

Invasion dynamics of *Acer negundo* L. in ribbon forests of the Altai Krai: ecological impacts and predictive habitat modeling

Natalia V. Ovcharova¹, Marina M. Silantyeva¹,
Alexey V. Vaganov^{1,2}, Anastasia A. Masanina¹

1 Altai State University, 61 Lenin Ave., Barnaul, 656049, Russia

2 Sakhalin Branch of the Botanical Garden-Institute FEB RAS, 21 Gorkov st., Yuzhno-Sakhalinsk, 693023, Russia

Corresponding author: Natalia V. Ovcharova (ovcharova_n_w@mail.ru)

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Abstract

This study examines the invasion dynamics of ash-leaved maple (box elder, *Acer negundo* L.) in the ribbon forests of Altai Krai, Russia, where it has become one of the dominant invasive species over the past thirty years. Originally introduced as an ornamental plant in the early 20th century, *A. negundo* has rapidly proliferated in lowland, steppe, and forest-steppe regions, significantly impacting local ecosystems. Our research analyzes the ecological and phytocoenotic conditions that facilitate *A. negundo*'s invasion, focusing on its distribution across various ribbon pine forests in the region. Through geobotanical surveys and forest management record analysis, we reveal the species' prevalence in diverse forest types and its effects on biodiversity, tree growth, and community dynamics. Key findings indicate that *A. negundo* flourishes in disturbed habitats, where it aggressively competes with native flora, suppressing their growth and altering successional pathways. This leads to low-diversity communities increasingly dominated by the invasive species and highlights the exacerbating role of logging and land-use changes. Using predictive modeling techniques, we assessed habitat suitability for *A. negundo* across Eurasia, identifying temperature as the primary limiting factor for its distribution. The model achieved a high AUC value of 0.97, indicating strong reliability. These findings suggest a significant potential for *A. negundo*'s range expansion throughout Altai Krai, especially in areas with reduced competition from native species. This research underscores the urgent need for effective management strategies to mitigate the effects of *A. negundo* in Altai Krai and similar regions.

Keywords

Acer negundo L., phytocoenotic features, invasive species, bioclimatic modeling, succession, MaxEnt algorithm

Introduction

Ribbon forests in the Altai Territory represent a unique ecological phenomenon within Russia, characterized by their growth along riverbeds and on sandy soils derived from ancient alluvial deposits. In the past three decades, these forests have faced substantial invasion by the ash-leaved maple, or boxelder (*Acer negundo* L.), a North American species now recognized as one of the ten most dangerous invasive plants in Russia.

Acer negundo was introduced to Europe in the 17th century as an ornamental plant and began to be used for landscaping in Siberian cities by the late 18th century. It was introduced to the Altai Territory in the early 20th century primarily for the establishment of protective forest plantations, with the most significant plantings occurring in the 1960s. Although it continues to be used in urban landscaping, *A. negundo* is no longer officially recommended for creating green spaces due to its invasive nature. In this region, it primarily thrives in the lowland areas of steppe and forest-steppe zones but does not extend into higher elevations (Silantyeva et al. 2021). In its native range, the ash-leaved maple is a component of diverse ecosystems, including mesotrophic deciduous, coniferous, and floodplain forests, as well as swamps and prairies (Panasenکو 2014). The global spread of *Acer negundo* has prompted extensive research into the mechanisms and vectors facilitating its invasion. A contemporary monitoring network has been established to foster data sharing among researchers, enhancing environmental and economic security. Initial studies of alien species in Russia began in the early 20th century, focusing on the ecological characteristics that enable invasive species to establish themselves. The invasion of *A. negundo* has garnered attention from researchers across multiple countries, including Belarus, Ukraine (Vykhor, Prots 2013), Poland (Yakhnovets and Yurchenko 2019), Lithuania, Latvia (Gudmonas, Gudžinkas 2011; Straigyte et al. 2015), and France (Saccone et al. 2010).

