

where the response variable Y is understory cover, species richness or evenness, μ is the intercept term, N_m , N_{sd} , BA, and SA are continuous variables while TP is a categorical variable, ε is the error term. According to the fitted models, we implemented each GLM using the function “glm” with Poisson error distribution in the package “nlme” (Pinheiro et al., 2017). Following the GLM analyses, we graphically present the partial effects of N_m , N_{sd} , BA, and SA on understory cover, richness, and evenness across the three topographic positions based on the method described by Chen et al. (2016).

To examine the effects of N_m , N_{sd} , BA, TP, and SA on understory community composition, we conducted permutational multivariate

analysis of variance (PERMANOVA) tests (Anderson, 2001) separately for total understory species, shrubs, and herbs. In PERMANOVA, we used Bray-Curtis dissimilarity to quantify pairwise distances of the community composition data and used 999 permutations to determine statistical significance. The PERMANOVA was implemented by using the function “*adonis2*” in the package “*vegan*” (Oksanen et al., 2014). Subsequently, we visualized the variation in understory community composition using detrended correspondence analysis (DCA) (Hill and Gauch, 1980). The DCA ordinations were implemented using the function “*decorana*” in the package “*vegan*” with default settings. To further identify relationships between environmental variables and community composition, environmental variables were overlaid on the DCA ordination using the function “*ordisurf*” in the package “*vegan*”. We also tested the correlations between site scores on DCA axes and environmental variables to present whether the DCA axis represented some kind of a gradient of an environmental factor. Indicator species are often used to present the relationship between the species occurrence values from a set of sampled sites and the classification of the same sites into site groups (De Cáceres and Legendre, 2009). We conducted indicator species analyses using the function “*multipatt*” in the package “*vegan*” to identify the unique species associated with site groups through combining sites for each stand age and topographic position (18 site groups after combination). We simultaneously computed the values of specificity (i.e., the positive predictive value of the species as an indicator of a site group) and sensitivity (i.e., the probability of finding the species in sites belonging to the site group) corresponding with each indicator value (De Cáceres and Jansen, 2016).

3. Results

3.1. Understory vegetation cover

Eighteen shrub species and twenty-three herb species were observed in this study. The percentage cover of the understory (all species combined) was significantly impacted by the direct effects of topographic position, stand age, and soil nitrogen quantity and heterogeneity (p -value < 0.05; Table 2). Topographic position had the strongest effect, explaining 18.55% of total variation of vegetation cover. Total vegetation cover in the understory was higher at sites with

flat locations and south-facing slopes than sites with north-facing slopes (p -value < 0.05; Fig. 1A). Total understory vegetation cover increased significantly with soil nitrogen quantity across the three topographic positions (p -value < 0.05; Fig. 1D), decreased with soil nitrogen heterogeneity at the flat locations (p -value < 0.05; Fig. 1G), and increased with stand age at the south-facing slopes (p -value < 0.05; Fig. 1J). Surprisingly, we did not detect any significant effects of soil-nitrogen heterogeneity on total understory vegetation cover (Table 2).

Shrub cover was significantly affected by stand age, soil nitrogen quantity and heterogeneity, topographic position, and overstory basal area (p -value < 0.05; Table 2), of which, stand age had the strongest effect (25.58% of variance explained). There were no significant differences in shrub cover among the three topographic positions (p -value \geq 0.05; Fig. 1B). Shrub cover increased with soil nitrogen quantity at the north- and south-facing slopes (p -value < 0.05; Fig. 1E), decreased with soil nitrogen heterogeneity at the flat locations (p -value < 0.05; Fig. 1H), increased with stand age at the flat locations and south-facing slopes (p -value < 0.05; Fig. 1K), and increased with overstory basal area at the south-facing slopes (p -value < 0.05; Fig. 1N).

Herb cover was significantly affected by stand age, overstory basal area, and soil nitrogen quantity (p -value < 0.05; Table 2), of which, stand age had the strongest effect (24.80% of variance explained). There were no significant differences in herb cover among the three topographic positions (Fig. 1C). Herb cover decreased with increasing soil nitrogen quantity at the north-facing slopes (p -value < 0.05; Fig. 1F) and decreased with increasing overstory basal area at the north- and south-facing slopes (p -value < 0.05; Fig. 1O).

3.2. Understory species richness and evenness

Total species richness in the forest understory was significantly affected by the direct effects of topographic position and soil nitrogen quantity, and the interaction effect of stand age and topographic position (p -value < 0.05; Table 2). The interaction between stand age and topographic position had the strongest effect (12.07% of variance explained; Table 2). Total understory richness was higher at sites with flat locations and south-facing slopes than sites with north-facing slopes (p -value < 0.05; Fig. 2A). Total species richness in the understory

Table 2

The effects of soil nitrogen quantity (N_m), soil nitrogen heterogeneity (N_{sd}), stand age (SA), overstory basal area (BA), and topographic position (TP) on understory cover, species richness, evenness, and community composition, are summarized separately for shrubs, herbs, and all plant species. The percentage of variance explained by each factor (%) is shown. Significant results (p -value < 0.05) are highlighted in bold.

