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RESEARCH PAPER

Vascular plants in the Trans-Siberian Railway within the Amur Region

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ABSTRACT

A comprehensive analysis of data on local floras of 16 railroad stations in the Amur section of the Trans-Siberian Railway (within the Amur Region) is presented: taxonomic and biomorphological structure, dynamics of numbers of native and alien species of vascular plants since 1911, and effects of natural biomes and socio-economic parameters on "railway flora". A comparative analysis of the native fraction and alien fraction of flora was carried out in the Amur section and Ussuriysk section. Additionally, a comparative analysis of the invasive fraction in the Amur section and in the Eastern European section of the Trans-Siberian Railway was performed.

Keywords: native species, alien species, natural biome, floristic characteristic, railway station local flora, invasion pathway, Trans-Siberian Railway

РЕЗЮМЕ

Котенко О.В., Виноградова Ю.К. Сосудистые растения Транссибирской железнодорожной магистрали в пределах Амурской области. Приведен комплексный анализ сведений о локальных флорах 16 железнодорожных станций Амурского участка Транссибирской магистрали: таксономическая, биоморфологическая структура, динамика численности аборигенных и чужеродных видов сосудистых растений с 1911 г., влияние естественных биомов и социально-экономических факторов на "железнодорожную флору". Проведен сравнительный анализ аборигенной и чужеродной фракций флоры Амурского и Уссурийского участков. Представлен сравнительный анализ инвазионного компонента флоры Амурского и Восточно-Европейского участков Транссиба.

Ключевые слова: аборигенные виды, чужеродные виды, естественный биом, флористические показатели, локальная флора железнодорожных станций, вектор инвазии, Транссибирская железнодорожная магистраль

The Trans-Siberian Railway connects two parts of the World differing in their profile of native species. Because over a half of Russia's foreign trade and transit cargo currently goes through the Trans-Siberian Railway, its role in unintentional introduction of plant species is rather big. The unique feature of the Trans-Siberian Railway is that it is a transport corridor passing through vast areas of relatively heavily disturbed landscapes throughout most of its length. Therefore, sites of species exchange with surrounding landscapes are limited to railway stations.

The Amur section (from railway station Yerofey Pavlovich in the west to the Kundur-Khabarovskiy station in the east) is one of the longest parts of the Trans-Siberian Railway: 1043 km or 11 % of its total length. According to the date of the first herbarial sampling, research on the flora of this section began in 1911, even before the commissioning of the railway. Fragmentary information about species of "railway flora" is available in the summary "Vascular plants of Soviet Far East" (Kharkevich 1985–1996), in books about the flora of Amur Region (Starchenko 2008), in a summary about alien flora of the Amur Region (Aistova 2009), and in the "Black book of the flora of the Far East" (Vinogradova et al. 2021). Nonetheless, a detailed comprehensive analysis of flora in the Amur section of the Trans-Siberian Railway has not yet been performed. In this regard, the following purposes are relevant:

1) revealing biogeographic patterns of plant dispersal via railroad traffic; this information will allow to compare the spread of species from Europe to the east and, conversely, from Asia to the west, as well as to assess the role of the ecological barrier in the spread of alien species in eastern regions of the Russian Federation;

2) identification of the involvement of anthropogenic factors in the movement of plant species;

3) risk assessment of the spread of alien species along the Trans-Siberian Railway in the future.

The purpose of this study was to determine and analyze species composition and structure of flora in the Amur section of the Trans-Siberian Railway.

MATERIAL AND METHODS

Flora was investigated in the Amur section of the Trans-Siberian Railway (within the Amur Region), including 16 major railway stations: Yerofey Pavlovich, Skovorodino, Magdagachi, Tygda, Shimanovskaya, Ledyanaya, Buzuli, Ust'-Pyora, Svobodny, Seryshevo, Belogorsk, Yekaterinoslavka, Zavitaya, Bureya, Arkhara, and Kundur-Khabarovskiy. The study area is located within two natural biomes: the Amur-Zeya Boreal Taiga biome (its south taiga variant and subtaiga variant) and the Zeya-Bureinsk biome (its near-Amur forest-steppe variant). The characteristics of natural biomes were taken from the map "Biomes of

Russia" (Ogureeva 2018). Geobotanical releves were carried out both at railway stations and on railroads between them. Sampling plots of 100 m^2 were set up along the transverse profile of the railway in three ecotopes: the railroad bed, slopes, and the right-of-way within the ballast section, in two to four replicates. A total of 115 sites were subjected to geobotanical analysis. In parallel, herbarium samples were collected by the route method. The work was done during 2020–2022, and the railway stations were visited 2–3 times during the growing season. Herbarium materials from LE, MHA, MW, VLA, and ABGI were used. Plant nomenclature is given according to the resource The world flora online (http://www.worldfloraonline.org/). For some taxa, we used names accepted in the book "Vascular plants of Soviet Far East" (Kharkevich 1985–1996). Native and alien species of vascular plants were identified according to the book "Flora of Amur Region and problems of its conservation: the Russian Far East" (Starchenko 2008). Invasive species are presented according to "The Black book of the flora of the Far East: invasive plant species in the ecosystems of the Far Eastern Federal District" (Vinogradova et al. 2021). Biomorphological structure was analyzed in accordance with a simplified classification (Kotenko et al. 2022).

