

Geospatial modelling of widely distributed oriental-beech forests syntaxa in the Northwestern Caucasus

Nikolay Shevchenko¹, Tatyana Braslavskaya¹, Anna Geraskina^{1,*}

¹Isaev Centre for Forest Ecology and Productivity of the Russian Academy of Sciences, Profsoyuznaya Street 84/32 bldg. 14, Moscow, 117997, Russian Federation

Abstract

SHEVCHENKO, N., BRASLAVSKAYA, T., GERASKINA, A., 2026. Geospatial modelling of widely distributed oriental-beech forests syntaxa in the Northwestern Caucasus. *Folia Oecologica*, 53 (3): 241–252.

For the first time in the Northwestern Caucasus, we applied the maximum entropy method (MaxEnt) to estimate the potential distribution of widespread oriental-beech forest syntaxa belonging to the alliance *Myosotido dissitiflorae–Fagion orientalis* Shevchenko et al. 2026. The models demonstrated good performance (AUC = 0.85–0.95) with variables characterizing precipitation, temperature, and altitude. Maps were constructed, and potential distribution areas of oriental-beech forests in the region were identified. The most significant bioclimatic predictors in the models of all studied syntaxa were found to be precipitation seasonality and annual precipitation. The potential distribution area of oriental-beech forest syntaxa was found to encompass the foothill, mid-mountain, and high-mountain zones of the central and eastern parts of the Northwestern Caucasus, with the exception of the western part of the region and the Black Sea coast, where these syntaxa are found only locally in well-watered mesorelief conditions. Geospatial modelling revealed significant similarities between oriental-beech and hornbeam forests in terms of their growing conditions in the Northwestern Caucasus. Therefore, the oriental-beech and hornbeam forests of the Northwestern Caucasus can be considered as mosaic elements within the oligo- or polydominant stands of broadleaf forests in the region. The resulting models of the potential distribution of oriental-beech forests can be used in geobotanical mapping, forest vegetation inventories, and clarification of syntaxa distribution boundaries in the Northwestern Caucasus and Northwestern Transcaucasia. The obtained results are essential for informed conservation planning and sustainable use of the region's unique oriental-beech forests, rich in endemic animal and plant species, under conditions of modern anthropogenic impact.

Keywords

bioclimatic predictors, geospatial modelling, MaxEnt, Northwestern Caucasus, oriental-beech forests

Introduction

Oriental-beech forests of the Northwestern Caucasus are unique highly productive communities with a high diversity of endemics and relics of forest flora which perform important environment-regulating functions (ORLOV, 1953; GROSSGEYM, 1948). They occupy about 1/4 of the forested area and 1/3 of the area of the broadleaf forests of the region (KOVAL et al., 1995). A regional feature of the oriental-beech forests in the Northwestern Caucasus is that they

almost completely lack Euxine and Mediterranean species, which brings these forests closer to the oriental-beech forests of the Central Georgia. And at the same time they differ from communities on the Black Sea coast and in the mountains of the Eastern Bulgaria, Northern Turkey, and Colchis (QUÉZEL et al., 1980; PASSARGE, 1981; WILLNER et al., 2017). According to Braun-Blanquet (ecological-floristic) classification of vegetation, oriental-beech forests belong to order (ord.) *Rhododendro pontici–Fagetalia orientalis* Passarge 1981 within class (cl.) *Carpino-Fage-*

*Corresponding author:

e-mail: angersgma@gmail.com

© 2026 Authors. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>)

tea sylvaticae Jakucs ex Passarge 1968. Most of the studies on syntaxonomic analysis of oriental-beech forests of the Northwestern Caucasus were performed in a limited area and are based on a small number of vegetation relevés (KOROTKOV and BELONOVSKAYA, 1987; FRANTSUZOV, 2006; SOKOLOVA, 2022). A recent new analysis of these forests (SHEVCHENKO et al., 2026) using 178 relevés made it possible to identify 4 new associations (one of them with 2 subassociations) and a new North-Caucasian alliance (all.) of oriental-beech forests, that is *Myosotido dissitiflorae–Fagion orientalis* Shevchenko et al. 2026. Mapping and geospatial modelling of oriental-beech forest syntaxa of this region, as well as assessment of the contribution of various environmental factors to their spatial distribution, are necessary for well-grounded planning of forest protection and rational use in the setting of their continued extensive exploitation.

Scientific foundations of sustainable forest management increasingly include methods of regression analysis that make it possible to create models of correlation between environmental factors (predictors) and forest ecosystems, analyse predictors, test biological hypotheses, and use these data to predict the future development dynamics of forests and their biotic components. In most cases, the tasks of mapping various characteristics of forest ecosystems are solved using geospatial modelling methods (SHIT et al., 2021). The maximum entropy method (MaxEnt) has become very popular among machine learning methods for building regression models (PHILLIPS et al., 2017). Applying spatial distribution extrapolation based on the maximum entropy method, MaxEnt estimates the environmental suitability threshold of the studied objects in various geographical locations, analysing presence-only data for these objects in some locations with known values of environmental factors together with information on the geospatial distribution of all values of the same factors (ELITH et al., 2011).

The most significant methodological limitations of using the MaxEnt program (PHILLIPS et al., 2017) in modelling potential ranges include sampling bias, overfitting, multicollinearity of predictors, ignoring biotic interactions, spatial heterogeneity of field data, and uncertainty arising from extrapolation to new environmental conditions. Therefore, MaxEnt results should be considered as an assessment of the potential ecological suitability of an area, rather than an exact prediction of the actual distribution of a species, and, whenever possible, confirmed by independent field observations and additional models.

The scientific novelty of the research lies in mapping syntaxa and identifying predictors that determine the modern distribution of oriental-beech forests in the Northwestern Caucasus using open datasets and our own geobotanical descriptions of forest communities. Only recently have studies on geospatial modelling of vegetation in Western and Eastern Europe (unions, orders in the Braun-Blanquet classification, and sometimes associations) or habitat types based on remote sensing predictors begun to appear in vegetation science (FISCHER et al., 2019; KOZHEVNIKOVA, 2019; PERRIN, 2023; GAFUROV, 2024). In

general, the analysis of the influence of climate change at the plant community level is very rare (HADINEJAD et al., 2025), despite the fact that the impact of climate change on the ranges of individual plant species is widely modeled, including using the MaxEnt algorithm (DAD and RASHID, 2025). Community-level analysis has been performed, for example, for deciduous forests in the Central Highlands of Vietnam (TUAN et al., 2026). For the Caucasus, similar studies using this approach have only been carried out by the authors of the article for hornbeam forests of the Northwestern Caucasus (SHEVCHENKO et al., 2025).

The purpose of the study is to use geospatial modelling methods in order to determine the limits and area of potential range of oriental-beech forest syntaxa belonging to the alliance (all.) *Myosotido dissitiflorae–Fagion orientalis* in the Northwestern Caucasus and to evaluate the influence of various bioclimatic factors on their distribution.

The following hypotheses were used in the study: 1. Will the potential range of the oriental-beech forests in the region occupy most of the foothill and mountain areas of the central and eastern parts of the forest belt of the Northwestern Caucasus? 2. Will the potential ranges of the hornbeam and oriental-beech forests in the region coincide completely? 3. Will precipitation-related predictors outweigh temperature predictors?