Research by Gusev (2016) and Gusev et al. (2017) identified the *Acer negundo* – *Calamagrostis epigeios* community emerging 13 years post-succession. Their findings indicated that *Acer negundo* reduces species diversity, suppresses tree growth, increases synanthropization, and disrupts the natural evolution of plant communities. Furthermore, they noted a lack of change in species dominance within 30 to 40-year-old maple communities. Subsequent investigations suggested that early stages of secondary succession are particularly vulnerable to alien species like *A. negundo*, leading to delayed succession and the establishment of long-term communities that facilitate further invasions. Kostina et al. (2015) demonstrated that *A. negundo* gradually colonizes disturbed forests, particularly in areas affected by bark

beetle outbreaks. Various hypotheses have been proposed to explain the success of alien species invasions, addressing introduction vectors and distribution pathways (Di Castri 1990; Pyšek, Prach 1993; Stohlgren et al. 1999; Stohlgren 2002; Vila et al. 2007).

Acer negundo is native to diverse environments across North America, primarily found in lower elevation regions of Canada, the United States, and Mexico (Enquist et al. 2016). Its adaptability to various habitats, including disturbed sites and urban areas, contributes to its extensive distribution (Maitner et al. 2018). The species flourishes in a range of forest ecosystems, such as oak-hickory and elm-ash-cottonwood forests (USDA Forest Service, 1988). The invasive status of *A. negundo* in Europe, South America, and parts of Asia raises concerns about its ecological impacts. Several studies have employed distribution modeling techniques to predict its potential spread in non-native regions. For example, research utilizing species distribution models (SDMs) has indicated that *A. negundo*'s range is likely to expand under changing climatic conditions (Lamarque et al. 2013). These models commonly incorporate environmental variables such as temperature, precipitation, and soil characteristics to assess suitable habitats for invasion.

The impact of *A. negundo* invasion varies across geographical regions due to local environmental conditions and existing flora. Studies in Belarusian Polesia and the Middle Urals revealed significant declines in native species richness due to *A. negundo* invasion, with specific dynamics differing based on regional floristic conditions (Kozłowski et al. 2020). This underscores the necessity for region-specific management strategies when addressing invasions. The invasion of *A. negundo* poses considerable challenges for biodiversity conservation. Its ability to drastically reduce native plant richness through mechanisms such as phenotypic plasticity and canopy cover effects highlights the urgent need for monitoring and managing this invasive species (Dąbrowski et al. 2021). Effective management strategies must incorporate ecological assessments that consider local conditions and community dynamics.

Reports indicate significant declines in native plant species richness resulting from *A. negundo* invasion. In invaded areas, total plant species richness has decreased by 21% to 43%, with specific declines in herbaceous (24% to 43%) and woody species richness (8% to 44%) (Kozłowski et al. 2020). Furthermore, the increase in alien herb proportions by 35% in invaded plots supports the invasional meltdown hypothesis, indicating that *A. negundo* facilitates the establishment of other invasive species. This situation emphasizes the need for targeted monitoring and management strategies to mitigate the adverse impacts of *A. negundo* on native biodiversity. Understanding the distribution patterns of *A. negundo* is essential for developing effective management strategies to mitigate its invasive effects. Modeling the potential range of invasive species is crucial for monitoring and managing their spread. This process involves assessing ecological niches, predicting habitat suitability in response to climate change (Thakuri et al. 2019; Shabania et al. 2020), and identifying potential invasion routes and vulnerable areas.

Distribution modeling can help identify areas at risk and inform conservation efforts by prioritizing regions for monitoring and control measures. Additionally, integrating ecological data with predictive models can enhance our understanding of how climate change may influence the future distribution of *A. negundo*. The mechanisms behind *Acer negundo*'s invasion in forest communities across Eurasia have been extensively explored, with focus on factors such as allelopathy, crown closure effects, and mycorrhizal associations (Veselkin and Prokina 2016; Veselkin et al. 2019; Tsandekova 2020; Dubrovin, Krupina 2020; Veselkin et al. 2021). The anatomical and morphological characteristics of *Acer negundo* in various habitats have also been well-documented. American studies have examined the water potential of *A. negundo*, revealing differences in growth between female and male trees based on water availability. Female trees tend to thrive in humid environments due to their more efficient water usage, while male trees show better adaptability to drier conditions (Dawson, Ehleringer 1993; Ward et al. 2002).

The objective of this study is to evaluate the ecological and phytocoenotic conditions that facilitate the invasion of *Acer negundo* into the ribbon forests of Russia. Furthermore, we aim to model the ecological niches and potential range of this species across Eurasia.