Taxonomic analysis of the flora of the Amur section was performed on 379 species of vascular plants; however, 58 species were excluded from subsequent analyses because they were not found by us and are present only in the old herbarium collections with no data on a specific habitat. The other part of the study (biomorphological analysis; assessment of climatic and social factors; a comparative analysis of local flora in the Amur and Ussuriysk sections; and a comparative analysis of the invasive fraction of flora in the Amur and European section) was performed on 321 plant species.

For a comparison of local floras of the Amur section and other sections, we used data from a joint project "From West to East and back again – Trans-Siberian Railway as a continental pathway of plant invasions". The Ussuriysk section from Tel'man to Vladivostok (Galkina et al. 2021) and the European section from Moscow to Kirov (Vinogradova et al. 2020) were included in the analysis.

Data were processed statistically by means of the PAST 4.08 software. Possible effects of socioeconomic parameters on local floras were determined by the Spearman correlation coefficient. To evaluate a possible impact of socioeconomic parameters on the flora of the railway stations, we used statistical data on the size and density of population, data on the area of towns and villages, and information about passenger traffic of long-distance and local trains (https://rosstat.gov.ru/folder/210/document/13204).

RESULTS AND DISCUSSION

Taxonomic analysis of flora

In the Amur section of the Trans-Siberian Railway, 379 species of vascular plants were registered; among them, 265 are native and 114 are alien species, including 49 invasive ones (Tokhtar et al. 2022). The 379 species belong to 216 genera from 57 families. The top 10 families represent 74 % of the total number of species (Table 1).

Thirty-four families have only one genus, and six families have two genera. Amaranthaceae, Asparagaceae, Onagraceae, and Salicaceae are represented by 3 genera. There were also families represented by 4 genera (Boraginaceae and Cyperaceae), 5 genera (Scrophulariaceae), 6 genera (Ranunculaceae), and 7 genera (Polygonaceae). The largest numbers of genera are registered in Apiaceae (9 genera), Caryophyllaceae (10), Lamiaceae (10), Brassicaceae (13), Fabaceae (13), Rosaceae (14), Poaceae (24), and Asteraceae (35 genera).

Biomorphological analysis of the flora

Perennial herbaceous plants predominate in the flora of the Amur section: 189 species (59 %); the fraction of

Table 1. Taxonomic analysis of vascular plants observed in the Amur section of the Trans-Siberian Railway.

Family	Aboriginal fraction		Alien fraction	
	Number	%	Number	%
Asteraceae	37	14	23	20
Poaceae	33	12	12	11
Rosaceae	25	9	5	4
Fabaceae	18	7	11	10
Cyperaceae	15	6	0	0
Caryophyllaceae	13	5	2	2
Ranunculaceae	13	5	0	0
Salicaceae	9	3	0	0
Lamiaceae	8	3	6	5
Violaceae	8	3	0	0
Polygonaceae	7	3	3	3
Juncaceae	7	3	2	2
Brassicaceae	6	2	9	8
Apiaceae	6	2	4	4
Scrophulariaceae	6	2	2	2
Geraniaceae	5	2	1	1
Equisetaceae	5	2	0	0
Boraginaceae	4	2	1	1
Plantaginaceae	3	1	1	1
Valerianaceae	3	1	0	0
Asparagaceae	3	1	0	0
Onagraceae	2	1	2	2
Chenopodiaceae	2	1	2	2
Rubiaceae	2	1	2	2
Crassulaceae	2	1	0	0
Papaveraceae	2	1	0	0
Pinaceae	2	1	0	0
Primulaceae	2	1	0	0
Ulmaceae	2	1	0	0
Campanulaceae	2	1	0	0
Iridaceae	2	1	0	0
Alliaceae	2	1	0	0
Amaranthaceae	1	1	4	4
Urticaceae	1	1	2	2
Aceraceae	1	1	1	1
Balsaminaceae	1	1	1	1
Convolvulaceae	1	1	1	1
Araceae	1	1	0	0
Asclepiadaceae	1	1	0	0
Betulaceae	1	1	0	0
Caprifoliaceae	1	1	0	0
Dryopteridaceae	1	1	0	0
Grossulariaceae	1	1	0	0
Lythraceae	1	1	0	0
Orchidaceae	1	1	0	0
Polemoniaceae	1	1	0	0
Commelinaceae	1	1	0	0
Liliaceae	1	1	0	0
Euphorbiaceae	0	0	2	2
Berberidaceae	0	0	1	1
Cannabaceae	0	0	1	1
Cucurbitaceae	0	0	1	1
Cuscutaceae	0	0	1	1
Elaeagnaceae	0	0	1	1
Linaceae	0	0	1	1
Malvaceae	0	0	1	1
Portulacaceae	0	0	1	1