Materials and methods

Study area

In the Northwestern Caucasus, the main massifs of oriental-beech forests grow predominantly in the mid-mountain zone, stretching from the basin of the Pshekh River in the west to the basin of the Zelenchuk River in the east. They form a wide reach of woodland covering the northern slopes of the Peredovoy Range and the slopes of the low mountains that occupy the northern depression between the Skalisty and Peredovoy Ranges. Fragments of beech forests are also found in the high-mountain part of the Main Range and in the foothills occupied by hornbeam-oak forests. The most highly productive beech forests in the Northwestern Caucasus are widespread at altitudes from 700 to 1,300 m asl, where they occupy the largest area and predominate over other forest formations (ORLOV, 1953; KHUTORTSOV, 1967).

The study area (Fig. 1) includes mountainous and foothill territories in the south of the Krasnodar Krai and in the Republics of Adygea and Karachay-Cherkessia (west of Mount Elbrus) between 43.5° and 44.8° N (approximately 120 km long) and between 38.5° and 41.5° E (approximately 450 km). In the floristic zoning systems of the Caucasus, the north-western part of the northern macro-slope of the Greater Caucasus is assigned to the province of the Transkuban region (KUZNETSOV, 1909), later to the Kuban region (GROSSGEYM, 1948), whereas the central part of the southern macro-slope is assigned to the Iberian province (KUZNETSOV, 1909) or to the Kartalinsky district (GROSSGEYM, 1948). On the eastern boundary of the study

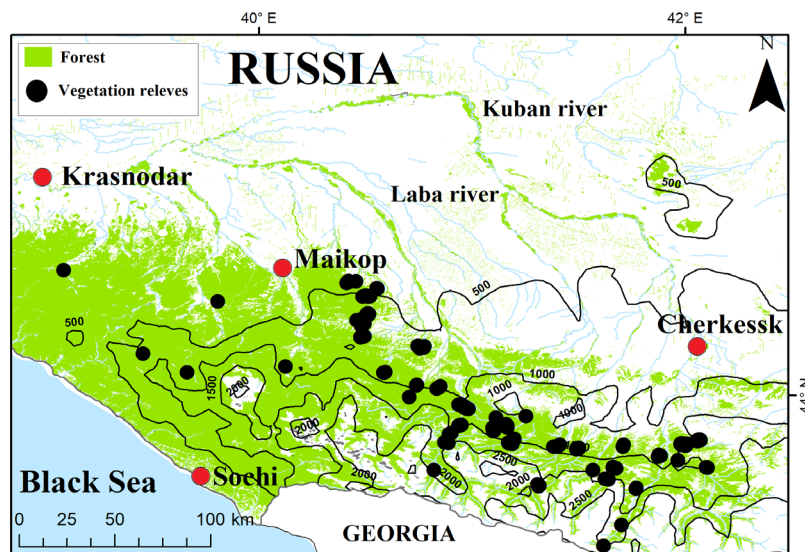


Fig. 1. Map of vegetation relevé points of oriental-beech forests belonging to all. MF in the Northwestern Caucasus. All. – alliance; MF – *Myosotido dissiflorae*–*Fagion orientalis*.

Detailed description of Fig. 1: A map of the studied area with the countries: Russia and Georgia, the cities: Krasnodar, Maikop, Sochi, Cherkessk, rivers: Kuban River, Laba River; and also the Black Sea. The vegetation description points are located in the forest belt of the Northwestern Caucasus in Russia.

area, complex mountain structures belonging to the area of the Alpine orogeny (GVOZDETSKIY, 1963) have altitudes up to 4,047 m asl (Dombay-Ulgen mountain). By true altitudes, the territory is divided into the following altitudinal zones (Safarov, Olisaev, 1990): below 200 m asl – foothill, 200–600 m asl – low-mountain, 600–1,400 m asl – mid-mountain, 1,400–2,000 m asl – high-mountain, 2,000–2,400 m asl – subalpine, above 2,400 m asl. — alpine.

The climate in the potential range of beech forests of the Northwestern Caucasus is temperate, with mild winters and humid summers. Mean annual temperature is 8–9 °C, mean temperature of warmest month (July–August) is 18–19 °C, and that of coldest month (January) is 2–3 °C below zero. The duration of the active growing season (with a daily maximum temperature of 10 °C or higher) is 170–175 days. Annual precipitation on this territory ranges from 930 mm in the western regions to 750 mm in the eastern regions (GVOZDETSKIY, 1963).

Target syntaxa

Oriental-beech forests in the Caucasus are represented by two ecological-floristic types: on the northern macro-slope, it is the North Caucasian type without evergreen understory species and with the constant participation of nemoral herblike species widespread in Europe; on the southern macro-slope, the Iberian type, again without evergreen species in the understory and at the same time with some boreal species in the ground cover (SOCHAVA, 1949). Broadleaf and dark coniferous-broadleaf forests of the North Caucasian type (mesophytic, hygro- and xeromesophytic) with *Fagus orientalis* dominating in the tree layer (SHEVCHENKO et al., 2026) and mesophilous species common to cl. *Carpino-Fagetea sylvaticae* Jakucs ex Passarge

1968 dominating in the grass layer are assigned to ord. *Rhododendro pontici*–*Fagetalia orientalis* Passarge 1981 (MUCINA et al., 2016). Communities of the order are common in the South-Eastern Europe and in the Asia Minor: in the Balkan and Turkish Black Sea regions (Soó, 1964; HORVAT et al., 1974; QUÉZEL et al., 1980, 1992; TZONEV et al., 2006; KAVGACI et al., 2012, 2023), in the Caucasus and Transcaucasia (Soó, 1964; PASSARGE, 1981; FRANTSUZOV, 2006; GHOLIZADEH et al., 2020; ERMAKOV et al., 2023), as well as in the Mountainous Crimea (MUCINA et al., 2016; DUBINA et al., 2019).

Data collection and optimized MaxEnt modelling

Field studies of forest vegetation were conducted by the authors in 2014–2018 together with a systematic traversing of the least fragmented forests of the Northwestern Caucasus occupying the maximum areas in river valleys. During these studies, 191 vegetation relevés of oriental-beech forests were performed. The geographical coordinates of the relevés (decimal, up to the fifth digit after the dot) were recorded using a Garmin 67 GPS navigator.

As a result of the conducted analysis of the relevés (SHEVCHENKO et al., 2026), oriental-beech forest syntaxa of the Northwestern Caucasus were identified as part of all. *Myosotido dissitiflorae*–*Fagion orientalis* Shevchenko et al. 2026. Geospatial modelling was performed for syntaxa represented by more than 10 relevés: association (ass.) *Aro maculati*–*Fagetum orientalis* Shevchenko et al. 2026 (50) (ass. AF), ass. *Myosotido dissitiflorae*–*Fagetum orientalis* subass. *typicum* Shevchenko et al. 2026 (93) (ass. MFt), ass. *Myosotido dissitiflorae*–*Fagetum orientalis* subass. *piceetosum orientalis* Shevchenko et al. 2026 (26) (ass. MFp), and ass. *Lonicero caprifolii*–*Fagetum*

orientalis Shevchenko et al. 2026 (22) (ass. LF), as well as for the entire all. *Myosotido dissitiflorae–Fagion orientalis* (191) (all. FM).

Geospatial modelling of potential range of oriental-beech forest syntaxa in modern conditions was performed using the MaxEnt software, version 3.4.1, available from the MaxEnt software website at www.cs.princeton.edu/~schapire/maxent/, where the spatial distribution is extrapolated using the maximum entropy method (ELITH et al., 2011). When building the model, the default settings were used, i.e. all classes of spatial objects were involved, the maximum number of iterations (500) and the maximum number of background points (10,000) were used (PHILLIPS and DUDÍK, 2008), the regularization multiplier was set to 1.0, and the convergence threshold was set to 0.00001. The output format chosen was cloglog, which provided habitat suitability values ranging from 0 to 1. The replicated run type is crossvalidate, and the apply threshold rule is 10 percentile training presence. This threshold is one of the most common in MaxEnt modelling, as it allows for the exclusion of a small proportion (10%) of training points that may be due to georeferencing errors, inaccurate location determinations, or species registration in atypical habitats. This approach reduces the impact of outliers and yields a more conservative and robust estimate of the species' potential distribution.

