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Ecosystem Inventory

Pinus densiflora var. *ussuriensis* Forest Alliance

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Abstract

The *Pinus densiflora* var. *ussuriensis* forest is a unique pine forest type in Northeast China. The species grows normally under extremely adverse conditions because it has a strong tolerance to poor soils and drought. It also benefits the ecological environment significantly through water conservation, soil improvement and windbreak and sand fixation, thus making it an important pioneer species for improving site conditions. This paper systematically analyzes the geographical distribution, ecological and community characteristics, species composition and classification of *Pinus densiflora* var. *ussuriensis* forests in China through field surveys and literature review. The main findings are:

(1) Based on the dominant species of each layer, *Pinus densiflora* var. *ussuriensis* forests can be divided into two categories of associations: *Pinus densiflora* var. *ussuriensis* - *Rhododendron dauricum* - *Carex callitrichos* association and *Pinus densiflora* var. *ussuriensis* + *Quercus mongolica* - *Lespedeza bicolor* - *Carex caespitosa* association.

(2) According to sample plot surveys, a total of 134 vascular plant species, belonging to 59 families and 104 genera, were recorded in natural *Pinus densiflora* var. *ussuriensis* forests. Amongst them were one fern species, two gymnosperm species and 131 angiosperm species.

(3) The composition of life forms in *Pinus densiflora* var. *ussuriensis* forests is dominated by terrestrial herbs, with fewer woody plants and with vines making up the smallest proportion.

(4) The *Pinus densiflora* var. *ussuriensis* forests located on the hillocks of Xingkai Lake are in decline. If the soil in this area continues to increase in wetness, this community may eventually evolve into a broad-leaved mixed forest.

Keywords

Pinus densiflora var. *ussuriensis*, species diversity, community characteristics

Introduction

Northeast China has four vegetation regions, among which the area from Lesser Khingan Mountains to Changbai Mountains belongs to the temperate coniferous and broad-leaved mixed forest region (Wu 1980). This vegetation region is further divided into two vegetation zones: the northern Lesser Khingan-Wandashan Mountain Forest Zone and the southern Taipingling-Changbai Mountain Forest Zone (Zhou 1997). The zonal vegetation of the northern Lesser Khingan-Wandashan Mountain Forest Zone is broad-leaved mixed forest dominated by *Pinus koraiensis* (*Zhou 1997*).

Within the Lesser Khingan-Wandashan Mountain Forest Zone, there is a relatively special area: the Muling-Sanjiang Plain region. This region has low-lying terrain, abundant water systems and rich groundwater (Zhou 2011). Such geological conditions have resulted in distinct characteristics: due to frequent surface water accumulation, *Pinus koraiensis* broad-leaved forests cannot survive, thus resulting in large patches of grassland and swamp. The forested areas are small, with some deciduous broad-leaved forests dominated by *Quercus mongolica* distributed on hills and isolated mountains (Zhou 1997). Consequently, the species composition is relatively simple and there are about 900 species of vascular plants (Wang et al. 2022).

Another characteristic of this area is that, in the hillocks between the Xingkai Lakes and the low mountains and hills of the Muling River Basin, there are small patches of *Pinus densiflora* var. *ussuriensis* forests embedded in the deciduous broad-leaved forests (Zhou 1997). This is the only type of pine forest in this area and it plays important ecological functions in soil and water conservation.

Research on *Pinus densiflora* var. *ussuriensis* forests is limited. The earliest detailed description of its community characteristics is in Yiliang Zhou's book "Vegetation Geography of Northeast China" from the early 1890s (Zhou 1997) . Since then, research on *Pinus densiflora* var. *ussuriensis* forests has been relatively scattered, mainly focusing on floristic characteristics, forest management and conservation. In 1992, Chengyang Xu, Hong Li and Jing Zhang studied the impact of the ecological environment on the growth of natural *Pinus densiflora* var. *ussuriensis* forests. They explored the relationships between tree height, diameter at breast height and environmental factors (Xu et al. 1992). In 2000, Yue Zhang and others mainly studied the floristic characteristics of *Pinus densiflora* var. *ussuriensis* forests, finding that the proportion of floristic components was

highest in the northeast (Zhang et al. 2000). In 2012, Yuanfa Sun conducted a detailed survey of *Pinus densiflora* var. *ussuriensis* in Jidong County, Heilongjiang Province, counting its distribution range and population size (Sun 2012). Subsequently, Lei Jiao and Yu Zhang proposed conservation measures for *Pinus densiflora* var. *ussuriensis* in Jidong County (Jiao and Zhang 2013).