annual/biennial herbaceous plants is 31 % (99 species), and woody plants are represented by the lowest number of species: 10 % (33 species).

Among the woody plants, native species predominate over alien ones (43 species vs 5, respectively). A similar pattern was documented for perennial herbaceous plants (242 native vs 66 alien species). Among the annual and biennial plants, native species slightly predominate over alien ones only on the railway right-of-way (24 native species vs 17 alien ones), whereas on the railroad bed and slopes, this group demonstrated predominance of alien species (61 native species vs 79 alien ones). The predominance of alien annual/biennial plants on the railroad bed and slopes of the railway indicates that the Trans-Siberian Railway is one of the main pathways for the dissemination of alien plants in the region (Table 2).

From the northwest to the southeast of the study area, the number of annual and biennial plants increases (Fig. 1). For instance, in the south taiga variant of the Amur-Zeya biome, we found 85 species of perennial plants and 45 annual/biennial herbaceous species, whereas in the subtaiga variant of the Amur-Zeya biome, there were 87 and 46 species, and in the near-Amur forest-steppe variant of the Zeya-Bureya biome, 124 and 79 species, respectively. No variation of the number of woody plants was detected.

Stages of research on flora in the Amur section of the Trans-Siberian Railway

The stages of the compilation of the flora list for the Amur section proved to be determined both by the intensity of studies on nature in the region and by the operating mode of the Trans-Siberian Railway (Kotenko & Vinogradova 2022c). Judging by the results of the analysis of the herbarium materials and according to the number of the registered native and alien species, there were four stages in the history of flora research in the Amur section (Fig. 2).

The first stage: 1907–1940. It is characterized by the first herbarium sampling of native and alien species performed in the Amur section during its construction and immediately after its commissioning. The native species that was documented first, *Galium boreale* L. (LE), was sampled in 1911 between railway stations Yerofey Pavlovich and Magdagachi. A little later, in 1915, the native *Lonicera edulis* Turcz. (LE) was sampled at railway station Ulyagir. The first registered alien species was *Tripleurospermum inodorum* (L.) Sch. Bip. (LE): it was sampled in 1926 by E. Serpukhova at the Kundur-Khabarovskiy railway station 10 years after the Amur section was put into operation.

The second stage: 1941–1980. It showed an increase in the number of finds of both native and alien species. This stage resulted from the work of A.P. Til'ba, V.S. Shaga, V.N. Voroshilov, S. Loboda, T. Nekrasova, S. Shatovkina, S.D. Kalinin, M.I. Ryzhikh, N.V. Ermakova, N.A. Kostyuk, N.S. Probatova, V.P. Seledets, E.G. Rudyka, P.G. Gorovoi, T.N. Ul'yanova, and N. Krasikova. More herbarium collections of alien species were carried out as compared to native plants. Among native taxa, the following species were sampled: *Artemisia tanacetifolia* L., *Taraxacum mongolicum* Hand.- Mazz. (Asteraceae), *Stellaria dichotoma* L. (Caryophyllaceae), *Carex bohemica* Schreb. (Cyperaceae), *Dryopteris expansa* (C.Presl) Fraser-Jenk. & Jermy (Dryopteridaceae), *Melilotus suaveolens* Ledeb. (Fabaceae), *Amethystea caerulea* L. (Lamiaceae), *Agrostis stolonifera* L., *Bromus inermis* Leyss., *Leymus chinensis* (Trin.) Tzvelev (Poaceae), *Chamaerhodos erecta* (L.) Bunge, *Potentilla anserina* L., *Potentilla multifida* L. (Rosaceae). 21 alien species were collected: *Cirsium setosum* (Willd.) Besser, *Helianthus annuus* L., *Saussurea amara* (L.) DC., *Senecio vulgaris* L., *Tragopogon orientalis* L. (Asteraceae), *Amaranthus albus* L., *A. retroflexus* L. (Amaranthaceae), *Echium vulgare* L. (Boraginaceae), *Gypsophila davurica* (Turcz.) Fenzl (Caryophyllaceae), *Convolvulus arvensis* L. (Convolvulaceae), *Trifolium pratense* L. (Fabaceae), *Dracocephalum moldavica* L., *Galeopsis bifida* Boenn., *Lophanthus chinensis* Benth., *Phlomoides tuberosa* (L.) Moench (Lamiaceae), *Malva pusilla* Sm. (Malvaceae), *Plantago media* L. (Plantaginaceae), *Potentilla argentea* L., and *P. bifurca* L. (Rosaceae), *Linaria vulgaris* Mill., *Odontites vulgaris* Moench (Scrophulariaceae).