Materials and methods

Ecological and coenotic features of *Acer negundo*

This study investigates the distribution of *Acer negundo* within the Barnaulsky, Kasalinsky, and Kulundinsky ribbon pine forests (see Fig. 1). These forests are characterized by narrow, parallel formations that extend nearly 400 km southwest from the ancient Ob floodplain. At the Altai Krai boundary with the Republic of Kazakhstan, these forests converge with the Loktevsky ribbon forest, collectively forming a substantial forest island known as the Srostinsky pine forest. This complex continues along the ancient river delta to the Irtysh River, where it intermingles with the terraced sands of the river (Forest Plan, 2022).

The research spanned four years, from 2019 to 2022, and included 148 geobotanical descriptions focusing on maple communities and mixed communities where *Acer negundo* was a significant component. Supplementary data were gathered from forest management records in the Forest Fund of the Altai Territory, covering the period from 2008 to 2018. This dataset included information from 563 localities reported by Roslesinform employees, along with 950 localities with coordinates collected during field expeditions conducted in the Altai Territory from 2002 to 2022. Additionally, 500 localities were documented based on herbarium specimens, which utilized herbaria such as ALTB, WIR, LE, NS, and NSK.

The geobotanical descriptions were analyzed using the TURBOVEG and JUICE software packages, facilitating a detailed examination of community species compo-

sition, projective cover, and constancy. Projective cover was assessed on a five-point scale: less than 5%, 15%, 16 to 25%, 26 to 50%, and more than 50%. Phytocenological tables were compiled to classify the constancy of each species into categories: less than 20%, 21% to 40%, 41% to 60%, 61% to 80%, and 81% to 100%.

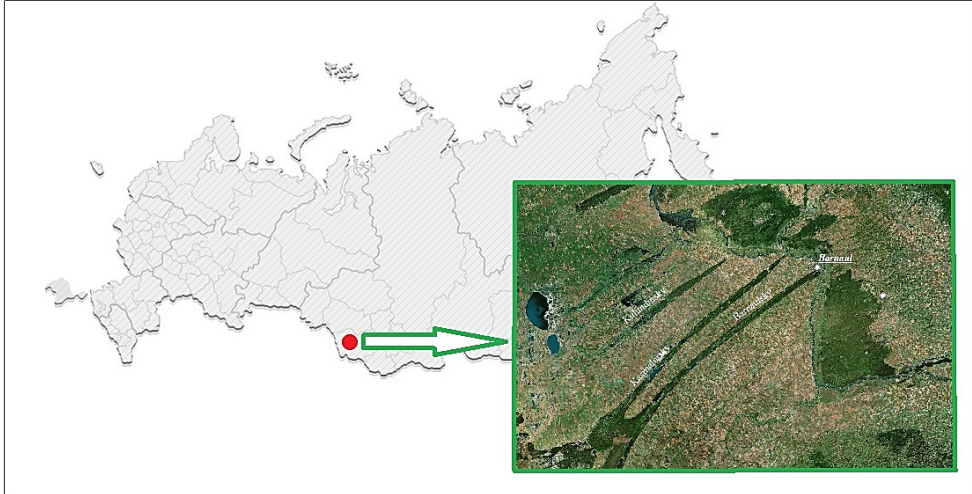


Figure 1. Map of the Kulundinsky, Kasmalinsky, and Barnaulsky ribbon pine forests.

Current and probabilistic predictive distribution of *Acer negundo*

The study also examined the current distribution and probabilistic predictive model for *Acer negundo*. Geographic coordinates were sourced from the Global Biodiversity Information Facility (GBIF) datasets (GBIF 2022a), and erroneous coordinates were removed using a GeoJSON polygon filter. The preliminary dataset contained 100,888 geographic coordinate records, with a final shapefile consisting of 65,535 valid records. Distribution maps were generated using DIVA-GIS 7.5 software. For Eurasia, a bioclimatic predictive model was developed using geographical coordinates from the MW and iNaturalist datasets (GBIF 2022b). The model focused on specific geographic regions, resulting in 14,047 points after duplicates were eliminated. To address spatial non-uniformity, the SDMtoolbox (Brown 2014) was employed, leading to the use of 6,632 actual localities for predictive modeling. After finalizing the dataset, a shapefile containing 14,047 unique points was compiled.