To date, research on the community structure of *Pinus densiflora* var. *ussuriensis* forests remains limited and attempts to classify its vegetation have reached no definitive conclusion. Therefore, it is urgently necessary to systematically analye the community structure, species composition and habitat conditions of *Pinus densiflora* var. *ussuriensis* forests to provide essential baseline data for in-depth future studies.

Materials and Methods

Overview of the study area

The natural distribution area of *Pinus densiflora* var. *ussuriensis* forests is narrow, with small patches only found along the shores of Xingkai Lake in Russia and in the south-eastern region of Heilongjiang Province, China, particularly around Xingkai Lake and the low mountain hills of the Muling River Basin (Zhou 1997).

The Xingkai Lake Nature Reserve is located in the south-eastern part of Mishan City, Jixi City, Heilongjiang Province. *Pinus densiflora* var. *ussuriensis* forests are mainly located on the large hillocks between the Great and Small Xingkai Lakes. These hillocks extend southeast from the north-western edge of the Great Lake, with geographical coordinates ranging from 131°58'30" to 133°07'30"E and 45°01'00" to 45°34'30"N. Due to the influence of the massive water body of Xingkai Lake, the region has a unique microclimate, characterized by a humid to semi-humid temperate continental monsoon climate. In spring, the melting lake water absorbs a large amount of heat, causing the temperature to be 1°C to 3°C lower than other areas at the same latitude. In autumn, the freezing lake water releases heat, delaying the frost-free period by about 15 days compared to inland areas at the same latitude. The annual average temperature is between 2.9°C and 3.1°C, with an annual average precipitation of 650-750 mm, about 70% of which occurs in summer. The prevailing wind in the spring and summer is from the southwest, with an annual average wind speed of 3.0-4.0 m/s and about 38 windy days per year. The area receives an average of 2574 hours of sunshine annually, with an active accumulated temperature of 2250°C and a frost-free period of 147 days. Winters in Xingkai Lake are extremely cold, with ice formation starting in November and leading to complete freezing of the lake surface within about 15 days. The ice thickness reaches 0.8-1.5 m and the thawing occurs in mid- to late April. In all, the lake remains frozen for about 150 days (Yang et al. 2020, Yang et al. 2021).

The distribution area in the Muling River Basin is mainly located in the low mountain hills of the middle and upper reaches of the Muling River. The river flows from the southwest, starting in Muling City and extends to Jixi City and other areas in the northeast, with *Pinus*

densiflora var. *ussuriensis* forests distributed intermittently throughout this region. This area also has a temperate continental monsoon climate. Spring is dry and windy, summer is mild and rainy, autumn has early frosts and winter is cold and dry. The average annual temperature ranges from 2.8°C to 4.9°C, with an annual evaporation ranging from 1251.1-1341.5 mm and an annual accumulated temperature ≥ 10°C ranging from 2490.7 to 2831.6°C. The average annual rainfall is about 509.4-517.3 mm and mostly is concentrated between June and September. The average relative humidity is 66%. The area receives 2280.8-2498.2 hours of sunshine annually, with a frost-free period of about 120 days(Xu et al. 1992, Jiao and Zhang 2013, Ji and Che 2014, Hou 2020).

Plot Survey

In the Great Hillock of Xingkai Lake, Heping Forest Farm in Jixi City and in Xinancha Forest Farm in Jidong County, 3 6 20 m × 20 m tree plots were established. Within each tree plot, a 5 m × 5 m subplot was established for shrubs and four 1 m × 1 m subplots were established for herbaceous plants at the corners of each shrub subplot.

In the tree plots, all woody plants with a height ≥ 5 m were numbered and measurements were taken for each tree, recording its height, diameter at breast height (DBH), height to the first branch and crown width. In the shrub subplots, all woody plants with a height < 5 m were numbered and, for each individual, the scientific name, number of individuals, cover, average height, basal diameter and crown width were recorded. In the herbaceous plots, the scientific names, abundance, cover and average height of all herbaceous species were recorded.

Table 1

Table 1.

Sample plot information.

Site number	Sample site	Aspect	Slope	Position on slope	Latitude (°N)	Longitude (°E)	Altitude (m)
S1	Mishan - Xingkai Lake Hukang	Southwest	15°	Upper slope	45.3466742	132.3069948	99.6
S2	Mishan - Xingkai Lake Hukang	Southwest	20°	Mid-slope	45.3486517	132.3097488	99.8
S3	Mishan - Xingkai Lake Hukang	Southwest	20°	Upper slope	45.2671735	132.7066088	99.8
S4	Mishan - Xingkai Lake Hukang	Southwest	15°	Upper slope	45.2755584	132.6909948	101.5
S5	Liuwangkou Tun, Xingkaihu Farm	Southwest	10°	Upper slope	45.2803	132.6913	92.80
S6	Liuwangkou Tun, Xingkaihu Farm	Southwest	10°	Upper slope	45.2696	132.7127	83.70