Table 2. The number of native (N) and alien (A) species in different biomorphological groups within railway ecotopes.

Ecotope	Woody plants		Perennial herbaceous plants		Annual and biennial herbaceous plants	
	N	A	N	A	N	A
Railroad bed	13	2	51	18	24	38
Railroad slopes	20	3	107	26	37	41
Right-of-way	10	0	84	22	24	17

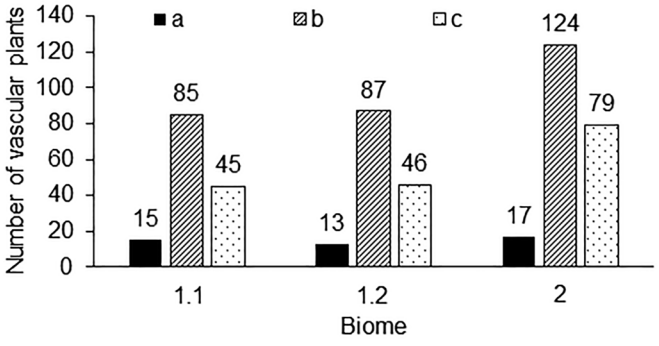

Figure 1 Biomorphological groups in different biomes. Biomes: 1.1: Amur-Zeya boreal taiga biome, south taiga variant; 1.2: Amur-Zeya boreal taiga biome, subtaiga variant; 2: Zeya-Bureya near-Amur forest-steppe biome, near Amur forest-steppe variant. Biomorphological groups: a: woody plants; b: perennial herbaceous plants; c: annual and biennial herbaceous plants

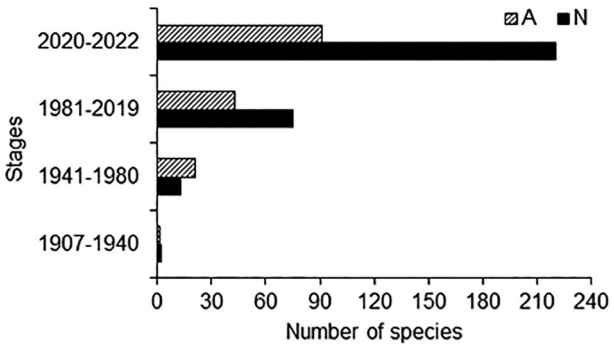

Figure 2 Stages of research on local flora of the Amur section. A: alien species, B: native species

Third stage: 1981–2019. It features an increase in research interest in "railway flora" and a sharp rise in the number of finds of both native and alien species. A.E. Kozhevnikov, V.M. Starchenko, E.V. Boiko, G.F. Darman, E.V. Aistova, and S.G. Kudrin collected 75 native and 43 alien species.

The fourth stage: 2020–2022. This is the beginning of purposeful research into the flora of the Amur section of the Trans-Siberian Railway. The largest number of samples native (220) species and alien species (91) was registered at this stage.

Thus, finds of native and alien species in the Amur section until the 1980s were few and far between. Later, there was a gradual increase in the number of alien species found at railway stations of the Amur section; this increase was due to purposeful floristic studies involving the Trans-Siberian Railway.

The influence of natural and climatic factors on the flora

In the Amur Region, the Trans-Siberian Railway passes through three variants of two natural biomes, which correspond to a taiga zone, a coniferous-deciduous forest zone, and a forest-steppe zone. From the west to east, the average annual air temperature goes up (from -4.0°C to -0.6°C), as does the average annual precipitation (from 421 to 641 mm). The total number of vascular plant species in biomes, on the contrary, diminishes from the west to east (Ogureeva 2018): Amur-Zeya biome (1260 species), and Zeya-Bureya biome (1075). Abundance of vascular plants per 100 km^2 is higher in Amur-Zeya biome (500–600); for Zeya-Bureya biome, this parameter is lower (400–550).