To test the obtained models, 25% of the points that initially did not participate in the training were used. Although the 1.0 setting is used by default, in our case, the training set size is several times larger than the number of predictors. Under these conditions, default regularization performs its primary function – preventing multicollinearity and stabilizing weights without suppressing biologically significant responses, as evidenced by response curves free of artifactual peaks.

Predictors in the models were 19 bioclimatic variables (bioclim) presented in the WorldClim version 2.1 open climate database (www.worldclim.org; accessed on 18 April 2025), which allow interpolation of observed data for the period from 1950 to 2000 (current) (HIJMAN et al., 2005) with a resolution of 30 arcseconds (~1 km²). The projection used in this work is WGS 84 / Pseudo Mercator. The following indicators were used: bio1 – annual

mean temperature (°C); bio2 – mean diurnal range (mean of monthly (max temp – min temp)); bio3 isothermality (bio2/bio7) × 100; bio4 – temperature seasonality (standard deviation for the year × 100); bio5 – max temperature of warmest month (°C); bio6 – min temperature of coldest month (°C); bio7 – temperature annual range (bio5–bio6) (°C); bio8 – mean temperature of wettest quarter (°C); bio9 – mean temperature of driest quarter (°C); bio10 – mean temperature of warmest quarter (°C); bio11 – mean temperature of coldest quarter (°C); bio12 – annual precipitation (mm); bio13 – precipitation of wettest month (mm); bio14 – precipitation of driest month (mm); bio15 – precipitation seasonality (coefficient of variation – CV); bio16 – precipitation of wettest quarter (mm); bio17 – precipitation of driest quarter (mm); bio18 – precipitation of warmest quarter (mm); bio19 – precipitation of coldest quarter (mm), and elevation.

Optimized MaxEnt model

For each syntaxon, a sample of points where it was registered was used to calculate pairwise Pearson correlation coefficients between 20 predictors of the WorldClim database using the ArcGIS and Excel programs (WARREN et al., 2010). For further research, after conducting correlation analysis, the following bioclimatic predictors were proposed: for all. MF – bio5, bio8, bio12, bio15; for ass. AF – bio1, bio15, bio18; for ass. LF – bio1, bio8, bio12, bio15; for ass. MFt – bio8, bio12, bio15, bio18; ass. MFp – bio5, bio12, bio15.

After that, strongly correlated ($|r| > 0.7$) predictors were excluded from the modelling. Non-correlating predictors were used for model construction. Its reliability was assessed using the built-in AUC (area under receiver operating characteristic (ROC) curve) plotting function; the curve reflects the sensitivity of the modelled object to the predictors of the model and the object specificity. An AUC value above 0.75 and close to 1 indicates a high degree of reliability (ELITH, 2002). To assess the relative contribution of predictors to the construction of the model, the jack-knife analysis was used.

The True Skill Statistic (TSS) metric was used to assess the predictive ability of models built in Maxent.

Table 1. Number of occurrence records per species before and after applying spatial thinning with a minimum distance of 1 km. The thinning procedure reduced the total number of points by 5.9%, removing spatial clusters to minimize spatial autocorrelation and sampling bias, while maintaining a representative geographic coverage of the study area.

No.	Syntaxon	Records before thinning	Records after thinning	% Reduction
1	All. MF	208	191	5.9
2	Ass. AF	56	50	10.7
3	Ass. LF	23	22	4.3
4	Ass. MFt	101	93	7.9
5	Ass. MFp	28	26	7.1

All. MF – alliance *Myosotido dissitiflorae–Fagus orientalis*; Ass. AF – association *Aro maculate–Fagetum orientalis*; Ass. LF – association *Lonicero caprifolii–Fagetum orientalis*; Ass. MFt – association *Myosotido dissitiflorae–Fagetum orientalis* subass. *typicum*; Ass. MFp – association *Myosotido dissitiflorae–Fagetum orientalis* subass. *piceetosum orientalis*.

Table 2. Contribution of bioclimatic predictors (%) to the construction of models of the potential range of oriental-beech forests belonging to the alliance *Myosotido disitiflorae-Fagus orientalis* in the North Western Caucasus.

No.	Syntaxon	AUC	TSS	Prediction	Contribution in model (%)
1	All. MF	0.95	0.80	bio12	40.8
1	All. MF	0.95	0.80	bio15	27.5
1	All. MF	0.95	0.80	bio 8	16.7
1	All. MF	0.95	0.80	bio5	15.0
2	Ass. AF	0.90	0.74	bio18	54.5
2	Ass. AF	0.90	0.74	bio15	26.8
2	Ass. AF	0.90	0.74	bio1	18.4
3	Ass. LF	0.80	0.67	bio12	48.0
3	Ass. LF	0.80	0.67	bio15	27.4
3	Ass. LF	0.80	0.67	bio8	11.4
3	Ass. LF	0.80	0.67	bio1	13.2
4	Ass. MFt	0.95	0.67	bio15	45.9
4	Ass. MFt	0.95	0.71	bio12	21.0
4	Ass. MFt	0.95	0.71	bio18	19.4
4	Ass. MFt	0.95	0.71	bio8	13.7
5	Ass. MFp	0.80	0.66	bio15	54.3
5	Ass. MFp	0.80	0.66	bio12	31.9
5	Ass. MFp	0.80	0.66	bio5	13.8

All. MF – alliance *Myosotido disitiflorae-Fagus orientalis*; Ass. AF – association *Aro maculate-Fagetum orientalis*; Ass. LF – association *Lonicero caprifolii-Fagetum orientalis*; Ass. MFt – association *Myosotido dissiflorae-Fagetum orientalis* subass. typicum; Ass. MFp – association *Myosotido dissiflorae-Fagetum orientalis* subass. *piceetosum orientalis*; AUC – area under the receiver operating characteristic (ROC) curve; TSS – true skill statistics; bio1 – annual mean temperature, bio5 – max temperature of warmest month (°C); bio8 – mean temperature of wettest quarter (°C); bio12 – annual precipitation (mm); bio15 – precipitation seasonality (coefficient of variation – CV); bio18 – precipitation of warmest quarter (mm).

Data processing was performed in ArcGIS 10.6.1. TSS is a threshold-dependent criterion that accounts for both omission and false inclusion errors and is robust to species prevalence. Model quality was interpreted as follows: TSS values > 0.65 were considered evidence of high predictive ability.

To reduce spatial sampling error, we visually inspected the occurrence data for clustering and assessed spatial autocorrelation. Some syntaxa exhibited clusters with similar, identical coordinates. To address this issue, we applied spatial thinning, setting the minimum nearest neighbor distance to 1 km. To further verify the spatial distribution of occurrence and the absence of sampling error, we plotted all filtered occurrence points on a map of the study area boundary and ecological layers. These distribution maps confirmed adequate spatial coverage and served as the basis for subsequent niche modelling. After thinning, 191 unique, spatially confirmed occurrence points remained; 208 occurrence points were used in the initial stage. Background points were also restricted to the study area (Table 1). After evaluating the reliability of the model and determining the contribution of each predictor to it, a map of the most likely (with an environmental suitability threshold above 0.5) distribution range of the syntaxon under study was built. MaxEnt maps were visualized using the ArcGIS 10.6.1 program (SCHEDEMAN and VAN ZONNEVELD, 2010).