Attribute	Source	Df	All		Shrubs		Herbs	
			Variance explained (%)	p -value	Variance explained (%)	p -value	Variance explained (%)	p -value
Understory cover	N_m	1	7.48	0.005	10.30	< 0.001	4.89	0.023
	N_{sd}	1	4.03	0.038	4.20	< 0.017	1.40	0.223
	SA	1	6.77	0.007	25.58	< 0.001	24.80	< 0.001
	BA	1	0.57	0.436	4.41	0.019	5.54	0.015
	TP	2	18.55	< 0.001	5.90	0.015	0.12	0.939
Species richness	N_m	1	4.63	0.039	0.18	0.668	6.75	0.012
	N_{sd}	1	0.76	0.403	0.02	0.900	1.17	0.296
	SA	1	0.13	0.727	8.34	0.004	1.31	0.266
	BA	1	1.28	0.277	4.68	0.033	0.08	0.789
	TP	2	10.58	0.007	15.56	< 0.001	8.76	0.017
Species evenness	SA \times TP	2	12.07	0.004	4.60	0.106	12.49	0.003
	N_m	1	2.83	0.142	0.05	0.849	12.21	< 0.001
	N_{sd}	1	0.03	0.885	0.31	0.645	1.08	0.292
	SA	1	0.07	0.822	1.10	0.383	23.77	< 0.001
	BA	1	6.24	0.029	0.28	0.660	0.04	0.847
Community composition	TP	2	2.95	0.325	5.82	0.133	4.94	0.078
	N_m	1	6.07	0.002	5.33	0.018	1.85	0.195
	N_{sd}	1	0.90	0.429	0.78	0.035	0.96	0.687
	SA	1	11.45	0.001	6.31	0.001	10.46	0.001
	BA	1	9.29	0.001	5.03	0.001	12.22	0.001
	TP	2	11.23	0.001	16.10	0.001	5.23	0.026