According to the total number of recorded vascular plant species in the Amur section of Trans-Siberian Railway, the biomes can be ranked in the following order: the south taiga variant of the Amur-Zeya biome (145 species) ≤ the subtaiga variant of the Amur-Zeya biome (146) < the near-Amur forest-steppe variant of the Zeya-Bureya biome (220). A total of 118 species are common between two studied biomes, among which, 79 are native and 39 are alien, including 24 invasive plants. A similar ranking of the biomes was noted regarding the number both native species [the south taiga variant of the Amur-Zeya biome (106 species), the subtaiga variant of the Amur-Zeya biome (107), and the near-Amur forest-steppe variant of the Zeya-Bureya biome (140)] and alien species [the south taiga variant of the Amur-Zeya biome (39), the subtaiga variant of the Amur-Zeya biome (39), and the near-Amur forest-steppe variant of the Zeya-Bureya biome (80)]. Apparently, the dispersal of alien plants by railway in the Amur section of the Trans-Siberian Railway does not proceed directly from the European part of Russia. The spread of plants proceeds from a more developed and more favorable (in terms of climatic conditions) Khabarovsk city agglomeration, which is confirmed by a comparison of herbarium specimens of invasive species collected in the Amur Region and on the Khabarovsk Territory not only on the railroad but also in other habitats (Vinogradova et al. 2021). For example, out of 87 invasive species common between these two regions, 52 species have been collected on the Khabarovsk Territory earlier than in the Amur Region.

In all three variants of biomes, the highest species diversity is seen on railroad slopes. In the south taiga variant of the Amur-Zeya biome and in the near-Amur forest-steppe variant of the Zeya-Bureya biome, the smallest number of species was found on the right-of-way (32 and 108 species respectively). In the subtaiga variant of the Amur-Zeya biome, the number of recorded species was the lowest on the railroad bed (54 species).

Possible effects of socioeconomic parameters

Correlations were analyzed between floristic characteristics of local flora of 16 railway stations (the total number of species and numbers of native, alien noninvasive, alien invasive, woody, perennial, and annual/biennial plant species) and socioeconomic parameters (population size and density, the area of a town/village on whose territory a station is located, and passenger traffic of long-distance and local trains).

The number of recorded plant species was the highest at Svobodny railway station (81 species) and the lowest at the Tygda station (22 species). The ratio of native, alien, and invasive species turned out to be similar among the 16 analyzed stations (Fig. 3). The native fraction prevails at all railway stations (Kotenko & Vinogradova 2022a). The number of native species varies from 14 (Tygda station) to 57 (Ledyanaya station). The number of alien species varies from 8 (Tygda station) to 34 (Svobodny station).

The examined floristic characteristics, with the exception of the total number of species and the number of invasive species, seem to be strongly influenced by human population size (Table 3). There was a strong positive correlation of this parameter with the number of woody plants (rs = 0.94742) and the number of native species (rs = 0.92672); we also found a positive correlation with the number of perennial (rs = 0.74486) and annual/biennial herbaceous plants (rs = 0.72375) and an average positive relationship with the number of alien species (rs = 0.51103).

Passenger traffic (= long-distance passenger train traffic + local passenger train traffic) appears to have a strong correlation with the number of alien (rs = 0.95551) and invasive (rs = 0.87348) species. There were also strong correlations of passenger traffic with numbers of woody (rs = 0.90374) and annual/biennial herbaceous plants (rs = 0.86094).

The area of a town/village correlates most strongly with the number of woody plants (rs = 0.9737), while the correlation with the number of native species is slightly weaker (rs = 0.87957). There is only an average correlation between the area of a town/village and the number of both polycarpic and monocarpic plant species (rs = 0.69995 and rs = 0.51525, respectively).

A strong positive correlation was noted between population density and the number of invasive species (rs = 0.87493) and the number of polycarpic herbaceous plant species (rs = 0.83266). The correlation (rs = 0.69612) between population density and the number of native plant species was moderate.

There was no correlation between the total number of recorded species and any socioeconomic parameters.

A comparison between Amur section flora and Ussuriysk section flora along the Trans-Siberian Railway

The native flora fraction is predominant in both the Amur section and Ussuriysk section of the Trans-Siberian Railway (223 species or 69 % in the Amur section and 133 species or 63 % in the Ussuriysk section). The total list of native species of the Amur and Ussuriysk sections contains 298 species. Fifty-eight native species (19 %) are common between the two railway sections; 166 species (56 %) were found in the Amur section but not in the Ussuriysk section, and 74 species (25 %) were found only in the Ussuriysk section. According to the leading families of the native flora fraction, the two sections differ in the richness ranking of families and by the presence of the Brassicaceae among leading families in the Ussuriysk section. In the Amur section, leading families of the native flora fraction are as follows (descending order): Asteraceae (28 species, 9 %) → Poaceae (22 species, 7 %) = Rosaceae (22 species, 7 %) → Fabaceae (15 species, 7 %) → Cyperaceae (14 species, 5 %) → Ranunculaceae (11 species, 4%). In the Ussuriysk section, the ranking of leading families of native flora is different: Fabaceae (12 species, 4 %) = Poaceae (12 species, 4 %) → Asteraceae (11 species, 3 %) = Rosaceae (11 species, 3 %) → Ranunculaceae (10 species, 3 %) → Cyperaceae (6 species, 2 %) → Brassicaceae (5 species, 1 %).