Site number	Sample site	Aspect	Slope	Position on slope	Latitude (°N)	Longitude (°E)	Altitude (m)
S7	South Fork Forest, Chicken East and West	Southwest	20°	Mid-slope	45.0181379	131.1118699	404.9
S8	South Fork Forest, Chicken East and West	South	35°	Upper slope	45.0250836	131.1221641	337.1
S9	South Fork Forest, Chicken East and West	South	45°	Mid-slope	45.0190816	131.1154875	310.8
S10	South Fork Forest, Chicken East and West	East	50°	Upper slope	44.9974858	131.0928815	413.5
S11	South Fork Forest, Chicken East and West	South	50°	Upper slope	45.0188718	131.1121523	435.8
S12	South Fork Forest, Chicken East and West	South	40°	Upper slope	45.0205656	131.1129329	459.8
S13	Jixi Heping Forest	South	35°	Mid-slope	45.4459644	130.9735044	428.8
S14	Jixi Heping Forest	Southwest	40°	Upper slope	45.4505443	130.9901770	454.5
S15	Jixi Heping Forest	Southwest	50°	Lower slope	45.4147683	130.9575652	325.7
S16	Jixi Heping Forest	Southwest	60°	Mid-slope	45.4150583	130.9562751	328.8
S17	Jixi Heping Forest	Southwest	35°	Mid-slope	45.4275936	130.9750248	341.7

Data Analysis

Verification of Scientific Names

All species present in *Pinus densiflora* var. *ussuriensis* forest plots and census surveys were verified according to the "Flora of China" (Chinese Academy of Sciences Flora of China Editorial Committee 2019) (http://www.iplant.cn/foc) (Flora of China Editorial Committee 2024). This resulted in our final species list for *Pinus densiflora* var. *ussuriensis* forests.

Calculation of Importance Values

The importance values for each layer's species were calculated, based on the plot data records using the following formulae:

Importance Value for Tree Layer = (Relative Density + Relative Basal Area at Breast Height + Relative Height) / 3

Importance Value for Shrub and Herbaceous Layers = (Relative Density + Relative Cover + Relative Height) / 3

Classification and Naming of Associations

Quantitative classification was performed using the JUICE programme (Tichý and Jason 2006). The results of the quantitative classification were corrected, based on literature, references and expert experience to determine a reasonable classification scheme. Associations were named using the scientific names of the species with the highest importance value in each layer, following the principles of the revised scheme of the Chinese vegetation classification system (Guo et al. 2020).

Results and Analysis

Species Composition

This survey combined plot survey and reconnaissance methods, resulting in the identification of 134 vascular plant species belonging to 104 genera and 59 families (Suppl. material 1). Amongst them were one fern species from one genus and one family, two gymnosperm species from two genera and two families and 131 angiosperm species from 101 genera and 56 families.

Table 2

Table 2.

Species Composition of *Pinus densiflora* var. *ussuriensis* forest.

	Number of Families	Number of Genera	Number of Species
Ferns	1	1	1
Gymnosperms	2	2	2
Angiosperms	52	99	130

In descending order of species abundance, the families with the most species were: Asteraceae 11 genera, 18 species, Rosaceae 9 genera, 12 species, Fabaceae 6 genera, 9 species, Lamiaceae 5 genera, 5 species, Caryophyllaceae 4 genera, 5 species, Poaceae 3 genera, 5 species, Apiaceae 4 genera, 4 species, Campanulaceae 2 genera, 4 species, Cyperaceae 2 genera, 4 species, Violaceae 1 genus, 4 species, Crassulaceae 3 genera, 3 species, Ranunculaceae 3 genera, 3 species, Rubiaceae 2 genera, 3 species, Caprifoliaceae 2 genera, 3 species, Asparagaceae 2 genera, 3 species, Rhamnaceae 1 genus, 3 species, Ericaceae 2 genera, 2 species, Betulaceae 2 genera, 2 species, Berberidaceae 2 genera, 2 species, Amaryllidaceae 1 genus, 2 species, Celastraceae 1 genus, 2 species and Iridaceae 1 genus, 2 species. Additionally, there were 33 families containing only one genus and one species each.

The dominant families with the highest proportions of species were as follows: Asteraceae 13.53%, Rosaceae 9.02%, Fabaceae 6.77%, Lamiaceae, Poaceae and Caryophyllaceae each 3.76%, Apiaceae, Campanulaceae, Cyperaceae and Violaceae each 3.01%.