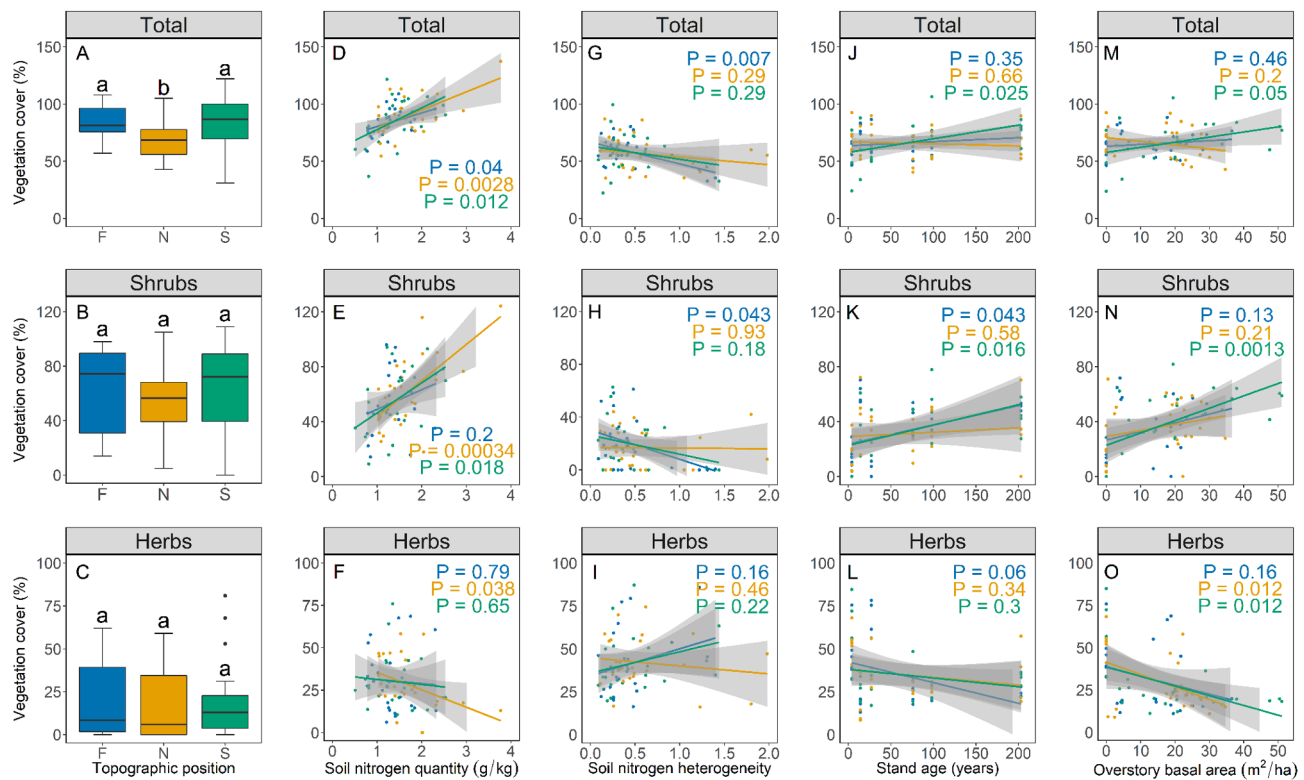


Fig. 1. Understory cover across flat location (F = blue), north-facing slope (N = orange), and south-facing slope (S = green) for all plant species (panel A), shrubs (panel B), and herbs (panel C), and the partial dependence of understory cover on soil nitrogen quantity (panels D, E, F), soil nitrogen heterogeneity (panels G, H, I), stand age (panels J, K, L), and overstory basal area (panels M, N, O) for total species, shrubs, and herbs across three topographic positions, respectively. Lowercase letters indicate significant differences of understory cover between topographic positions (p -value < 0.05). Each p -value corresponds to regression line for individual topographic position. Grey areas show 95% confidence intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

significantly decreased along with soil nitrogen quantity at the north-facing slopes (p -value < 0.05; Fig. 2D), decreased along with stand age (p -value < 0.05; Fig. 2J), and increased along with overstory basal area (p -value < 0.05; Fig. 2M) at the flat locations and south-facing slopes.

Shrub richness was significantly affected by topographic position, stand age, and overstory basal area (p -value < 0.05; Table 2), with topographic position having the strongest effect (15.56% of variance explained). Shrub richness was higher at sites with flat locations and south-facing slopes than sites with north-facing slopes (p -value < 0.05; Fig. 2B). Shrub richness significantly increased along with stand age at the north-facing slopes (p -value < 0.05; Fig. 2K) and increased along with overstory basal area at the flat locations and south-facing slopes (p -value < 0.05; Fig. 2N). Herb richness was significantly affected by soil nitrogen quantity, topographic position, and the interaction between stand age and topographic position (p -value < 0.05; Table 2). The interaction effect of stand age and topographic position had the strongest effect (12.49% of variance explained; Table 2). Herb richness was higher at sites with flat locations and south-facing slopes than sites with north-facing slopes (p -value < 0.05; Fig. 2C). Herb richness significantly increased along with soil nitrogen heterogeneity (p -value < 0.05; Fig. 2I) and overstory basal area (p -value < 0.05; Fig. 2O) at the flat locations, and decreased along with stand age (p -value < 0.05; Fig. 2L) at the flat locations.

Total species evenness was significantly affected by overstory basal area (6.24% of variance explained), and there were no significant differences in total species evenness among the three topographic positions (p -value ≥ 0.05; Fig. 3A). Total species evenness increased along with stand age at the north-facing slopes (p -value < 0.05; Fig. 3J) and decreased along with overstory basal area at the north- and south-facing slopes (p -value < 0.05; Fig. 3M). We failed to detect any

significant effect of stand age, soil nitrogen quantity and heterogeneity, topographic position, and overstory basal area on shrub evenness (p -value ≥ 0.05; Table 2). Stand age and soil nitrogen quantity had significant effects on herb evenness (p -value < 0.05; Table 2), of which, stand age had the strongest effect (23.77% of variance explained). There were no significant differences in herb species evenness among the three topographic positions (p -value ≥ 0.05; Fig. 3C). Herb evenness decreased along with soil nitrogen quantity at the north-facing slopes (p -value < 0.05; Fig. 3F) and decreased along with stand age at the flat locations and north-facing slopes (p -value < 0.05; Fig. 3L).

3.3. Understory community composition

Total understory community composition was most strongly affected by stand age, followed by topographic position, overstory basal area, and soil nitrogen quantity (p -value < 0.05; Table 2). When considering all species together, sites in 4- and 27-year age classes were separately grouped on the left and right of Axis 1 in ordination space, corresponding with lower levels of soil nitrogen quantity, soil nitrogen heterogeneity, and overstory basal area (Fig. 4). Older sites were grouped near the center of ordination space, with higher levels of soil nitrogen quantity, soil nitrogen heterogeneity, and overstory basal area (Fig. 4). The Axis 1 had a significant positive correlation with overstory basal area ($r = 0.60$, p -value < 0.05). The indicator species analysis indicated that younger sites had different overall community composition from older sites (Table 3). During boreal forest succession, overall community composition shifted from shade-intolerant species (indicator species such as *C. angustifolium*, *Carex schmidtii*) to shade-tolerant species (indicator species such as *R. dauricum*, *Vaccinium vitis-idaea*) (Table 3).