In both sections, the profile of plant life forms demonstrates the predominance of polycarpic herbs and a low number of woody species, while monocarpics occupy an intermediate position in terms of the number of species. Life forms of native plant species in the Amur and Ussuriysk sections are distributed as follows: perennial herbaceous plants (152 species or 68 % in Amur section; 89 species or 67 % in Ussuriysk section) → annual or biennial herbaceous plants (42 species or 19 % in Amur section; 27 species or 20 % in Ussuriysk section) → woody plants (29 species or 13 % in Amur section; 17 species or 13 % in Ussuriysk section).

In both the Amur and Ussuriysk sections, the number of native species is the highest on the slopes (162 and 91 species, respectively) and the lowest on the railroad bed (83 and 45 species, respectively). On the railway right-of-way, the number of native species is moderate; in the Amur section, it is 123 species, and in the Ussuriysk section, 78 species.

The number of native species increases from the northwest to southeast in the Amur section, and vice versa in the Ussuriysk section. For instance, in the Amur section, 140 native species were noted in the Zeya-Bureya biome and 106 native species in the Amur-Zeya biome. In the Ussuriysk section, the highest number of native species was observed in the Amur-Ussuriysk subtaiga biome (100 species), and the lowest in the Sikhote-Alin southern biome (40 species).

The total number of alien species for the Amur and Ussuriysk sections is 128. Of these, 41 species grow in both railway sections, 59 species only in the Amur section, and 28 species only in the Ussuriysk section. In terms of the ranking of four leading families, the taxonomic profile of the alien flora fraction is similar between the Amur section and Ussuriysk section: Asteraceae (22 species in Amur section; 21 in Ussuriysk section) → Poaceae (14 in Amur section; 9 in Ussuriysk section) → Fabaceae (10 in Amur section; 9 in Ussuriysk section) → Brassicaceae (7 species in Amur section; 4 in Ussuriysk section) (Kotenko & Vinogradova 2022b). Nine families are present in the Amur section but not in the Ussuriysk section: Berberidaceae, Cannabaceae, Cuscutaceae, Elaeagnaceae, Euphorbiaceae, Geraniaceae, Linaceae, Malvaceae, and Portulacaceae. Six families are present only in the Ussuriysk section: Alismataceae, Betulaceae, Polemoniaceae, Ulmaceae, Vitaceae, and Typhaceae. In both the Amur section and Ussuriysk section, the spectrum of life forms is dominated by annual/biennial herbaceous plants and the proportion of woody plants is low. In both sections, the largest number of alien species grows on railroad slopes (Amur section: 71; Ussuriysk section: 54), and the smallest number on the right-of-way (41) in the Amur section and on the railroad bed (40) in the Ussuriysk section. In the Amur section, the number of alien species increases from the northwest to southeast: the south taiga variant of the Amur-Zeya biome (39 species) → the

Table 3. Correlation between floristic and the socioeconomic parameters (Spearman's rho)

Species cathegory	Population size	Passenger traffic	Town/ village area	Population density
native species	0.92672	0.41251	0.87957	0.69612
alien species	0.51103	0.95551	0.37476	0.41562
invasive species	0.38781	0.87348	0.34272	0.87493
woody plants	0.94742	0.90374	0.9737	0.22478
perennial herbaceous plants	0.74486	0.37547	0.69995	0.83266
annual and biennial herbaceous plants	0.72375	0.86094	0.51525	0.08703
All vascular plant species	**0.45904**	**0.28668**	**0.27676**	**0.22613**

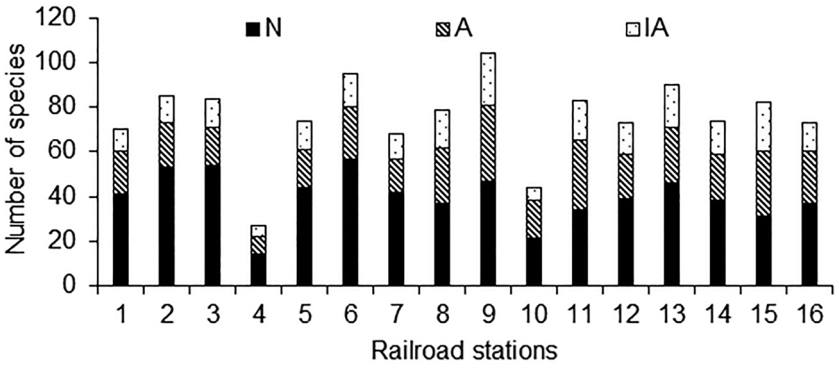

Figure 3 Ratio of flora fractions at the studied stations. Railroad stations: 1. Yerofey Pavlovich; 2. Skovorodino; 3. Magdagachi; 4. Tygda; 5. Shimanovskaya; 6. Ledyanaya; 7. Buzuli; 8. Ust'-Pyora; 9. Svobodny; 10. Seryshevo; 11. Belogorsk; 12. Yekaterinoslavka; 13. Zavitaya; 14. Bureya; 15. Arkhara; 16. Kundur-Khabarovskiy. A fraction of flora: N, native; A, alien; IA, invasive