The species distribution modeling and mapping were performed using the Biodiversity and Climate Change Virtual Laboratory (Hallgren 2016), applying the MaxEnt algorithm (Phillips et al. 2022) for modeling. The initial modeling utilized WorldClim climatic variables (Phillips et al. 2006; Philips and Dudik 2008), with a predictive map generated based on land areas at a resolution of 2.5 arc minutes. Given that the climate across *A. negundo* habitats is diverse, we incorporated mul-

tiple WorldClim climatic variables (BIO1–BIO19, www.worldclim.org) during the initial modeling stage: BIO1 – annual mean temperature; BIO2 – mean diurnal range (mean of monthly temp); BIO3 – isothermality (BIO1/BIO7) x 100; BIO4 – temperature seasonality (coefficient of variation); BIO5 – max temperature of warmest month; BIO6 – min temperature of coldest month; BIO7 – temperature annual range (BIO5 – BIO6); BIO8 – mean temperature of wettest quarter; BIO9 – mean temperature of driest quarter; BIO10 – mean temperature of warmest quarter; BIO11 – mean temperature of coldest quarter; BIO12 – annual precipitation; BIO13 – precipitation of wettest month; BIO14 – precipitation of driest month; BIO15 – precipitation seasonality (coefficient of variation); BIO16 – precipitation of wettest quarter; BIO17 – precipitation of driest quarter; BIO18 – precipitation of warmest quarter; BIO19 – precipitation of coldest quarter (WorldClim 1.4, www.worldclim.org). The contributions of each variable were assessed using a jackknife test (Phillips 2006).

Results

Ecological and coenotic features of *Acer negundo*

The invasion of *Acer negundo* into ribbon forest communities is heavily influenced by ecological factors, particularly climatic and edaphic conditions (such as soil composition, acidity, and water content), as well as the topography of ribbon pine forests situated in the valleys of ancient hollows within the Altai Territory. An essential ecological factor facilitating the invasion of maple is the anthropogenic influence, which has both direct and indirect impacts on ribbon pine forests. The Barnaulsky and Kasmalinsky ribbon forests span two natural zones from northeast to southwest, encompassing the steppe regions within the Kulunda Plain (including sub-zones like dry-steppe, arid-steppe, and moderate-arid-steppe) and the forest-steppe area (specifically the southern forest-steppe subzone) within the Priobsky Plateau. The Kulundinsky forest, stretching 100 km in length, lies predominantly within the southern forest-steppe subzone of the forest-steppe region. The small rivers within the ancient hollows flow either towards the Kulunda Plain (Kulunda) or towards the Ob River (Kasmala, Barnaulka). Soddy-podzolic soils, originating from ancient alluvial hollows, are prevalent in ribbon pine forests. These soils vary, with soddy-podzolic sandy-sandy loam soils forming in elevated areas and soddy-podzolic gleyed soils developing in depressions due to continuous contact with groundwater.

Over the past three to four decades, *Acer negundo* has seen increased prevalence in ribbon pine forests, with pure maple stands covering extensive areas. The ash-leaved maple has been observed to hinder forest succession in various ecosystems. *Acer negundo* is distributed across all ribbon forests in the Altai Territory, with varying occurrence and abundance, particularly thriving in the Barnaul forestry, closest to the regional center of Barnaul (Silantyeva et al. 2021).

In addition to *Acer negundo*, other alien species have been identified in these forests, altering the species composition and expanding their distribution. These species include green ash, Siberian crabapple, small-leaved lime, brittle willow, and European white elm. The mechanisms of succession driven by the invasive *Acer negundo* in ribbon forests within the forest-steppe and steppe zones exhibit similarities. Maple invasion during early succession stages impedes secondary succession, fostering the development of long-standing communities that act as a platform for further invasion. These maple-dominated communities are characterized by low species diversity, suppressed tree growth, significant synanthropization, habitats spanning several hectares, and long-term existence. This pattern is consistent across both Kasmalinsky and Kulundinsky ribbon forests.