Community composition of shrubs was most strongly affected by

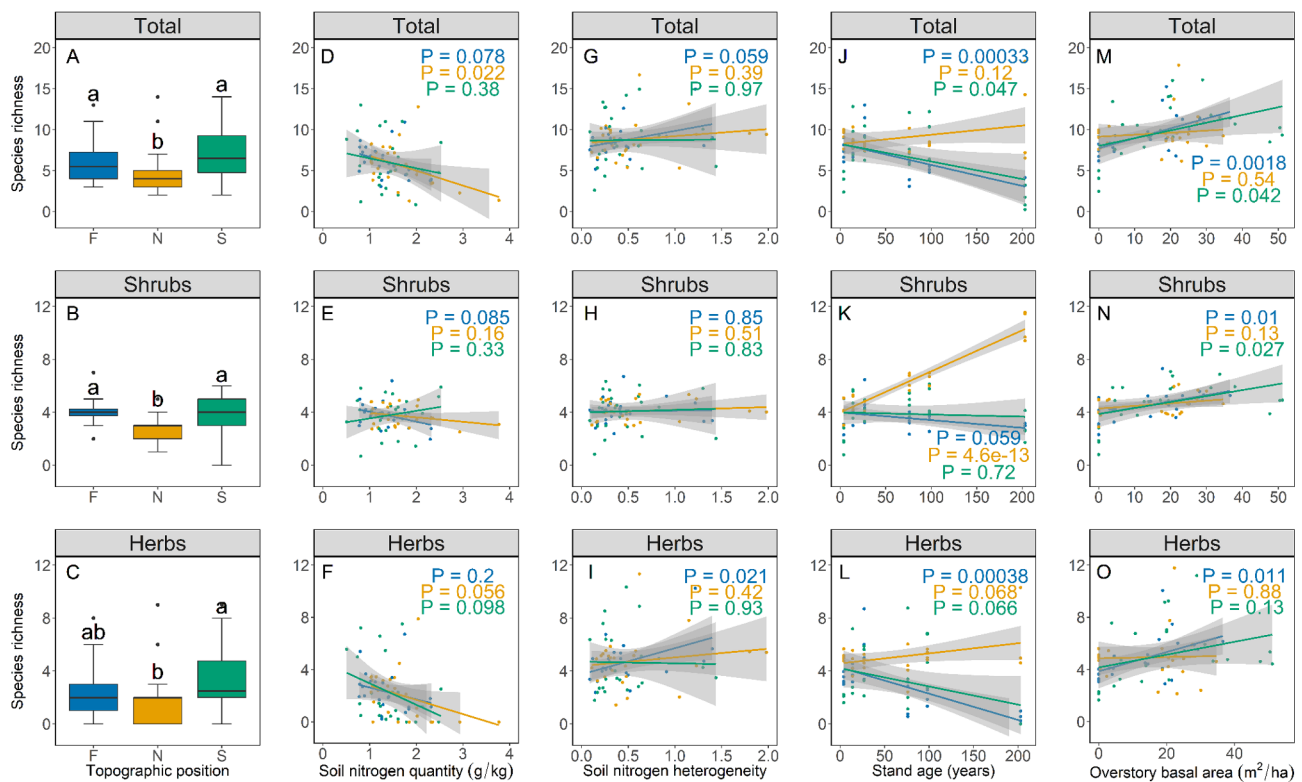


Fig. 2. Understory species richness across flat location (F = blue), north-facing slope (N = orange), and south-facing slope (S = green) for total species (panel A), shrubs (panel B), and herbs (panel C), and the partial dependence of understory species richness on soil nitrogen quantity (panels D, E, F), soil nitrogen heterogeneity (panels G, H, I), stand age (panels J, K, L), and overstory basal area (panels M, N, O) for all plant species, shrubs, and herbs across three topographic positions, respectively. Lowercase letters indicate significant differences of understory species cover between topographic positions (p -value < 0.05). Each p -value corresponds to regression line for individual topographic position. Grey areas show 95% confidence intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

topographic position, followed by stand age, overstory basal area, and soil nitrogen quantity and heterogeneity (p -value < 0.05; Table 2). Shrub communities in 4- and 27-year age classes clustered separately in ordination space at the top-right and bottom-right, possessing lower soil nitrogen quantity, soil nitrogen heterogeneity, and overstory basal area (Fig. 4). Older sites were grouped on the centroid, with greater levels of soil nitrogen quantity, soil nitrogen heterogeneity, and overstory basal area (Fig. 4). The Axis 1 and Axis 2 were negatively correlated with overstory basal area ($r = -0.40$ and -0.51 , p -value < 0.05). The indicator species analysis indicated that younger sites had a different composition of shrub species when compared to older sites (Table 3). The composition shifted from shade-intolerant shrubs (indicator species such as *Rubus sachalinensis*, *V. uliginosum*) to shade-tolerant shrubs (indicator species such as *L. palustre*, *R. dauricum*) during boreal forest succession (Table 3).