In descending order of species abundance, the genera with the most species were: *Artemisia* eight species, *Viola* four species, *Adenophora*, *Rhamnus*, *Carex* and *Vicia* each with three species. There were 12 genera each containing two species: *Patrinia*, *Allium*, *Setaria*, *Lespedeza*, *Polygonatum*, *Galium*, *Prunus*, *Potentilla*, *Euonymus*, *Deyeuxia*, *Silene* and *Iris*. There were 85 genera containing only one species each. The dominant genera were as follows: *Artemisia* 6.02%, *Viola* 3.01%, *Adenophora*, *Rhamnus*, *Carex* and *Vicia* each with 2.26%.

Table 3

Table 3.
Number of genera and species in each family.

Family	No. of genera	No. of species
Asteraceae	11	18
Rosaceae	9	12
Fabaceae	6	9
Lamiaceae	5	5
Apiaceae	4	4
Caryophyllaceae	4	5
Crassulaceae	3	3
Ranunculaceae	3	3
Poaceae	3	5
Ericaceae	2	2
Betulaceae	2	2
Berberidaceae	2	2
Rubiaceae	2	3
Caprifoliaceae	2	3
Asparagaceae	2	3
Campanulaceae	2	4
Cyperaceae	2	4
Liliaceae	1	1
Cupressaceae	1	1
Plantaginaceae	1	1
Euphorbiaceae	1	1
Menispermaceae	1	1
Cucurbitaceae	1	1
Polemoniaceae	1	1
Apocynaceae	1	1
Gracilariaceae	1	1

Family	No. of genera	No. of species
Malvaceae	1	1
Fagaceae	1	1
Orchidaceae	1	1
Orobanchaceae	1	1
Onagraceae	1	1
Geraniaceae	1	1
Oleaceae	1	1
Vitaceae	1	1
Solanaceae	1	1
Paeoniaceae	1	1
Brassicaceae	1	1
Dioscoreaceae	1	1
Pinaceae	1	1
Phrymaceae	1	1
Dennstaedtiaceae	1	1
Sapindaceae	1	1
Araliaceae	1	1
Amaranthaceae	1	1
Urticaceae	1	1
Commelinaceae	1	1
Salicaceae	1	1
Papaveraceae	1	1
Ulmaceae	1	1
Polygalaceae	1	1
Amaryllidaceae	1	2
Celastraceae	1	2
Iridaceae	1	2
Rhamnaceae	1	3
Violaceae	1	4

Life Form Composition

In the *Pinus densiflora* var. *ussuriensis* forest, terrestrial herbaceous plants are the most abundant, accounting for nearly 80% of the total. Amongst terrestrial herbaceous plants, erect forbs comprised the highest proportion, making up about 40% of the total species and more than 50% of the herbaceous plants. Rhizomatous plants are next, accounting for approximately 15% of the total species and about 20% of the herbaceous plants.

Succulent plants and ferns had the lowest proportions, each accounting for only about 1% of the total.

Woody plants in the *Pinus densiflora* var. *ussuriensis* forest made up about 20% of the total. The only evergreen tree species was *Pinus densiflora* var. *ussuriensis*. Deciduous shrubs comprised the highest proportion amongst woody plants, accounting for about 15% of the total species. Deciduous trees accounted for about 6% of the total. Vines had the lowest proportion, making up less than 1% of the total.

Table 4

Table 4.

Life type spectrum (%) of 134 species of plants in *Pinus densiflora* var. *ussuriensis* forests.

Woody plant	Tree				Dioecious	Vine
	Ever-green	Deciduous			Deciduous	Deciduous
22.54	0.70	6.34			14.79	0.70
Terrestrial herb	Perennial herb					Pteridophytes
	Rootstock	Upright miscellaneous	Trailing and climbing	Lotus seat	Succulent	Parasitic
77.46	15.49	42.25	11.97	4.93	1.41	1.41

Association Classification

Based on the JUICE programme classification results, *Pinus densiflora* var. *ussuriensis* forests can be divided into two categories of associations. The association categories are named according to the species with the highest importance values in each layer. The specific results are as follows:

Table 5

Table 5.

List of *Pinus densiflora* var. *ussuriensis* forest associations

Association	Vegetation Types	Number of voucher plots
Pinus densiflora var. *ussuriensis* + *Quercus mongolica* - *Lespedeza bicolor* - *Carex caespitosa* association	Evergreen coniferous forest	6
Pinus densiflora var. *ussuriensis* - *Rhododendron dauricum* - *Carex callitrichos* association		11

Pinus densiflora var. *ussuriensis* + *Quercus mongolica* - *Lespedeza bicolor* - *Carex caespitosa* association

Forest of this association is distributed on the hillocks between the Great and Small Xingkai Lakes at an altitude of 80-100 m. It typically grows on sunny lake-facing slopes with a gradient of about 10°-20°. The vertical structure of the community is distinct, exhibiting the typical appearance of a coniferous forest. It can be divided into four layers: tree layer, sub-tree layer, shrub layer and herbaceous layer. The tree layer has a cover of about 70%, with a diameter at breast height (DBH) of 15 (3-37) cm and a height of 13 (5-17) m. It can be divided into two sub-layers: the dominant species in the large tree sub-layer is *Pinus densiflora* var. *ussuriensis*, occasionally mixed with broad-leaved tree species such as *Populus davidiana* and *Acer pictum*, all of which have an average height of about 14 m. The sub-tree layer is mainly composed of *Quercus mongolica*, with occasional *Acer truncatum* and *Acer pictum* mixed in.