Results

When modelling the potential range in the Northwestern Caucasus of oriental-beech forest syntaxa belonging to all. MF using the MaxEnt software, good performance results of geospatial models were obtained: with AUC = 0.80–0.95; TSS = 0.66–0.80 (Table 2). This allows us to conclude that the constructed maps reliably characterize the features of the potential distribution of the studied syntaxa.

In general, oriental-beech forests of all. MF (Table 1S, Fig. 2a) are found in the valleys of the rivers Kuban, Belaya, Bolshaya Laba, Zelenchuk, Kefar, Urup, Teberda, Psheha, Gubs, Mara, Aksaut, etc. (Krasnodar Krai, Republic of Adygea, Karachay-Cherkess Republic), from low-mountain to high-mountain regions with the altitude range (244) 560–1,690 m. These forests grow in well-drained areas of different slopes, mainly in the north-western, northern and western exposures. The soils are loamy and clay stony, medium-thick and shallow brown forest soils. Traces of selective logging were noted in almost all communities; no traces of fire were found. Total potential range (with an environmental suitability threshold above 0.5) of the forests of this alliance is 16,848 km². The northern boundary of its potential range corresponds to the northern boundary of the forest distribution in the Northwestern Caucasus, descend-

ing to 300–500 m asl, the southern one rises along the valleys of mountain rivers of the northern macro-slope of the Greater Caucasus Range to an altitude of 2,000–2,500 m asl, the western one runs along the upper reaches of the Belaya River, and the eastern one — along the upper reaches of the Kuban River. The largest contribution (Table 2) to the construction of the model ($\geq 10\%$) is made by the annual precipitation (bio12); mean temperature of wettest quarter (bio8); max temperature of warmest month (bio5) and precipitation seasonality (bio15).

Forests of ass. AF (Table 2S, Fig. S1a, Fig. 2b) are distributed mainly in mid-mountain regions (sometimes on the upper boundary of the low-mountain zone) at altitudes from 540 to 1,200 (1,400) m, in the valleys of the Bolshaya and Malaya Laba, Belaya, Gubs and Psefir rivers (Republic of Adygea, Krasnodar Krai). Forests grow on gentle and sloping slopes of the northern, north-western or north-eastern exposures, on well-moistened thick loamy and clay brown and gray forest soils. The potential range (with an environmental suitability threshold above 0.5) for this association is 5,412 km². The northern boundary of the potential range corresponds to the northern boundary of forest distribution in the Republic of Adygea and partly in the Krasnodar Krai, descending to an altitude of 350–400 m asl, the southern one rises along the northern macro-slope of the Greater Caucasus Range to an altitude of 1,000 m asl, the western one runs along the valley of the Belaya River, and the eastern one — along the Bolshaya Laba River. The area most suitable (area of 1,953 km²) for the distribution of the association (with an environmental suitability threshold above 0.7) is confined to the upper reaches of the interfluvium of the Belaya and Malaya Laba rivers. The greatest contribution (Table 2) to the construction of the model ($\geq 10\%$) is made by precipitation of

warmest quarter (bio18), which is the predominant factor, and by precipitation seasonality (bio15) and annual mean temperature (bio1).

Forests of ass. LF (Table 3S, Fig. S1b, Fig. 2c) are distributed mostly in the valleys of the Urup, Teberda, Bolshaya Laba, Pshekh and Gubs rivers (Karachay-Cherkess Republic, Republic of Adygea and Krasnodar Krai), in the mid-mountain zone at altitudes of 600–1,330 m, less often in the low-mountain zone (370–500 m), occasionally in the foothills (96 m) and in the high-mountain zone (1,500 m). Forests occupy well-drained gentle and sloping (sometimes steep) slopes of the north-western and north-eastern, less often — southern exposure. The soils are loamy stony brown forest soils. The area of distribution (with an environmental suitability threshold above 0.5) of the association is 11,157 km². The northern boundary of the potential range of this syntaxon does not extend beyond the northern boundary of the modern distribution of forests in the region, in the south, the boundary in places rises along the valleys of rivers flowing down from the northern macro-slope of the Greater Caucasus Range to an altitude of 2,000–2,100 m asl, in the west, the boundary runs along the coast of the Black Sea, and in the east — along the upper reaches of the Kuban River. The most significant contribution (Table 2) to the construction of the model was made by the following bioclimatic predictors: annual precipitation (bio12), precipitation seasonality (bio15) and mean temperature of wettest quarter (bio8).

Typical communities of ass. MFt (Table 4S, Fig. S1c, Fig. 2d) are found from low-mountain to high-mountain regions of the valleys of the Kuban, Belaya, Bolshaya Laba, Zelenchuk, Kefar, Urup, Teberda, Pshekh, Gubs, Mara, Aksaut, etc. rivers, in the altitude range of (244) 560–1,690 m. These forests grow in well-drained areas of different slopes,

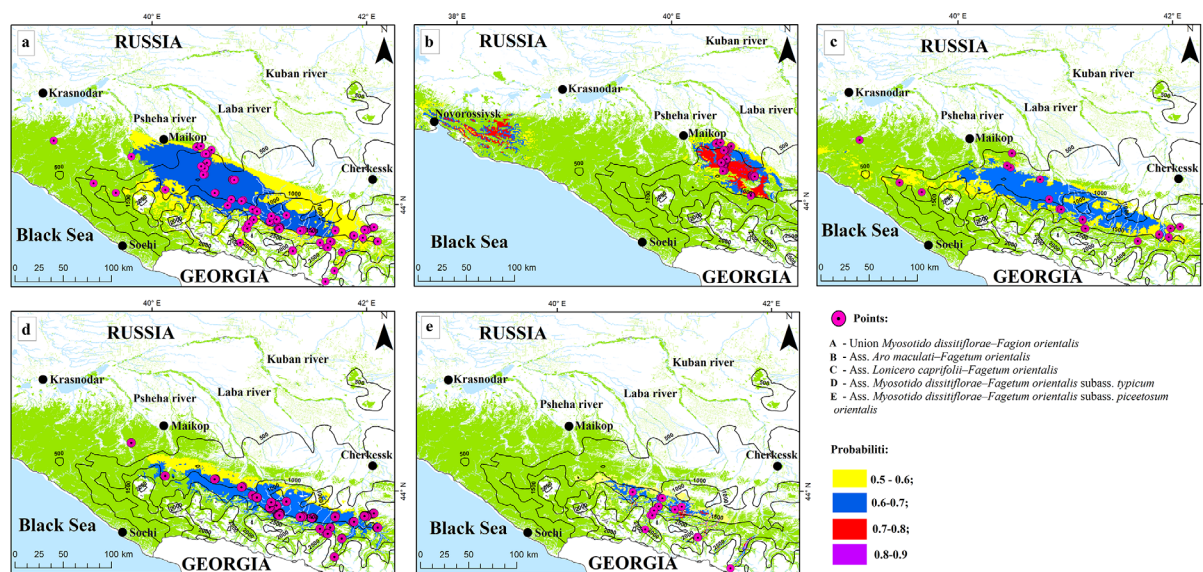


Fig. 2. Maps of potential ranges of the most common syntaxa of oriental-beech forests belonging to all. MF in the Northwestern Caucasus, with an environmental suitability threshold above 0.5. All. – alliance; MF – *Myosotido dissitiflorae*-*Fagetum orientalis*.