Community composition of herbs was most strongly affected by overstory basal area, stand age, and topographic position, in that order (p -value < 0.05; Table 2). Herb communities clustered separately in ordination space: sites from the 4- and 14-year age classes grouped on the left, while sites from the 27-year age class grouped on the right of Axis1. These three age classes were typified by low levels of soil nitrogen quantity, soil nitrogen heterogeneity, and overstory basal area (Fig. 4). The Axis 1 and Axis 2 were positively correlated with overstory basal area ($r = 0.67$ and 0.29 , p -value < 0.05). The indicator species analysis indicated that herb species typically dominated early successional communities with indicator species such as *C. angustifolium*, *C. schmidtii*, and *Fragaria orientalis* (Table 3).

4. Discussion

Throughout stand development, understory recovery is associated with a variety of factors, especially those related to soil nitrogen, overstory characteristics, and topography (Chipman and Johnson, 2002; Hart and Chen, 2008; Kumar et al., 2017; Liu et al., 2017). Our study is, to our knowledge, the first to simultaneously investigate these factors and their relative effects on understory cover, diversity, and composition through post-fire stand development in boreal forests. Specifically, we addressed the interaction effect between topographic position and stand age on understory recovery. Our results supported the idea that understory shrubs and herbs respond differently to these factors during post-fire understory recovery, which is consistent with previous studies (Hart and Chen, 2008; Azeria et al., 2011; Bartels and Chen, 2013; Kumar et al., 2017).

In boreal forests, soil nitrogen quantity is often a major limiting factor for plant growth (Näsholm et al., 2013). Our results supported the hypothesis that soil nitrogen quantity would have positive effects on the cover of total understory and shrubs but failed to support that soil nitrogen quantity would have positive effect on the cover of herbs. We found that, as quantities of soil nitrogen increased, shrub cover tended to increase while herb cover tended to decrease. Contrary to our hypothesis, we found that understory richness tended to decrease with increasing soil nitrogen quantity. We also found that the quantity of soil nitrogen had significant effects on composition of total understory and shrubs. It is possible that the nutrient-demanding shrub species possessed a competitive advantage for nitrogen absorption over herb