The shrub layer is relatively sparse, with about 30% cover and an average height of around 1 m. The main species include *Quercus mongolica* in shrub form, *Lespedeza bicolor*, *Rhamnus davurica*, *Prunus padus*, *Eleutherococcus senticosus*, *Lonicera praeflorens*, *Lonicera chrysantha*, *Sophora flavescens*, *Corylus heterophylla* and saplings of *Pinus densiflora* var. *ussuriensis*, *Acer truncatum* and *Acer pictum. Juniperus davurica* is occasionally found in clusters.

The herbaceous layer is sparse, with about 30% cover and an average height of about 50 cm. It is mainly composed of drought-tolerant herbaceous plants, commonly including *Carex rigescens*, *Deyeuxia angustifolia*, *Polygonatum odoratum*, *Artemisia gmelinii*, *Carex lanceolata*, *Carex breviculmis*, *Viola dissecta* and *Maianthemum bifolium*, with occasional occurrences of *Vicia amoena*, *Campanula punctata* and *Artemisia dracunculus*. In densely shaded areas, herbaceous plants that prefer moist environments, like *Viola selkirkii*, *Patrinia scabiosifolia* and *Stellaria longifolia*, can be found. At the forest edge, plants like *Sedum aizoon*, *Leontodon hispidus* and *Urtica angustifolia* are common, while invasive species like *Oenothera biennis* and *Chenopodium album* can be found near roads.

The vines *Vitis amurensis*, *Thladiantha dubia* and *Dioscorea nipponica* are also sparsely distributed within the forest across the herbaceous and shrub layers, adding complexity to the community structure.

Tables 6, 7 Table 8

Pinus densiflora var. *ussuriensis* - *Rhododendron dauricum* - *Carex callitrichos* association

Forest of this association is distributed in the low mountain hills of the middle and upper reaches of the Muling River Basin, at slopes of about 40°-60° and an altitude of 300-600 m. In the sunny, dry and barren stony dark brown soils of the mid-upper slopes of this

area, there are large areas of pure *Pinus densiflora* var. *ussuriensis* forest. This is a typical high-altitude distribution area for *Pinus densiflora* var. *ussuriensis* forest.

Table 6.

Characterisation of the number of tree layers in the *Pinus densiflora* var. *ussuriensis* + *Quercus mongolica* - *Lespedeza bicolor* - *Carex caespitosa* association.

Serial number	Scientific name	Frequency	Density (plants/600 m^2)	Diameter at breast height (cm)	Tree height (m)	Breast height section area (cm^2/600 m^2)	Significant value (%)
1	*Pinus densiflora* var. *ussuriensis*	6	70.3	18.2	14.7	34935.1	63.5
2	*Quercus mongolica*	4	8.8	18.1	16.0	2570.7	11.9
4	*Tilia amurensis*	1	1.5	18.1	17.5	440.2	7.7
5	*Acer tegmentosum*	1	2.0	18.8	14.0	733.1	6.8
6	*Populus davidiana*	2	1.3	10.9	15.6	121.8	6.6
7	*Acer pictum*	1	0.5	8.8	8.5	35.8	3.5

Table 7.

Characterisation of the number of shrub layers in the *Pinus densiflora* var. *ussuriensis* + *Quercus mongolica* - *Lespedeza bicolor* - *Carex caespitosa* association.

Serial number	Scientific name	Frequency	Density (plants/100 m^2)	Coverage (%)	Basal diameter (cm)	Height (cm)	Significant value (%)
1	*Quercus mongolica*	2	46.5	7.0	1.5	89.0	13.6
3	*Lespedeza bicolor*	4	23.5	10.4	0.6	76.8	10.6
4	*Prunus padus*	1	1.0	1.0	2.0	185.0	8.4
5	*Acer tegmentosum*	1	3.5	5.0	1.3	290.0	7.8
2	*Rhamnus arguta*	1	0.5	10.0	2.7	178.0	7.7
7	*Eleutherococcus sessiliflorus*	3	8.0	8.0	1.1	92.7	6.8
6	*Pinus densiflora* var. *ussuriensis*	1	12.0	5.6	1.9	107.5	6.7
8	*Euonymus verrucosus*	2	17.5	2.8	0.7	102.3	6.4
9	*Acer pictum*	2	17.0	1.7	0.9	116.0	6.0
10	*Lonicera praeflorens*	1	13.5	5.0	0.2	41.0	5.6
11	*Lespedeza juncea*	1	13.0	5.0	0.1	44.0	5.5
12	*Tilia amurensis*	1	0.5	0.5	2.7	210.0	3.8
13	*Lonicera chrysantha*	1	1.0	2.0	1.3	140.0	3.5
14	*Prunus tomentosa*	1	7.5	2.0	0.4	55.0	3.3