While the ribbon pine forests share common ecological and phytocoenotic features that facilitate *Acer negundo* invasion during secondary successions, specific characteristics are detailed in the study by Elesova et al. (2021). The phytocoenotic preferences of *Acer negundo* in ribbon forests were evaluated based on Pavlova classification of pine forests (1963) with minor adjustments. Four main formations of pine and birch-pine forests involving *Acer negundo* were identified: dry lichen and steppe, moderately moist herbaceous-shrub or berry, mesophytic grass, and birch-pine mesophytic grass. These formations exhibit varying coenotic indicators, including total species count, average species count per 100 m², percentage of adventive species, and the number of grass family representatives (Poaceae). The adventitious component in the flora of the studied pine forests ranges from 4% to 5% across different forest types (Table 1).

Table 1. Coenotic features of the Kasmalinsky, Barnaulsky, and Kulundinsky ribbon pine forest formations that include *A. negundo*

Indicators	Main pine forest formations			
	Dry lichen and steppe	Moderately moist grass-shrub	Mesophilic grass	Birch-pine grass
Species number	67	123	187	246
Average number of species per 100 m ²	17	25	28	19
Adventitious species ratio (%)	3 (4%)	6 (5%)	9 (5%)	10 (4%)
Number of graminoid species (%)	10 (15%)	8 (7%)	10 (5%)	20 (8%)

Geobotanical data analysis reveals that *Acer negundo* is more prevalent in the northeastern regions of ribbon forests, where mesophilic grass associations dominate. Towards the south, steppe-grass, grass-lichen, and dead soil forests replace these associations, with xerophytic shrubs predominating in the undergrowth, leading to sporadic or absent occurrences of *Acer negundo* in these areas.

Secondary successions in ribbon forest communities, including those with *A. negundo*, are driven by both anthropogenic factors (such as logging, fires, recre-

ation, and the introduction of alien dendroflora species) and natural influences. However, it is the anthropogenic factor that predominantly drives changes in these communities.

Potential (predicted) habitat of *Acer negundo*

In our study, the predictive model's performance is evaluated based on the area under the curve (AUC), which indicates the relative probability of *A. negundo* occurrence. We achieved an AUC value of 0.97 for *A. negundo*, reflecting an excellent model performance level (ranging from 0.9 to 1). Our modeling analysis (see Fig. 2) revealed that the spread of *A. negundo* into new regions is influenced by various factors, primarily including BIO4 (temperature seasonality/coefficient of variation, optimal range 10 to 15°C), BIO7 (temperature annual range, up to 36°C), BIO9 (mean temperature of the driest quarter, ranging from -15 to -2°C), and BIO11 (mean temperature of the coldest quarter, ranging from -8°C to below -40°C).