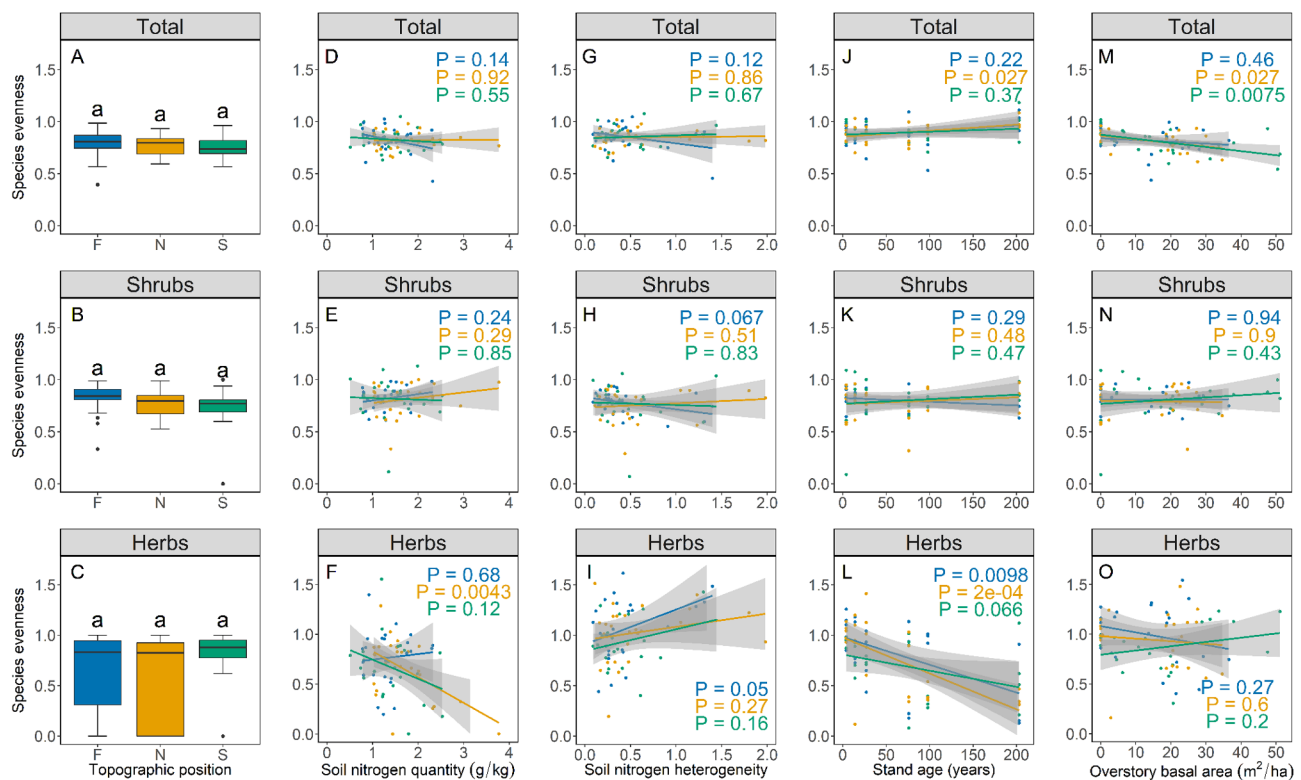


Fig. 3. Understory species evenness across flat location (F = blue), north-facing slope (N = orange), and south-facing slope (S = green) for total species (panel A), shrubs (panel B), and herbs (panel C), and the partial dependence of understory cover on soil nitrogen quantity (panels D, E, F), soil nitrogen heterogeneity (panels G, H, I), stand age (panels J, K, L), and overstory basal area (panels M, N, O) for all plant species, shrubs, and herbs across three topographic positions, respectively. Lowercase letters indicate significant differences of understory species evenness between topographic positions (p -value < 0.05). Each p -value corresponds to regression line for individual topographic position. Grey areas show 95% confidence intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

species, allowing for rapid recolonization and dominance of shrubs in the understory (Kumar et al., 2017). The understory vegetation of boreal forests is often dominated by ericaceous dwarf shrubs and dense carpets of feather mosses (Hart and Chen, 2006). Thus, the quantity of soil nitrogen fixed by the symbioses between cyanobacterial communities, ericaceous shrubs, and feather mosses will increase as the cover of ericaceous dwarf shrubs and feather mosses increase during boreal forest succession (Zackrisson et al., 2004; Bay et al., 2013). The distribution and abundance of ericaceous shrubs and feather mosses would affect the quantity of soil nitrogen, which in turn affects understory species distribution and cover (Bay et al., 2013). Contrary to our hypotheses, quantity and heterogeneity of soil nitrogen had little effect on understory species richness and evenness. This finding suggests that dominance of nitrogen-fixing shrubs may weaken the positive effect of soil nitrogen on understory diversity through interspecific competitive exclusion. Therefore, the increasing dominance of shrubs will intensify the interspecific competitive exclusion through increasing levels of soil nitrogen fixed by the symbioses between cyanobacterial communities and ericaceous shrubs (Hargrave et al., 2011).

Stand age was important in explaining the variance in understory cover, shrub richness, herb evenness, and understory composition. Similar to the previous studies (Kumar et al., 2017; Liu et al., 2017), we found that understory shrub cover increased while herb cover decreased as the stand ages. The total understory cover tended to increase with stand age, suggesting that a higher proportion of shrubs than herbs colonized study sites along with stand age after fire disturbance (Liu et al., 2017). Immediately after a stand-replacing disturbance,

abundant resources and growing space allow for rapid colonization and development of understory communities dominated by fast-growing, nutrient-demanding, and shade-intolerant herbaceous species (De Grandpré et al., 1993; Hart and Chen, 2006; Azeria et al., 2011). As the stand ages, the ecosystem gradually becomes light-limited as the canopy closes (Hart and Chen, 2006; Azeria et al., 2011) and shade-tolerant shrub species (i.e. *L. palustre*) eliminate shade-intolerant herb species (i.e. *C. angustifolium*) (Lavoie and Mack, 2012).

We found that topographic position was a key driver of understory cover, richness, and composition, which is similar to the findings of other studies (Chipman and Johnson, 2002; LaRade and Bork, 2011; Liu et al., 2017). In addition, there was a significant interaction effect between stand age and topographic position on understory species richness, showing understory richness would increase along with stand age at the north-facing slope. Different topographic positions create different levels of light availability and soil moisture on the forest floor, and then affect understory cover, richness, and composition (Gracia et al., 2007; Liu et al., 2017). In the northern hemisphere, south-facing slopes receive a greater amount of solar radiation, resulting in a relatively warmer and drier microclimate (Warren, 2008). This potentially benefits shade-intolerant species with high light requirements (Kumar et al., 2017). At flat locations and north-facing slopes, the understory is mainly composed of shade-tolerant and mesic-loving species (Gracia et al., 2007; Liu et al., 2017). Thus, the different tolerance levels possessed by plants for light and moisture availability may determine their presence or absence in habitats with different topography.