Serial number	Scientific name	Frequency	Density (plants/100 m ^{2})	Coverage (%)	Basal diameter (cm)	Height (cm)	Significant value (%)
15	*Rhamnus schneideri* var. *manshurica*	2	1.0	2.5	1.0	99.0	3.0
16	*Rhamnus ussuriensis*	1	3.0	2.0	0.4	71.0	2.7
17	*Berberis amurensis*	2	2.0	1.0	0.2	61.0	1.9
18	*Sophora flavescens*	1	3.0	1.0	0.1	35.0	1.6

Table 8.

Characterisation of the number of herbaceous layers in the *Pinus densiflora* var. *ussuriensis* + *Quercus mongolica* - *Lespedeza bicolor* - *Carex caespitosa* association

Number	Scientific name	Frequency	Density (plants/ 100 m^2)	Coverage (%)	Height (cm)	Importance Value (%)
1	*Carex callitrichos*	11	56.50	29.74	21.00	12.45
2	*Iris uniflora*	7	71.00	2.80	31.00	10.20
3	*Spodiopogon sibiricus*	6	33.00	27.70	42.00	10.16
4	*Artemisia argyi*	4	34.00	18.88	21.00	7.99
5	*Artemisia vestita*	3	9.00	21.20	57.00	6.84
6	*Deyeuxia pyramidalis*	2	9.00	12.00	75.00	6.07
7	*Carex cespitosa*	1	1.00	28.50	32.00	6.06
8	*Galium maximoviczii*	3	34.00	1.00	27.00	5.32
9	*Gypsophila pacifica*	3	9.00	8.20	63.00	4.97
10	*Patrinia rupestris*	1	3.00	1.80	70.00	3.49
11	*Atractylodes lancea*	2	3.00	12.90	23.00	3.39
12	*Potentilla fragarioides*	2	3.00	13.50	19.00	3.33
13	*Artemisia stolonifera*	1	1.00	6.00	50.00	3.12
14	*Artemisia lavandulifolia*	1	1.00	3.00	62.00	3.12
15	*Adenophora pereskiifolia*	1	1.00	1.20	57.00	2.63
16	*Iris ruthenica*	1	3.00	1.80	34.00	2.03
17	*Neottianthe cucullata*	1	1.00	1.20	37.00	1.82
18	*Allium flavum*	1	1.00	1.20	37.00	1.82
19	*Polygala tenuifolia*	1	1.00	2.00	26.00	1.50
20	*Orostachys spinosa*	1	1.00	6.00	6.00	1.34
21	*Viola dactyloides*	1	1.41	1.47	19.00	1.18
22	*Saposhnikovia divaricata*	1	1.00	1.40	7.00	0.63
23	*Pyrola asarifolia* subsp. *incarnata*	1	1.00	1.20	6.00	0.56

The vertical structure of the community is distinct and can be divided into four layers: large tree layer, small tree layer, shrub layer and herbaceous layer.

The tree layer can be divided into two sub-layers. The large tree layer is uniform and almost entirely composed of *Pinus densiflora* var. *ussuriensis*, with about 70% cover, a DBH of 13 (1-60) cm and a height of 10 (5-17) m. Occasionally, straight-trunked *Quercus mongolica* and rarely *Ulmus* trees are found. The small tree layer is mainly composed of poorly growing, multi-branched *Quercus mongolica*, with an average height of about 6 m.

The shrub layer is sparse with low species richness, a cover of about 20% and an average height of less than 1 m. It mainly consists of drought-tolerant deciduous shrubs, such as *Rhododendron dauricum*, *Lespedeza bicolor*, *Sophora koreensis* and *Spiraea salicifolia*, with occasional *Robinia pseudoacacia*, *Corylus* and seedlings of broad-leaved trees like *Betula platyphylla* and *Tilia amurensis*.