Detailed description of Fig. 2: On five maps (for each syntaxon) the thresholds of ecological suitability from 0.5 to 0.9 are indicated by color gradations. Geographical names (countries, cities, rivers, etc.) as in Figure 1.

mainly in the north-western, northern and western exposures. The soils are loamy and clay stony, medium-thick and shallow brown forest soils. The area of distribution (with an environmental suitability threshold above 0.5) of this syntaxon is 7,492 km². The northern boundary of its potential area runs at the altitudes from 500 to 1,000 m asl of the forest zone of the northern macro-slope, in the south the boundary in places rises along river valleys to an altitude of 2,500 m asl, in the west the boundary runs along the valley of the Belaya River, and in the east – along the upper reaches of the Kuban River. The most significant contribution (Table 2) to the construction of the model was made by the following bioclimatic predictors: precipitation seasonality (bio15), annual precipitation (bio12) and precipitation of warmest quarter (bio18).

Forests of ass. MFp (Table 5S, Fig. S1d, Fig. 2e) are distributed mostly in the mid-mountain and high-mountain regions of the Northwestern Caucasus: in the altitude range (500) 800–1,690 m, in the upper reaches of the Bolshaya Laba, Belaya, Zelenchuk, Teberda and Urup rivers (Karachay-Cherkess Republic, Republic of Adygea). They occupy sloping and steep slopes mainly of the north-western, south-eastern and south-western exposures on the above flood-plain terraces

in the valleys of mountain rivers. They grow on shallow (less often medium-thick) loamy brown forest soils with underlying stones, with or without signs of sheet erosion. The area of distribution (with an environmental suitability threshold above 0.5) of the forests of this subassociation is 4,685 km². The northern boundary of its potential area runs at altitudes not lower than 1,000 m asl of the forest zone, the southern boundary runs along the upper reaches of the rivers up to an altitude of 2,500 m asl, the western boundary runs along the valley of the Belaya River, and the eastern boundary is the Makhar River (in the upper reaches of the Kuban River). The following climatic predictors made the greatest contribution (Table 2) to the construction of a model of the potential range of this subassociation: precipitation seasonality (bio15), annual precipitation (bio12) and max temperature of warmest month (bio5).

Description of the bioclimatic predictors contributing most to the construction of the model

The greatest contribution to the construction of models of

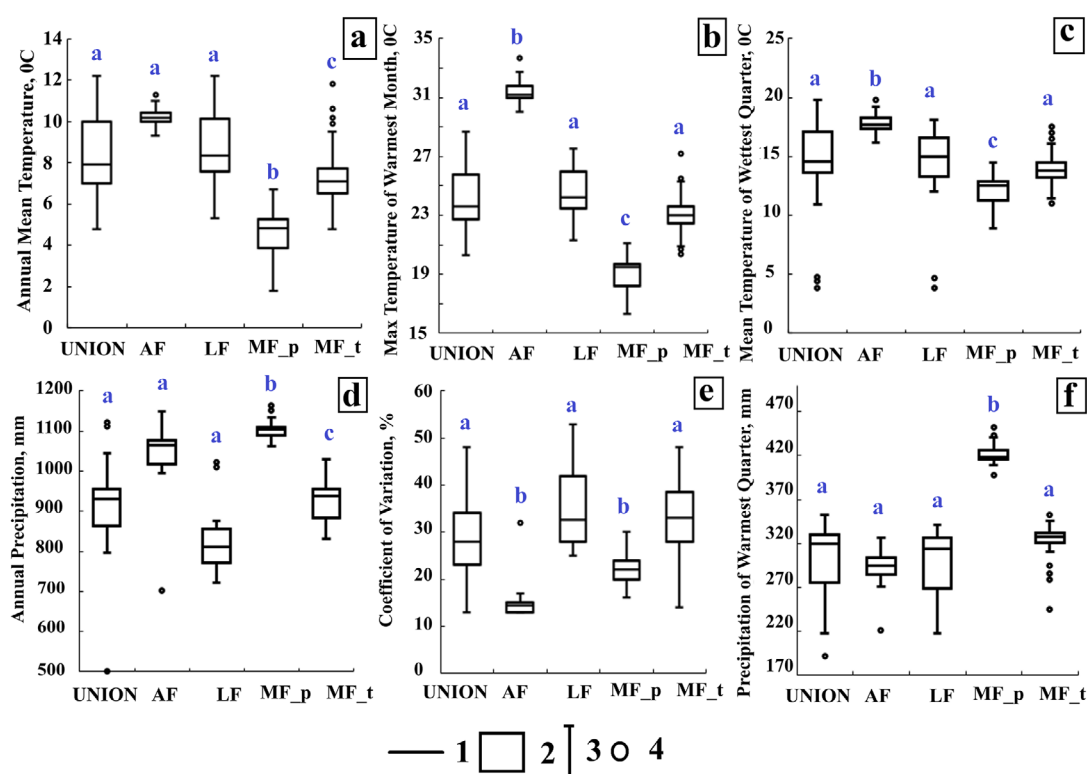


Fig. 3. Values of bioclimatic predictors contributing most to the construction of the model of oriental-beech forest syntaxa of the alliance *Myosotido dissitiflorae-Fagion orientalis* in the Northwestern Caucasus: Union – alliance MF – *Myosotido dissitiflorae-Fagion orientalis*; association AF – *Aro maculate-Fagetum orientalis*; association LF – *Lonicero caprifolii-Fagetum orientalis*; association MF_p – *Myosotido dissitiflorae-Fagetum orientalis* subass. *piceetosum orientalis*; association MF_t – *Myosotido dissitiflorae-Fagetum orientalis* subass. *typicum*; 1 – medians, 2 – interquartile ranges, 3 – ranges between minimum and maximum, 4 – outliers. Within each diagram, different lowercase letters indicate significant differences between syntaxa, whereas the same lowercase letters indicate insignificant differences.

Detailed description of Fig. 3: Six boxplots of variation of bioclimatic predictors (annual mean temperature, max temperature of warmest month, mean temperature of wettest quarter, annual precipitation, precipitation seasonality, precipitation of warmest quarter) are presented for each studied syntaxon of eastern beech forests.

the potential range of oriental-beech forest syntaxa in the Northwestern Caucasus was made by: annual mean temperature (bio1), max temperature of warmest month (bio5), mean temperature of wettest quarter (bio8), annual precipitation (bio12), precipitation seasonality (coefficient of variation) (bio15) and precipitation of warmest quarter (bio18).

Among the considered oriental-beech forest syntaxa, the highest value of the annual mean temperature (bio1) (Fig. 3a) was noted for ass. AF (10.2 ± 0.5 °C), whereas the lowest – for ass. MFp (4.4 ± 1.1 °C). The remaining considered syntaxa have intermediate comparable values (from 7.3 ± 1.1 °C to 8.7 ± 1.7 °C).

The highest values of the max temperature of warmest month (bio5) (Fig. 3b) as well as the mean temperature of wettest quarter (bio8) (Fig. 3c) are registered for ass. AF (31.4 ± 0.7 °C/ 17.8 ± 0.7 °C, respectively), the lowest — for ass. MFp (18.9 ± 1.2 °C / 12.1 ± 1.3 °C), for the considered syntaxa these indicators have intermediate comparable values (from 23.0 ± 1.1 °C to 24.5 ± 1.6 °C / from 13.9 ± 1.5 °C to 14.9 ± 2.5 °C).

The highest annual precipitation (bio12) (Fig. 3e) was noted for ass. MFp ($1,101.2 \pm 25.1$ mm), the lowest – for ass. LF (821.5 ± 38.1 mm), whereas the values for ass. AF, ass. MFt and for the entire all. MF are intermediate (877.8 ± 54.5 mm / 923.5 ± 45.8 mm, respectively).

The lowest value of precipitation seasonality (bio15) (Fig. 3d) was noted for the forests of ass. AF ($14.7 \pm 2.8\%$) and ass. MFp ($22.3 \pm 3.3\%$). In the remaining syntaxa, bio15 values are significantly higher (from $28.5 \pm 5.1\%$ to $34.4 \pm 7.3\%$), which is associated with a longer summer drought period.