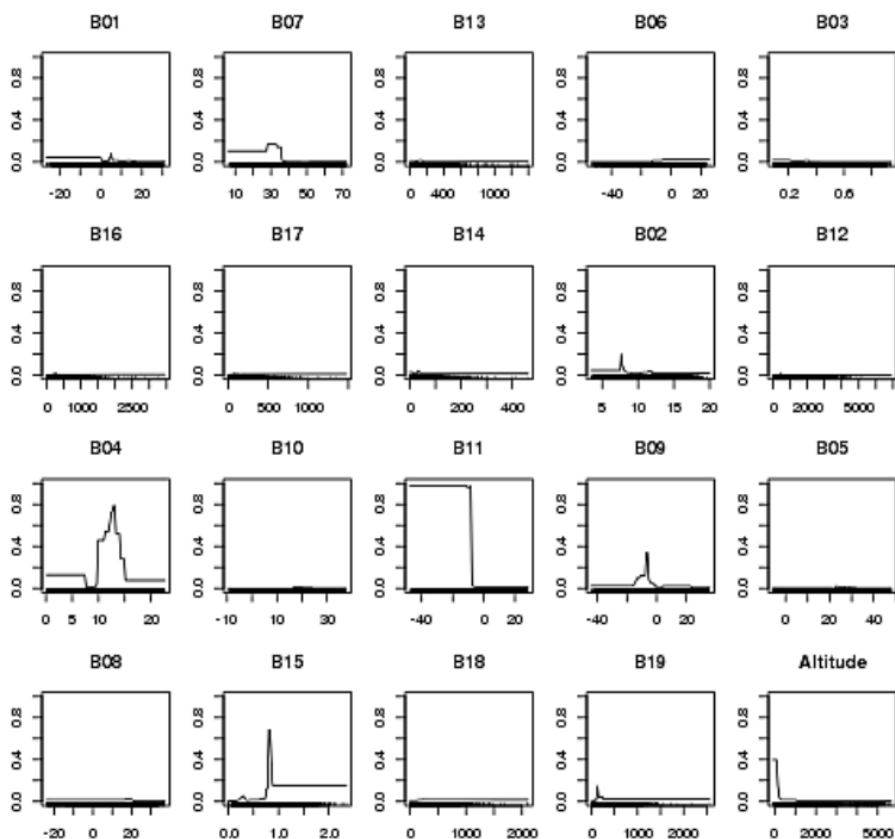


Figure 2. Results of bioclimatic modeling for *A. negundo* L. via BCCVL based on 19 climatic variables (WorldClim.org); BIO1–19, abscissa axis: BIO1–12 – temperature values, BIO13–19 – precipitation amount; ordinate axis: BIO1–19 – variable value from 0 to 1) and topographic variable (altitude).

A. negundo is typically a species found in lowland areas, a characteristic supported by the altitudinal zonation indicator in our predictive model. The species' average occurrence frequency (0.4) ranges from sea level to precisely 250 meters above sea level (Figs 3 and 4).

These gradations were used based on WorldClim bioclimatic variables with accurate data on the species distribution across Eurasia (red markers). For the Altai Territory, a map depicting the predicted suitable habitat for *A. negundo* L. was elaborated based on WorldClim bioclimatic variables (Fig. 4).

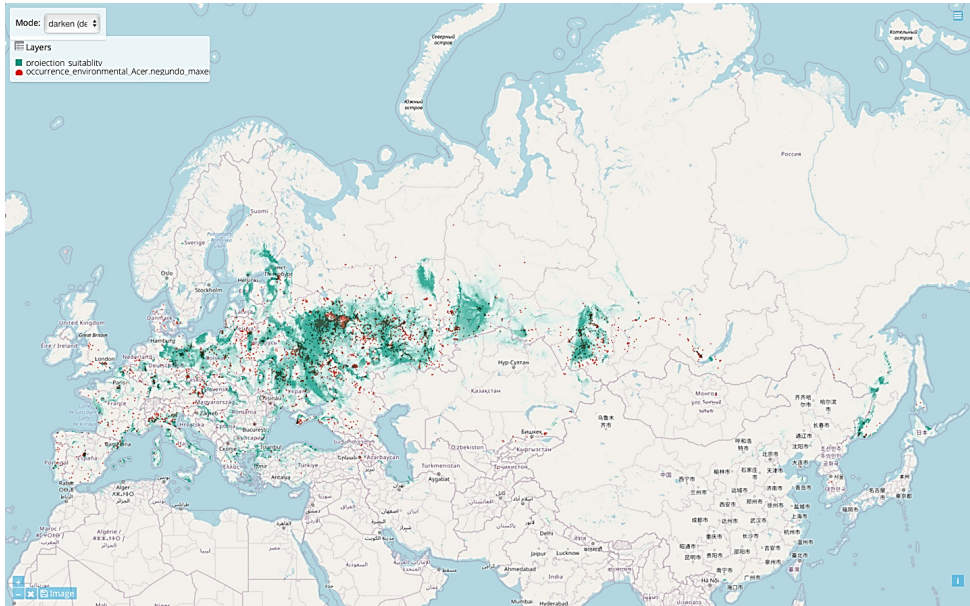


Figure 3. Map depicting the predicted suitable habitat for *A. negundo*. The gradations: 0.7-1 – ‘excellent’, dark green; 0.5-0.7 – ‘good’, green; 0.4-0.5 – ‘satisfactory’, light green; 0.2-0.4 – ‘bad’, gray-green; < 0.2 – ‘very bad’, colorless.