subtaiga variant of the Amur-Zeya biome (39) → the near-Amur forest-steppe variant of the Zeya-Bureya biome (80). By contrast, in the Ussuriysk section, the number of alien species goes up from southeast to northwest: the Sikhote-Alin southern biome (32 species) → the near-Khanka forest-steppe variant of the Zeya-Bureya biome (41) → the Amur-Ussuri subtaiga biome (58).

The number of invasive species included in the "Black book of the flora of the Far East" (Vinogradova et al. 2021) is almost identical between the two sections (Amur section: 49; Ussuriysk section: 48). In the Amur and Ussuriysk sections, such species are more common on railroad slopes (37 and 38, respectively). The lowest numbers of invasive species in the Amur section were noted on the right-of-way (28 species), whereas in the Ussuriysk section, on the railroad bed (30 species).

The number of aggressive invasive species listed among the top 100 most dangerous invasive species in Russia (Dgebuadze et al. 2018) is lower in the Amur section than in the Ussuriysk section (nine and 11, respectively). In both the Amur and Ussuriysk sections, the following species were noted: *Acer negundo* L., *Amaranthus retroflexus* L., *Ambrosia artemisiifolia* L., *Echinocystis lobata* (Michx.) Torr. et Gray, *Erigeron canadensis* L., *Hordeum jubatum* L., and *Impatiens glandulifera* Royle. *Bidens frondosa* L. and *Oenothera biennis* L. were found only in the Amur section, while *Erigeron annuus* (L.) Pers., *Galinsoga parviflora* Cav., and *Impatiens parviflora* DC. were noted only in the Ussuriysk section. Most often, these species in the Amur section are found on the railroad bed (six species) and on its slopes (six species) and somewhat less often on the right-of-way (five species). Three of them (*Amaranthus retroflexus*, *Erigeron canadensis*, and *Hordeum jubatum*) are registered in two biomes, and six species (*Acer negundo*, *Ambrosia artemisiifolia*, *Bidens frondosa*, *Echinocystis lobata*, *Impatiens glandulifera*, and *Oenothera biennis*) only in one biome. Judging from the number of aggressive invasive species, the biomes of the Amur section can be ranked in the following order: the south taiga type of the Amur-Zeya biome (1 species) → the subtaiga variant of the Amur-Zeya biome (3) → the near-Amur forest-steppe variant of the Zeya-Bureya biome (8).

In the Ussuriysk section, the largest number of aggressive invasive species was found on the railway slopes (10), and the lowest number on the right-of-way (6). On the railroad bed, eight aggressive invasive species were registered. Five species from the top 100 list were found in the Ussuriysk section in three biomes (*Acer negundo*, *Hordeum jubatum*, *Ambrosia artemisiifolia*, *Bidens frondosa*, and *Erigeron canadensis*), two species (*Amaranthus retroflexus* and *Impatiens glandulifera*) in two biomes, and four species in only one biome (*Echinocystis lobata*, *Erigeron annuus*, *Impatiens parviflora*, and *Galinsoga parviflora*). By the number of aggressive invasive species, the biomes of the Ussuriysk section can be ranked as follows: the Amur-Ussuriysk subtaiga biome (nine species) → the near-Khanka forest-steppe variant of the Zeya-Bureya biome (seven) = the Sikhote-Alin southern biome (seven).

A comparison of the invasive flora fraction between the Amur section and a section of the Trans-Siberian Railway on the territory of the Eastern European plain (hereafter: "european section")

The number of invasive species is almost two times higher in the Amur section than in the european section (49 vs 28). In both the Amur section and european section, the number of recorded invasive species is the largest on the railway slopes (39 and 23, respectively) and the lowest on the right-of-way (28 and six, respectively). On the railroad bed, 32 species were found within the Amur section, and 14 species within the european section.