The highest precipitation of warmest quarter (bio18) (Fig. 3f) was recorded for ass. MFp (422.0 ± 12.3 mm), while the values for the remaining considered syntaxa are comparable (from 293.6 ± 17.4 mm to 318.1 ± 15.4 mm).

Discussion

Geospatial modelling of oriental-beech forest syntaxa of all. MF (ord. *Rhododendro pontici-Fagetalia orientalis*) in the Northwestern Caucasus showed (Fig. 2a) that the potential range of the whole alliance covers the distribution territory of the region's broadleaf forests in the foothill, mid-mountain and high-mountain zones, with the exception of the foothill and low-mountain zones of the western part of the region and along the Black Sea coast (Northwestern Transcaucasia). This spatial distribution is due to the fact that oriental-beech forest syntaxa have a strong dependence on well-moistened soil throughout the year and do not tolerate well periods of prolonged drought. The territories of the western part of the region close to the Black Sea coast are characterized by a long period of summer drought, therefore this territory is unsuitable for the growth of oriental-beech forest syntaxa; alternatively, communities of oriental-beech forests occur locally and are confined to well-moistened meso-relief positions (such as the bottoms of gullies of forest rivers and the northern exposure of slopes).

The local persistence of oriental-beech forests in

the western part of the region, despite unfavorable macroclimatic conditions, demonstrates the significant role of mesorelief in the formation of ecological refugia. Ravine bottoms, narrow forest river valleys, and northern-facing slopes create their own microclimate, characterized by lower insolation, higher air and soil humidity, and reduced evaporation. Such habitats function as unique climatic refuges, allowing mesophilic forest communities to persist beyond their optimal climatic range. Consequently, spatial heterogeneity of the relief significantly increases the resilience of eastern beech forests to regional climate change.

Interestingly, modelling showed that the boundaries of the potential range of oriental-beech forest ass. AF almost completely coincided with the boundaries of hornbeam forest ass. *Aro maculati-Carpinetum betuli* (AC) belonging to all. *Crataego-Carpinion caucasicae* Passarge 1981 (ord. *Carpinetalia betuli* Fukarek 1968, cl. *Carpino-Fagetea sylvaticae* Jakucs ex Passarge 1968) (SHEVCHENKO and BRASLAVSKAYA, 2021). This can be due to several reasons. Firstly, the said association of oriental-beech forests can be considered as a late-successional stage of development of foothill and low-mountain broadleaf (oak-hornbeam, hornbeam and oak) forests that belong to all. *Crataego-Carpinion caucasicae* of the Northwestern Caucasus. Secondly, oriental-beech forests of ass. AF and hornbeam forests ass. AC can be considered as subcoenotic parcels as part of oligo- or poly-dominant tree stands of broadleaf forests of the region. At the same time oriental-beech forests of both ass. AF and ass. AC are confined to well-moistened soils on the slopes of forest gullies, gentle and sloping slopes of the northern, north-western or north-eastern exposures and have never been found on the southern slopes.

Due to orographically enhanced precipitation, high-mountain regions form habitats with the most stable moisture levels, which contributes to the preservation of the most mesophilic varieties of beech forests. However, such communities have a narrow ecological amplitude and therefore may be particularly sensitive to changes in the regional hydrological regime.

The potential range of oriental-beech forest ass. AF (Fig. 2b), as well as the potential range of hornbeam forest ass. AC, covers not only the eastern part of the Northwestern Caucasus, but also the foothill and low-mountain zone of Northwestern Transcaucasia along the Black Sea coast from Tuapse to Novorossiysk. As in the case of hornbeam forests ass. AC, in oriental-beech forests of this part of the Black Sea coast (ZERNOV, 2006) diagnostic species of ass. AF (*Arum maculatum* L., *Fagus orientalis* Lipsky, *Galium aparine* L., *Pachyphragma macrophyllum* (Hoffm.) N.Busch, *Symphytum caucasicum* Bieb.) are widespread. Therefore, it is reasonable to expect that in the Northwestern Transcaucasia along the Black Sea coast, the communities of not only hornbeam forest ass. AC, but also of oriental-beech forest ass. AF can be seen.

The distribution of ass. AF along the northwestern Black Sea coast predicted by the models is of significant biogeographical significance. The presence of diagnostic species of this association in this region indicates fa-

favorable environmental conditions for the formation of oriental-beech communities. Consequently, the modelling results can serve as the basis for a targeted search for new localities and a refinement of the syntaxonomic diversity of broadleaf forests in northwestern Transcaucasia.

According to the results of geospatial modelling (Table 2), for all considered syntaxa of oriental-beech forests within all. MF in the Northwestern Caucasus, as in the case of hornbeam forest syntaxa within ord. *Carpinetalia betuli*, the assessment of the bioclimatic predictors contribution to the construction of models showed that predictors characterizing precipitation distribution turned out to be more important than variables characterizing temperature conditions. The contribution of predictors characterizing precipitation distribution to the construction of models ranges from 68.3 to 86.3%. Most significant in the construction of models were the bioclimatic predictors characterizing precipitation seasonality (bio15) and annual precipitation (bio12), their contribution to the model construction ranging from 45.2 to 86.2% (Table 2). According to the results of geospatial modelling, ass. AF and ass. MFp have the lowest values of the bioclimatic predictor characterizing precipitation seasonality (bio15), which is associated with a relatively uniform distribution of precipitation throughout the year in the territory of the potential range of these syntaxa (ORLOV, 1953; GVOZDETSKIY, 1963; et al.) as compared to other oriental-beech forest syntaxa.

They occupy the most humid areas with a relatively uniform precipitation distribution throughout the year, while other syntaxa are adapted to more pronounced climatic seasonality. Consequently, within all. MF, there is a pronounced gradient of hydrological specialization, which determines the ecological differentiation of syntaxa and their spatial distribution.

Potential ranges of the remaining oriental-beech forest syntaxa extend much further west, where precipitation is significantly less in summer than in winter, and there is a distinct prolonged period of summer drought; therefore, the value of the predictor characterizing precipitation seasonality (bio15) there is higher as compared to the forests of ass. AF and ass. MFp. Moreover, ass. MFp also has the highest value of the predictor characterizing annual precipitation (bio12), which is associated with its high-mountain distribution, where, due to the barrier function of the mountains, significantly more precipitation falls during the year as compared to other oriental-beech forest syntaxa occupying lower altitudinal zones.

The high contribution of predictors characterizing precipitation seasonality and annual precipitation totals over temperature indicates that the oriental-beech forests of the Northwestern Caucasus are not simply mesophytes, but stenohygromesophytes. Their competitive advantage is realized only in conditions where summer moisture deficits are minimized. The identified dependence on intra-annual moisture distribution (rather than absolute quantity) indicates that for these forests, it is not so much the average annual norm that is critical, but rather the ecosystem's buffering capacity – the ability of the soil and mesorelief to accumulate winter-spring precipitation and maintain moisture throughout the growing season.

In recent decades, there has been a persistent trend towards increase in the value of precipitation seasonality (bio15) in all altitudinal zones in the Northwestern Caucasus (ZHAURBEKOV, 2012). In the regional context, this means an increase in the duration of the summer drought season. If this trend continues in the near future, there is a high probability of a reduction potentially suitable area in the region for the growth of such oriental-beech forest syntaxa within all. MF as ass. AF and ass. MFp, whose flora has a high proportion of mesophilous species that are highly vulnerable to prolonged summer droughts.