Overstory basal area had significant effects on shrub and herb cover,

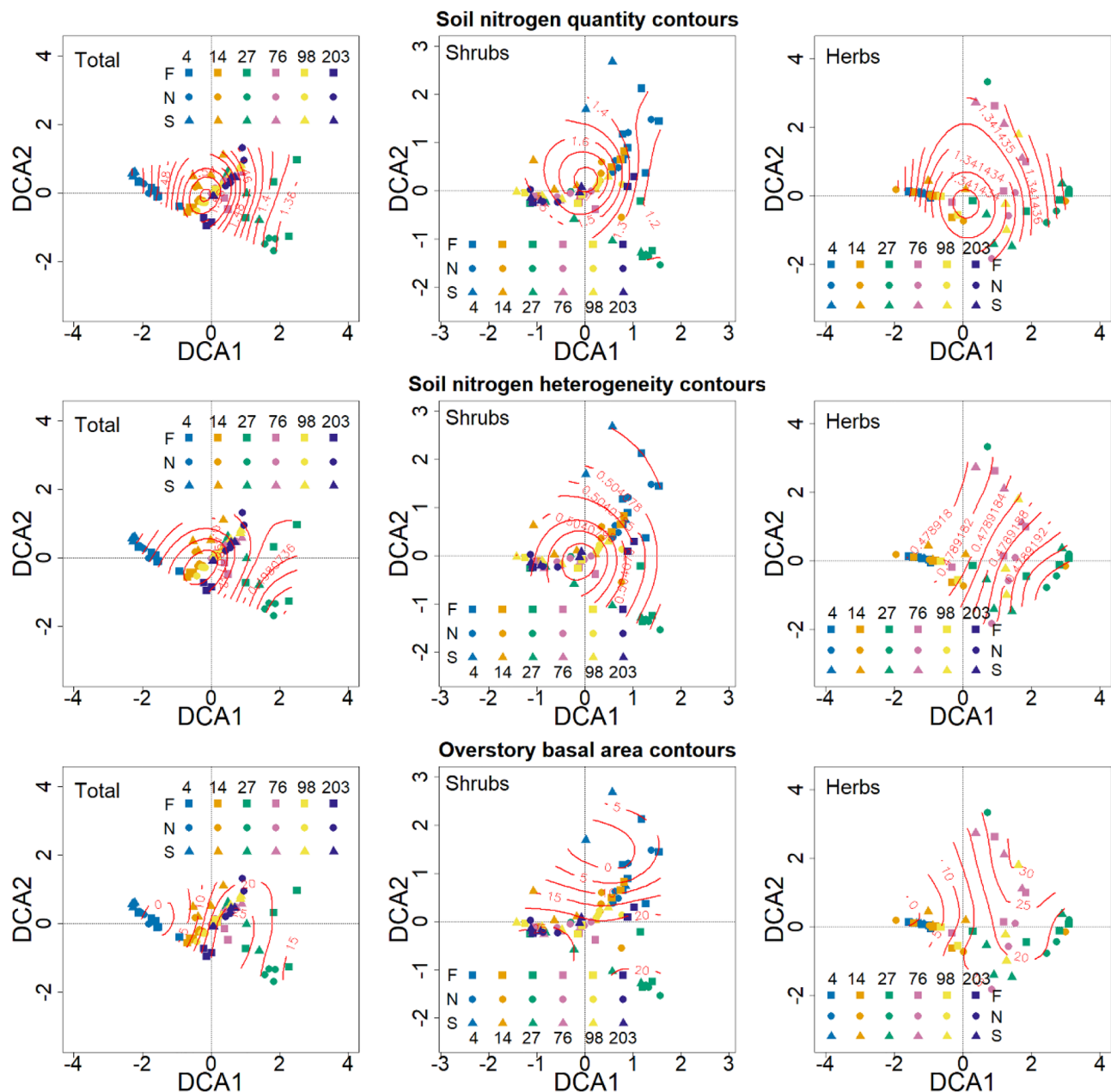


Fig. 4. Detrended correspondence analysis (DCA) for total species, shrubs, and herbs in different stand ages (SA) and topographic positions (TP). SA included 4 (blue), 14 (orange), 27 (green), 76 (pink), 98 (yellow), and 203 (purple). TP included flat location (F = square), north-facing slope (N = circle), and south-facing slope (S = triangle). In ordination space, sites nearest each other tend to have similar species composition, whereas those located farther apart are less similar. The red contours indicate isoclines for soil nitrogen quantity, soil nitrogen heterogeneity, and overstory basal area, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