The number of aggressive invasive species listed among the top 100 (Dgebuadze et al. 2018) is lower in the Amur section than in european section (nine and 15, respectively). Eight aggressive invasive species occur in both sections: *Acer negundo*, *Amaranthus retroflexus*, *Bidens frondosa*, *Erigeron canadensis*, *Echinocystis lobata*, *Hordeum jubatum*, *Impatiens glandulifera*, and *Oenothera biennis*. *Ambrosia artemisiifolia* is present only in the Amur section, whereas *Reynoutria* × *bohemica* Chrtek et Chrtkova, *Solidago canadensis* L., *Galinsoga parviflora*, *Heracleum sosnowskyi* Manden., *Impatiens parviflora*, *Lupinus polyphyllus* Lindl., and *Erigeron annuus* were found only in the european section.

In contrast to the european section, in the Amur section, there are no top 100 species that are present simultaneously in the three variants of the natural biomes. Three species (*Amaranthus retroflexus*, *Erigeron canadensis*, and *Hordeum jubatum*) were recorded in two variants of biomes, and six species (*Acer negundo*, *Ambrosia artemisiifolia*, *Bidens frondosa*, *Echinocystis lobata*, *Impatiens glandulifera*, and *Oenothera biennis*) were recorded in one variant. In the european section, two invasive species (*Amaranthus retroflexus* and *Erigeron canadensis*) occur in three biomes, six species (*Acer negundo*, *Impatiens glandulifera*, *I. parviflora*, *Oenothera biennis*, *Heracleum sosnowskyi*, and *Erigeron annuus*) in two biomes, and seven species (*Hordeum jubatum*, *Reynoutria* × *bohemica*, *Solidago canadensis*, *Bidens frondosa*, *Echinocystis lobata*, *Galinsoga parviflora*, and *Lupinus polyphyllus*) in one biome.

In both the european section and Amur section, the most aggressive invasive species were found on railroad slopes (european section: 12; Amur section: six). In the european section, their number is slightly lower on the railroad bed (nine), whereas in the Amur section, their number on the railroad bed is the same as that on the slopes (six). In both sections, their numbers are the lowest on the right-of-way (european section: 6, Amur section: 5).

CONCLUSIONS

A total of 379 species of vascular plants were identified in the Amur section of the Trans-Siberian Railway. Native species predominate: 265 (70 %). There are 114 alien species (30 %), of which 49 species are invasive.

Perennial herbaceous plants are the dominant group in the flora of the Amur section: 189 species (59 %). Annual/biennial herbaceous plants constitute 99 species (31 %), and woody plants 33 species (10 %). Among alien species, including invasive ones, the highest proportion belongs to

annual and biennial herbaceous plants: 57 species (58 %). Among perennial herbaceous plants, the proportion of alien species is 38 % (37 species). Among woody plants, the proportion of alien species is the lowest: 4 % (four species). The predominance of annual and biennial plants in the southeastern part of the Amur section of the Trans-Siberian Railway confirms that alien species of European origin do not spread directly from Europe but from the Khabarovsk urban agglomeration.

Stages of compilation of the list of alien plants in the Amur section are determined by the intensity of research into the flora of the region and by the mode of operation of the Trans-Siberian Railway.

For the Amur-Zeya biome and Zeya-Bureya biome, 118 species are common, of which 79 are native and 39 are alien, including 24 invasive. The greatest species diversity in both biomes is seen on railroad slopes.

Socioeconomic factors in descending order of their influence on the parameters of flora are as follows: population size → passenger traffic → the area of a town or village → population density.

The Amur section and the Ussuriysk section of the Trans-Siberian Railway are similar in the prevalence of the native flora fraction over the alien fraction. Perennial herbaceous plants are the dominant group in the alien flora fraction in both sections, and the proportion of woody plants is the lowest. In both sections, the largest number of alien species grows on railroad slopes. There are differences in the profile of families of the alien fraction: nine families occur in the Amur section but not in the Ussuriysk section: Berberidaceae, Cannabaceae, Cuscutaceae, Elaeagnaceae, Euphorbiaceae, Geraniaceae, Linaceae, Malvaceae, and Portulacaceae. Species of 6 families occur in the Ussuriysk section but not the Amur section: Alismataceae, Betulaceae, Polemoniaceae, Ulmaceae, Vitaceae, and Typhaceae. In the Amur section, the number of alien species increases from the northwest to southeast; in the Ussuriysk section, on the contrary, the number of alien species goes up from the southeast to northwest. The number of the most aggressive invasive species is lower in the Amur section than in the Ussuriysk section.

In the Amur section, the total number of invasive species is higher than that in the European section (49 vs 28), but the number of the most aggressive species listed among the top 100 is lower (9 vs 15).

The Trans-Siberian Railway is a key pathway of invasion of alien species in eastern Russia. Nonetheless, in the Amur section in particular, the dispersal of alien species has a secondary source, i.e. the urban agglomeration of Khabarovsk, proceeds in the direction from the southeast to northwest.

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