Discussion

Modeling approaches are essential for understanding the potential spread of *Acer negundo* and informing effective management strategies. Species distribution models (SDMs) are commonly used to predict suitable habitats for invasion based on environmental variables such as temperature, precipitation, and soil type (Lamarque et al. 2013). These models help identify regions at risk of invasion due to changing climatic conditions. Recent studies indicate that as climate conditions shift, suitable habitats for *A. negundo* may expand, increasing its invasive potential (Kozłowski et al. 2023). Such predictive modeling is crucial for proactive management efforts aimed at preventing further spread. Effective management strategies are vital for

mitigating the impacts of *A. negundo* invasion. Prevention is often cited as the best approach; avoiding the planting of this species or allowing it to set seed near sensitive areas is critical (Brademann A, McKenna K 2024). When control is necessary, methods such as mechanical removal combined with chemical treatments have proven effective (Diamond Mowers 2024). Following removal, revegetation with native species can help restore ecological balance and prevent re-establishment.

The distribution modeling of *A. negundo* provides significant insights into its native range and invasive potential. Its adaptability and phenotypic plasticity contribute to its success as an invader in various ecosystems. Continued research on the factors influencing its distribution will be essential for developing effective management strategies to mitigate its ecological impacts. The ribbon pine forests exhibit a diverse array of meso- and micro-relief features, resulting in varying soil moisture and temperature conditions, such as ridge tops, depressions, lakeside areas, and riverbanks. These features facilitate the formation of different types of pine forest ecosystems, including mesophilic grass, grass-vaccinium types, steppe-grass, grass-lichen, lichen, and dead soil forests. *A. negundo* predominantly establishes itself as pure maple forests within associations of mesophilic grass and grass-vaccinium pine forests.

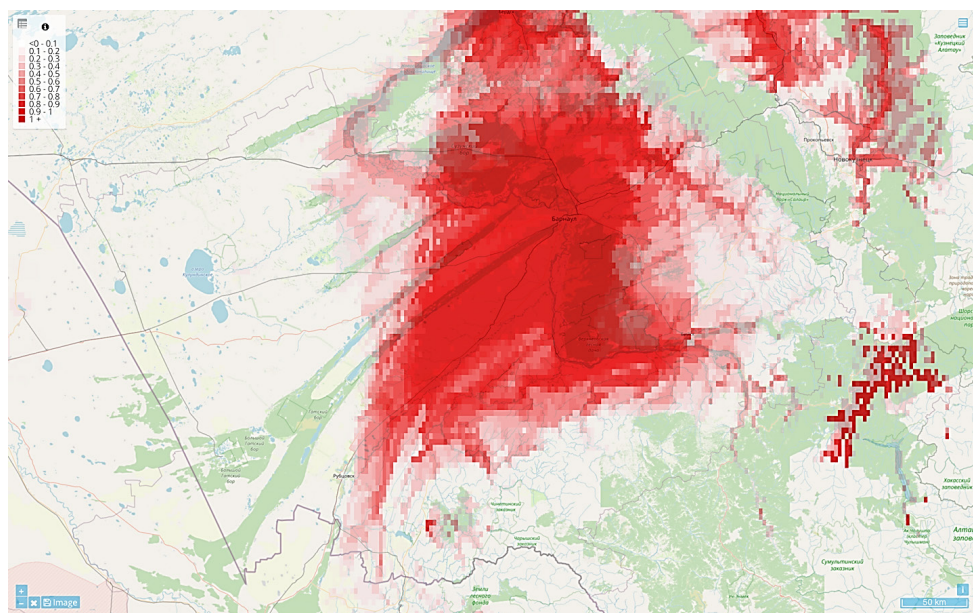


Figure 4. Map depicting the predicted suitable habitat for *A. negundo* (at the top left, scale range of 0–1) based on WorldClim bioclimatic variables (BIO1–19, temperature values, precipitation amount and topographic variable – altitude) for the Altai Krai.

Ribbon pine forests are characterized by soddy-podzolic soils, which have a light mechanical composition, contain up to 4% humus, and exhibit a slightly acidic to nearly neutral pH. The proximity of groundwater to the surface further influences these ecological conditions. These substrate characteristics, combined with the absence of a dense turf layer and various natural and anthropogenic factors, create favorable conditions for *A. negundo* to invade and thrive in these ecosystems. Local communities within ribbon pine forests are subject to anthropogenic transformations, including the removal of forest-forming species, litter accumulation, and mechanical disturbances of soil and vegetation cover, which facilitate the invasion of *A. negundo*. These disturbances alter the light and mineral regimes of the forests, leading to declines in local plant species and the development of pure maple forests in inter-ridge depressions.