shrub richness, total understory evenness, and understory composition. In boreal forests, wildfires can dramatically alter a site's light regime and microclimate by removing aboveground vegetation (Swanson et al., 2010). The open space and increased light availability promotes the colonization by herbaceous plants in the early successional stages (Hart and Chen, 2008). After that, the forest ecosystem will enter into a stage of overstory tree regeneration and the re-establishment of closed forest canopies. The development of the overstory after a disturbance exerts strong influences on the understory vegetation, substantially altering understory cover, species diversity, and composition (Halpern and Lutz, 2013). Overstory development, and its corresponding canopy closure, reduces light availability at the forest floor, leading to the replacement of shade-intolerant species by the shade-tolerant species (Bartemucci et al., 2006; Kumar et al., 2017). Development of the overstory also

influences the understory through resource competition for water and nutrients, which are essential to the understory (Barbier et al., 2008; Halpern and Lutz, 2013).

5. Conclusion

Our results demonstrate that multiple factors can determine understory recovery through influencing understory cover, richness, evenness, and composition as stands develop following fire disturbance in boreal forests. Our study highlights the importance of stand age, topographic position, overstory basal area, and soil nitrogen quantity in driving patterns of understory vegetation cover and composition after fire disturbance. We found soil nitrogen heterogeneity was a poor predictor of understory diversity and composition. Our results suggest

Table 3
Indicator species for stands of various ages and topographic positions.

Stand age	Topographic position	Indicator species	Life-form	Indicator value	Specificity	Sensitivity	p-value
4	Flat location	<i>Chamerion angustifolium</i>	Forb	0.573	0.328	1.000	0.001
4	North-facing slope	<i>Carex schmidtii</i>	Grass	0.574	0.329	1.000	0.001
14	Flat location	<i>Betula fruticosa</i>	Shrub	0.555	0.308	1.000	0.002
14	South-facing slope	<i>Rubus sachalinensis</i>	Shrub	0.496	0.246	1.000	0.033
27	Flat location	<i>Viola acuminata</i>	Forb	0.848	0.958	0.750	0.002
27	Flat location	<i>Fragaria orientalis</i>	Forb	0.779	0.607	1.000	0.001
27	Flat location	<i>Rubus arcticus</i>	Shrub	0.707	1.000	0.500	0.027
27	Flat location	<i>Salix pentandra</i>	Shrub	0.707	1.000	0.500	0.043
27	Flat location	<i>Vicia pseudo-orobus</i>	Forb	0.679	0.921	0.500	0.044
27	Flat location	<i>Salix raddeana</i>	Shrub	0.667	0.444	1.000	0.010
27	South-facing slope	<i>Ostericum maximowiczii</i>	Forb	0.669	0.447	1.000	0.004
27	North-facing slope	<i>Vaccinium uliginosum</i>	Shrub	0.704	0.496	1.000	0.001
76	Flat location	<i>Aquilegia oxysepala</i>	Forb	0.707	1.000	0.500	0.04
76	South-facing slope	<i>Linnaea borealis</i>	Shrub	0.802	0.857	0.750	0.001
76	South-facing slope	<i>Rhododendron dauricum</i>	Shrub	0.451	0.204	1.000	0.021
76	North-facing slope	<i>Pyrola asarifolia</i>	Forb	0.520	0.360	0.750	0.037
98	North-facing slope	<i>Ledum palustre</i>	Shrub	0.437	0.191	1.000	0.002

that levels of light and soil nitrogen resulting from different topographic positions and stand ages, exert profound effects on understory cover and composition during forest succession after wildfire.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRediT authorship contribution statement

Bo Liu: Conceptualization, Methodology, Investigation, Data curation, Formal analysis, Writing - original draft, Writing - review & editing. **Shekhar R. Biswas:** Conceptualization, Methodology, Formal analysis, Writing - review & editing. **Jian Yang:** Writing - review & editing. **Zhihua Liu:** Formal analysis, Writing - review & editing. **Hong S. He:** Writing - review & editing. **Yu Liang:** Writing - review & editing, Supervision, Funding acquisition. **Matthew K. Lau:** Formal analysis, Writing - review & editing. **Yunting Fang:** Writing - review & editing. **Shijie Han:** Writing - review & editing.

Acknowledgements

This study was funded by the National Key Research and Development Program of China (2016YFA0600804) and the National Natural Science Foundation of China (31800376, 31961133027, 31971486). S.R.B. was supported by a Zijiang Professorship start-up fund of East China Normal University (13903-120215-10407). M.K.L. was supported by the Chinese Academy of Sciences President's International Fellowship Initiative (PIFI, 2019PC0036). We thank Han Y.H. Chen for data analysis. We are grateful to the Huzhong Forestry Bureau and the Huzhong National Natural Reserve for their assistance in our field investigations, and Jianjian Kong, Lin Qi, Yuanzheng Yang, and Xiongxiang Bai for their help with the field work.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2020.118307>.

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