If this trend continues, we should expect a gradual shift in the ecological niches of oriental-beech forests toward more humid habitats – higher absolute altitudes, northern-facing slopes, and areas with favorable local hydrological regimes. There is a high probability of a reduction in the area of potentially suitable oriental-beech forest habitats in the foothill and low-mountain zones, where the impact of summer droughts is most pronounced. Changes in precipitation regimes may lead not only to spatial transformations of oriental-beech forest habitats but also to changes in their floristic composition and successional development patterns. The obtained results allow us to consider moisture regime indicators as key indicators of the resilience of oriental-beech forests in the Northwestern Caucasus to current climate change and emphasize the need to preserve areas that serve as climatic refugia, which in the future may become key centers for biodiversity conservation of the region's mesophilic broadleaf forests.

In the future, it is necessary to model changes in the potential ranges of oriental-beech forests under various climate scenarios and mathematical models up to 2080–2100. This will allow us to assess the scale of potential transformation of their ecological niches and identify areas most resilient to climate change. Furthermore, it is advisable to conduct a comparative analysis of the ecological niches of oriental-beech forests in various biogeographic regions of the Caucasus (Central, Eastern Caucasus, Transcaucasia) to identify common patterns of their distribution and the factors determining regional vegetation differentiation.

Conclusion

- According to geospatial modelling data, the potential range of oriental-beech forest syntaxa within all. MF covers the foothill, mid-mountain and high-mountain zones of the central and eastern parts of the Northwestern Caucasus, with the exception of the western part of the region and the Black Sea coast, where they can be found locally in well-moistened meso-relief positions.
- Geospatial modelling of all. MF syntaxa showed a strong similarity of growing conditions in the Northwestern Caucasus between the oriental-beech forest ass. AF and the hornbeam forest ass. AC (all. *Crataego–Carpinion caucasicae*), which is confirmed by the complete overlap of the boundaries of their potential ranges, the set and contribu-

tion of bioclimatic predictors to the geospatial models of their ranges.

- The most significant bioclimatic predictors of the considered oriental-beech forest syntaxa are variables characterizing precipitation seasonality (bio15) and annual precipitation (bio12), their contribution to the model construction ranging from 45.2 to 86.2%. For all. MF, such predictors are bio12, bio15, bio8 and bio5; for ass. AF — bio18, bio15, and bio1; for ass. LF — bio12, bio15, bio8 and bio1; for ass. MFp — bio15, bio12, bio18 and bio8; and for ass. MFt — bio15, bio12, and bio5.
- The resulting models of the potential distribution of oriental beech forests can be used in geobotanical mapping, forest vegetation inventories, and clarification of syntaxa distribution boundaries in the Northwestern Caucasus and North western Transcaucasia. The results can be used in developing biodiversity conservation measures and planning a network of specially protected natural areas, as well as in assessing the vulnerability of forest ecosystems to climate change.

Acknowledgements

The study was carried out with the financial support of the Russian Science Foundation No 25-24-00169, <https://rscf.ru/project/25-24-00169/>.

Supplementary material

Supplementary material for this article (Supplementary Tables 1S–5S and Supplementary Fig. S1) are openly available in Open Science Framework repository at <https://doi.org/10.5281/zenodo.22014924>

References

- DAD, J.M., RASHID, I., 2025. Effect of climate change on potential distribution of *Dactylorhiza hatagirea* (D. Don) Soó in the twenty-first century across the north-western Himalayas. *Folia Oecologica*, 52 (1): 48–61. <https://doi.org/10.2478/foecol-2025-0006>
- DUBINA, D.V., DZYUBA, T.P., EMELYANOVA, S.M., BAGRIKOVA, N.O., BORISOVA, O.V., BORSUKEVICH, L.M., VINOKUROV, D.S., GAPON, S.V., GAPON, YU.V., DAVIDOV, D.A., DVORETSKY, T.V., DIDUKH, YA.P., ZHMUD, O.I., KOZYR, M.S., KONSHCHUK, V.V., KUZEMKO, A.A., PASHKEVICH, N.A., RIFF, L.E., SOLOMAKHA, V.A., FELBABA-KLUSHINA, L.M., FITSAYLO, T.V., CHORNA, G.A., CHORNEY, I.I., SHEL'YAG-SOSONKO, YU.R., YAKUSHENKO, D.M., 2019. *Prodrom rastitel'nosti Ukrainy* [Prodrome of the vegetation of Ukraine]. Kiev: Naukova dumka. 783 p. (In Ukrainian).
- ELITH, J., 2002. Quantitative methods for modeling species habitat: comparative performance and an application to Australian plants. In *Quantitative methods for conservation biology*. N.Y.: Springer, p. 39–58.
- ELITH, J., PHILLIPS, S.J., HASTIE, T., DUDÍK, M., CHEE, Y.E., YATES, C.J., 2011. A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*, 17 (1): 43–57. <https://doi.org/10.1111/j.1472-4642.2010.00725.x>
- ERMAKOV, N.B., PLUGATAR, YU.V., LEIBA, V.D., 2023. Klassifikatsiya bukovykh (*Fagus orientalis*) lesov Zapadnogo Kavkaza [Classification of beech (*Fagus orientalis*) forests of the Western Caucasus]. *Vegetation of Russia*, 47: 112–132. <https://doi.org/10.31111/vegrus/2023.47.112> (In Russian with English summary).
- FISCHER, H.S., MICHLER, B., FISCHER, A., 2019. High resolution predictive modelling of potential natural vegetation under recent site conditions and future climate scenarios: case study Bavaria. *Tuexenia*, 39: 9–40. <https://doi.org/10.14471/2018.39.001>
- FRANTSUZOV, A.A., 2006. Floristicheskaya klassifikatsiya lesov s *Fagus orientalis* Lyspsky i *Abies nordmanniana* (Stev.) Spach v bassejne reki Beloy (Zapadnyy Kavkaz) [Floristic classification of forests with *Fagus orientalis* Lyspsky and *Abies nordmanniana* (Stev.) Spach in the Belaya river basin (Western Caucasus)]. *Vegetation of Russia*, 9: 76–85. <https://doi.org/10.31111/vegrus/2006.09.76>. (In Russian with English summary).
- GAFUROV, A., PROKHOROV, V., KOZHEVNIKOVA, M., USMANOV, B., 2024. Forest community spatial modeling using machine learning and remote sensing data. *Remote Sensing*, 16 (8), 1371. <https://doi.org/10.3390/rs16081371>
- GHOZIZADEH, H., NAQINEZHAD, A., CHYTRÝ, M., 2020. Classification of the Hyrcanian forest vegetation, Northern Iran. *Applied Vegetation Science*, 23 (1): 107–126. <https://doi.org/10.1111/avsc.12469>
- GROSSGEYM, A.A., 1948. *Rastitelnyy pokrov Kavkaza* [Vegetation blanket of the Caucasus]. Moskva: MOIP. 267 p. (In Russian).
- GVOZDETSKIY, N.A., 1963. *Kavkaz: ocherk prirody* [The Caucasus: an essay on nature]. Moskva: Gosudarstvennoe izdatel'stvo geograficheskoy literatury. 264 p. (In Russian).
- HADINEJAD, M., NAGHIPOUR, A.A., EBRAHIMI, A., NAIMI, B., 2025. Modeling the effect of climate change on the distribution of plant communities in Zayandeh-Rud basin, Iran. *Environmental Monitoring and Assessment*, 197: 479–503. <https://doi.org/10.1007/s10661-025-13861-6>
- KOVAL, I.P., SOLNTSEV, G.K., SHEVTSOV, B.P. (eds), 1995. *Spravochnik lesotaksatsionnykh normativov dlya Severnogo Kavkaza*. [Handbook of forestry-taxation norms for the North-Western Caucasus]. Moskva: VNIITsles-resurs. 90 p. (In Russian).
- HIJMANS, R.J., CAMERON, S.E., PARRA, J.L., JONES, P.G., JARVIS, A., 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25: 1965–1978. <https://doi.org/10.1002/joc.1276>
- HORVAT, I., GLAVAČ, V., ELLENBERG, H., 1974. *Vegetation Südsteuropas* [Vegetation of Southeast Europe]. Geobotanica Selecta, 4. Stuttgart: G. Fischer-Verlag. 768 p.
- KAVGACI, A., ARSLAN, M., BINGÖL Ü., ERDOĞAN, N., ČARNI, A., 2012. Classification and phytogeographical differentiation of oriental beech forests in Turkey and Bulgaria. *Biologia*, 67 (3): 461–473. <https://doi.org/10.2478/s11756-012-0029-6>
- KAVGACI, A., KARAKÖSE, M., KELEŞ, E.S., BALPINAR, N., ARSLAN, M., YALÇIN, E., NOVÁK, P., ČARNI, A., 2023. Classification of forest and shrubland vegetation in central and eastern Euxine Turkey and SW Georgia. *Applied*