The herbaceous layer is sparse with low species richness, only about 15% cover and an average height of about 30 cm. The main appearance of the herbaceous layer is composed of drought-tolerant plants from the genera *Carex* and *Iris*. Common species include *Brachypodium sylvaticum*, *Iris ruthenica*, *Elymus dahuricus*, *Glyceria leptolepis*, *Artemisia*, *Saussurea*, and *Scabiosa tschiliensis*. Occasionally, *Sedum aizoon*, *Adenophora triphylla*, *Rhododendron anthopogonoides*, *Umbilicaria esculenta* and *Umbilicaria orientalis* are found. In *Pinus densiflora* var. *ussuriensis* forests near farmland and villages, invasive species like *Senecio vulgaris* and *Erigeron annuus* can be seen. No interlayer plants are observed in forest of this latter association.

Tables 9, 10, 11

Table 9.

Characterisation of the number of tree layers in the *Pinus densiflora* var. *ussuriensis* - *Rhododendron dauricum* - *Carex callitrichos* association.

Serial numbe	Scientific name	Frequency	Density (plants/600 m^2)	Diameter at breast height (cm)	Tree height (m)	Breast height section area (cm^2/600 m^2)	Significant value (%)
1	*Pinus densiflora* var. *ussuriensis*	11	54.8	17.7	10.4	18108.6	75.1
2	*Quercus mongolica*	9	9.8	8.9	6.5	748.5	15.7
3	*Ulmus pumila*	1	0.1	19.0	6.3	38.6	9.2

Discussion

The two associations of *Pinus densiflora* var. *ussuriensis* forest exhibit different vegetation dynamics and succession characteristics due to varying environmental conditions and to having been subjected to different disturbances.

Table 10.

Characterisation of the number of shrub layers in the *Pinus densiflora* var. *ussuriensis* - *Rhododendron dauricum* - *Carex callitrichos* association.

Serial number	Scientific name	Frequency	Density (plants/100 m^2)	Coverage (%)	Basal diameter (cm)	Height (cm)	Significant value (%)
1	*Rhododendron dauricum*	4	29.5	42.5	0.3	77.3	33.0
2	*Quercus mongolica*	2	7.6	37.5	269.5	245.0	31.0
3	*Lespedeza bicolor*	10	13.1	11.4	0.4	74.7	26.4
4	*Maackia amurensis*	1	3.3	15.0	0.1	46.0	9.0
5	*Lespedeza juncea*	2	6.5	6.5	0.1	25.0	7.1
6	*Corylus heterophylla*	1	0.4	10.0	0.2	25.0	4.6

Table 11.

Characterisation of the number of herbaceous layers in the *Pinus densiflora* var. *ussuriensis* - *Rhododendron dauricum* - *Carex callitrichos* association.

Serial number	Scientific name	Frequency	Density (plants/ m^2)	Coverage (%)	Height (cm)	Significant value (%)
1	*Carex callitrichos*	11	34.9	14.3	26.2	27.0
2	*Carex cespitosa*	1	1.4	40.0	32.0	11.5
3	*Iris uniflora*	7	4.4	6.9	31.3	5.7
4	*Spodiopogon sibiricus*	6	3.3	6.3	41.8	5.3
5	*Artemisia vestita*	3	0.5	7.2	57.4	4.3
6	*Deyeuxia pyramidalis*	2	0.5	3.5	74.5	4.2
7	*Gypsophila pacifica*	3	0.5	4.7	62.7	4.0
8	*Patrinia rupestris*	1	0.2	3.0	70.0	3.6
9	*Atractylodes lancea*	2	0.2	11.0	22.5	3.6
10	*Potentilla fragarioides*	2	0.2	11.5	19.0	3.6
11	*Galium maximoviczii*	3	2.1	4.4	26.8	3.5
12	*Artemisia lavandulifolia*	1	0.1	3.0	62.0	3.3
13	*Artemisia argyi*	4	2.1	3.6	21.2	3.0
14	*Adenophora pereskiifolia*	1	0.1	2.0	57.0	2.8
15	*Viola dactyloides*	1	0.3	8.0	19.0	2.8
16	*Artemisia stolonifera*	1	0.1	1.0	50.0	2.3
17	*Iris ruthenica*	1	0.2	3.0	34.0	2.2

Serial number	Scientific name	Frequency	Density (plants/ m^2)	Coverage (%)	Height (cm)	Significant value (%)
18	*Neottianthe cucullata*	1	0.1	2.0	37.0	2.0
19	*Allium flavum*	1	0.1	2.0	37.0	2.0
20	*Polygala tenuifolia*	1	0.1	2.0	26.0	1.6
21	*Pyrola asarifolia* subsp. *incarnata*	1	0.1	2.0	6.0	0.8
22	*Saposhnikovia divaricata*	1	0.1	1.0	7.0	0.6
23	*Orostachys spinosa*	1	0.1	1.0	6.0	0.5