A complex network of roads within the ribbon forests acts as a conduit for the invasion of *A. negundo*, particularly near urban areas. This species can spread from populated regions and forest edges into disturbed areas. Depending on the extent of soil and vegetation cover disturbance and moisture levels, *A. negundo* can become the dominant species within transformed communities, altering both natural and anthropogenic secondary successions in the ribbon forests of the Altai Territory. In the southwestern regions of the Kasmalinsky and Barnaulsky ribbon forests, where dry steppe conditions are less favorable, *A. negundo* occupies deep roadside ditches that accumulate water or slopes adjacent to bushy swamps. The freezing of branches in this region can lead to forked growth, resulting in *A. negundo* predominantly manifesting as a multi-trunked tree.

Analysis of *A. negundo* distribution within pine forests reveals distinctive biological and morphological traits. In the Altai Territory, *A. negundo* typically grows up to 20 meters tall, with crown widths and trunk diameters ranging from 5 to 70 cm. Under moderate soil moisture conditions, individuals develop as single-trunked upright trees. In shaded environments, the trees tend to form multiple trunks that often exhibit strong bending. The species is susceptible to snow breakage and periodic freezing of annual shoots, resulting in bush-like forms and significant self-seeding. Within ribbon pine forests, *A. negundo* demonstrates rapid growth and reproduces both by seeds and vegetative shoots, which can reach heights of 2 to 2.5 meters during the growing season. Our findings support previous research by Mędrzycki (2011), indicating that maple begins seed reproduction approximately five years after establishment in open, unshaded areas. Conversely, individuals growing in shaded conditions beneath the forest canopy may take 15 years or longer to commence seed production. In ribbon forests, *A. negundo* is recognized for its salinity tolerance, shade tolerance, and resistance to air pollution (Silantyeva et al. 2021).

Predictive distribution modeling for *A. negundo* across Eurasia identifies temperature as the primary limiting factor for the species, accounting for 80% of its distribution constraints, while topography and precipitation have lesser influences. Importantly, the analysis did not find a significant correlation between precipitation

levels and the distribution of the species. Bioclimatic modeling corroborates that temperature is the key determinant of *A. negundo*'s habitat range. The predictive model achieved high validity across all variables (AUC=0.97), suggesting that the potential distribution of *A. negundo* extends significantly beyond its current habitat boundaries, indicating a broad ecological amplitude and substantial potential for habitat expansion.

In southern Siberia, the predictive distribution model highlights a significant proportion of potentially suitable habitat for *A. negundo*. Regions classified as excellent encompass a substantial portion of the Altai Territory (over 35%), as well as significant areas in Novosibirsk (about 20%) and Kemerovo (around 15%) regions, with smaller portions in the southern Tomsk region (less than 5%, see Figs 3, 4). The bioclimatic model indicates that *A. negundo* is predominantly confined to plain areas, while in the southern regions, its distribution is restricted to foothill and low-mountain areas. Its ecological niche in the Altai Territory centers around the floodplains of the Ob River and its major tributaries (Alei, Charysh, Chumysh, Barnaulka, Kasmala, and Kulunda rivers) as well as adjoining pine forests in river valleys and their tributaries.

Conclusion

The invasion of *Acer negundo* into ribbon forest communities is shaped by a combination of climatic, edaphic, and topographical factors within the ancient river valleys that host these forests. Anthropogenic influences significantly impact the ecological conditions, facilitating the invasion process. In the northeastern regions, where mesophytic communities dominate, box elder establishes itself rapidly and abundantly, particularly in disturbed areas. Conversely, in the southwestern regions characterized by xerophytic communities, its presence is sporadic or absent. Predictive distribution modeling indicates that temperature is the primary limiting factor for *A. negundo* in the Altai Territory under current climatic conditions, while precipitation and topography have minimal effects. Given its reproductive and dispersal capabilities, *Acer negundo* could potentially spread across more than half of the Altai Territory, provided strong limiting factors, such as competition from other species or insect pests, are absent.

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