Forest of the *Pinus densiflora* var. *ussuriensis* + *Quercus mongolica* - *Lespedeza bicolor* - *Carex caespitosa* association is located on the Great Hillock between the Great and Small Xingkai Lakes. This area has relatively high soil moisture and a thick humus layer, which results in a more complex stand structure and higher species richness, with about 102 species of vascular plants. The number and abundance of accompanying broad-leaved tree species in the tree layer are relatively high and they include *Quercus mongolica*, *Populus davidiana* and *Tilia amurensis*. The shrub layer is rich in species, with a notable presence of *Lespedeza* and *Rhamnus*. Additionally, vines such as *Vitis amurensis* are distributed within the forest. This area has a very small coverage of *Pinus densiflora* var. *ussuriensis* forest, with a low proportion of saplings and small-diameter individuals. The main disturbances affecting this association are:

(1) Changes in Soil Conditions: There are four hillocks on the northern shore of Xingkai Lake, in chronological order of their formation, Huanggang, Erdaogang, Taiyanggang and Dahuogang, with soil compositions transitioning from reddish-brown clay loam, yellow-brown sandy clay and sandy loam, light yellow clayey fine sand, to yellow-white fine sand (Hu 2001). This indicates that Dahuogang may be in the process of transitioning from arid, barren fine sand to more moister fertile clay loam. A few broad-leaved trees that prefer moist habitats, such as *Populus davidiana*, *Tilia amurensis* and *Acer pictum*, have invaded the edges of the *Pinus densiflora* var. *ussuriensis* forest. These invading broad-leaved trees generally have small diameters, low heights and are young in years. If soil moisture in this area continues to increase, it will be more conducive to the establishment and growth of broad-leaved trees, potentially altering the forest composition.

(2) Bank Collapse: The low-altitude *Pinus densiflora* var. *ussuriensis* forest is concentrated on the Great Hillock between the Great and Small Xingkai Lakes. The vast lake surface experiences strong winds and high waves, particularly from the southwest during spring and summer, with an average annual wind speed of 3-4 m/s. The lake winds accumulate sand and gravel on to the shore, forming the hillocks through aeolian processes. Over the past 30 years, the water level of Xingkai Lake has been rising, with significant changes in the extent of inundation, reducing the width of the narrowest part of the hillocks by nearly 50%. Many collapses have occurred on the hillocks (Yu et al. 2006),

frequently causing *Pinus densiflora* var. *ussuriensis* trees to fall, which severely damages the vegetation.

（3）Human Disturbance: The "Regulations on the Hillocks of the Heilongjiang Xingkai Lake National Nature Reserve" were implemented in 2011. Prior to the publication of these regulations, intense activities such as soil excavation, land use and road construction in the surrounding areas had already caused considerable damage to the *Pinus densiflora* var. *ussuriensis* forest on the hillocks (Jixi Daily 2011).

Particularly, both soil conditions and living environments had undergone stable and irreversible damage. Soil moisture in the area will continue to increase, leading to a gradual reduction in the *Pinus densiflora* var. *ussuriensis* forest area and the current area may eventually transition into broad-leaved mixed forest. In summary, this association is currently in decline. Therefore, it is essential to promptly preserve germplasm resources, strengthen breeding technology research, establish seed orchards and nurseries and actively implement ex-situ conservation measures.

In contrast, forest of the *Pinus densiflora* var. *ussuriensis* - *Rhododendron dauricum* - *Carex callitrichos* association, located in the middle and upper reaches of the Muling River Basin, is relatively stable. Forest of this association is primarily distributed on sunny slopes with high light intensity and dry, barren soil. The forest area is significantly larger, with a high proportion of saplings and small-diameter individuals. The stand structure is simple, with a distinct vertical structure. Species composition is straightforward, with only 74 species of vascular plants. The tree layer is almost entirely composed of *Pinus densiflora* var. *ussuriensis*. The shrub and herbaceous layers are extremely sparse and no vines are present.

This region is far from farmland and villages, meaning it has faced minimal human disturbance. The *Pinus densiflora* var. *ussuriensis* forest is sparse, with good light conditions and dry soil. The proportion of seedlings and saplings in the forest is as high as 40%, growing well without hindrance to self-renewal. Considering the local climate characteristics and the physical and chemical properties of the soil, forest of the *Pinus densiflora* var. *ussuriensis* - *Rhododendron dauricum* - *Carex callitrichos* association should be regarded as the climax vegetation of this area. The community is stable, with good natural regeneration. Dynamic monitoring should be conducted to formulate scientific conservation measures and rational utilisation plans for the *Pinus densiflora* var. *ussuriensis* forest moving forward.

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Conflicts of interest

The authors have declared that no competing interests exist.

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Supplementary material

Suppl. material 1: *Pinus densiflora* var. *ussuriensis* species list doi

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