- Vegetation Science*, 26 (4): e12753. <https://doi.org/10.1111/avsc.12753>
- KHUTORISOV, I.I., 1967. Materialy izucheniya vodoohrannopochvozashchitnoy roli gornyykh bukovykh i pikhtovykh lesov Severo-Zapadnogo Kavkaza [Materials of the study of the water-protective and soil-protective role of mountain beech and fir forests of the Northwestern Caucasus]. *Proceedings of the Caucasian State Nature Reserve*, 9: 312–415. (In Russian).
- KOROTKOV, K.O., BELONOVSKAYA, E.A., 1987. *Sintaksonomiya temnohvoynnykh lesov Kavkaza* [Syntaxonomy of dark coniferous forests of the Caucasus]. Moscow: USSR Academy of Sciences. 41 p. Deposited at VINITI, 25 February 1987, no. 1324-V87. (In Russian).
- KOZHEVNIKOVA, M.V., PROKHOROV, V.E., SAVELIEV, A.A., 2019. Prognostic modelirovaniye rasprostraneniya rastitelnykh soobshchestv poryadka Quercetalia pubescenti-petraeae Klika 1933 [Predictive modeling for the distribution of plant communities of the order Quercetalia pubescenti-petraeae Klika 1933]. *Tomsk State University Journal of Biology*, 47: 59–73. DOI: 10.17223/19988591/47/4
- KUZNETSOV, N.I., 1909. Printsipy deleniya Kavkaza na botaniko-geograficheskie provintsii [Principles of dividing the Caucasus into botanical-geographical provinces]. *Notes of the Imperial Academy of Sciences on the Physics and Mathematics Department*, 24 (1). 174 p. (In Russian).
- MUCINA, L., BÜLTMANN, H., DIERSSEN, K., THEURILLAT, J.-P., RAUS, T., ČARNÍ, A., ŠUMBEROVÁ, K., WILLNER, W., DENGGLER, J., GAVILÁN, GARCÍA, R., CHYTRÝ, M., HÁJEK, M., DI PIETRO, R., IAKUSHENKO, D., PALLAS, J., DANIÉLS, F.J.A., BERGMEIER, E., SANTOS GUERRA, A., ERMAKOV, N., VALACHOVIČ, M., SCHAMINÉE, J.H.J., LYSENKO, T., DIDUKH, Y.P., PIGNATTI, S., RODWELL, J.S., CAPELO, J., WEBER, H.E., SOLOMESHCH, A., DIMOPOULOS, P., AGUIAR, C., HENNEKENS, S.M., TICHÝ, L., 2016. Vegetation of Europe: hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. *Applied Vegetation Science*, 19 (1): 3–264. <https://doi.org/10.1111/avsc.12257>
- ORLOV, A.YA., 1953. Bukovye lesa Severo-Zapadnogo Kavkaza [Beech forests of the Northwestern Caucasus]. In SUKACHEV, V.N., ZONN, (eds). *Shirokolistvennyye lesa Severo-Zapadnogo Kavkaza*. Moskva: Izdatelstvo Akademii nauk SSSR, p. 244–381. (In Russian).
- PASSARGE, H., 1981. Über Fagetea im kartalinischen Kaukasus [About Fagetea in the Cartalinian Caucasus]. *Feddes Repertorium*, 92 (5-6): 413–431. <https://doi.org/10.1002/fedr.4910920507>. (In German).
- PERRIN, G., ROZO, C., BIRET, F., HUBERT-MOY, L., RAPINEL, S., 2023. Predicting the suitability area of heath alliances over France using open-source data. *Plant Biosystems – An International Journal Dealing with all Aspects of Plant Biology*, 157 (2): 379–391. <https://doi.org/10.1080/011263504.2023.2165562>
- PHILLIPS, S.J., DUDÍK, M., 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography*, 31 (2): 161–175. <https://doi.org/10.1111/j.0906-7590.2008.5203.x>
- PHILLIPS, S.J., ANDERSON, R.P., DUDÍK, M., SCHAPIRE, R.E., BLAIR, M.E., 2017. Opening the black box: an open-source release of Maxent. *Ecography*, 40 (7): 887–893. <https://doi.org/10.1111/ecog.03049>
- QUÉZEL, P., BARBÉRO, M., AKMAN, Y., 1980. Contribution à l'étude de la végétation forestière d'Anatolie septentrionale [Contribution to the study of forest vegetation in Northern Anatolia]. *Phytocoenologia*, 8 (3/4): 365–519. <https://doi.org/10.1127/phyto/8/1980/365>. (In French).
- QUÉZEL, P., BARBÉRO, M., AKMAN, Y., 1992. Typification de syntaxa a décrits en région méditerranéenne orientale [Typification of syntaxa described in the Eastern Mediterranean region]. *Ecologia Mediterranea*, 18 (1): 81–87. <https://doi.org/10.3406/ecmed.1992.1708>. (In French).
- SCHELDEMAN, X., VAN ZONNEVELD, M., 2010. *Training manual on spatial analysis of plant diversity and distribution*. Rome: Bioversity International 179 p.
- SHEVCHENKO, N.E., BRASLAVSKAYA, T.Y., 2021. Shirokolistvennyye lesa Severo-Zapadnogo Kavkaza. I. Poryadok Carpinetalia betulii P. Fukarek 1968 [Broad-leaved forests of the North-Western Caucasus. I. Order Carpinetalia betulii P. Fukarek 1968]. *Vegetation of Russia*, 42: 118–145. <https://doi.org/10.3111/vegrus/2021.42.118>. (In Russian with English summary).
- SHEVCHENKO, N.E., BRASLAVSKAYA, T.YU., DOROSHINA, G.YA., 2026. Shirokolistvennyye lesa Severo-Zapadnogo Kavkaza. II. Novye sintaksony poryadka Rhododendro pontici–Fagetalia orientalis Passarge 1981 [Broadleaf forests of the Northwestern Caucasus. II. New syntaxa of order Rhododendro pontici–Fagetalia orientalis Passarge 1981]. *Vegetation of Russia*, 53: 31–66. <https://doi.org/10.3111/vegrus/2026.53.31>. (In Russian with English summary).
- SHEVCHENKO, N.E., BRASLAVSKAYA, T. YU., GERASKINA, A.P., 2025. Geospatial modelling of the widespread broad-leaved forest syntaxa of order Carpinetalia betulii P. Fukarek 1968 in the North-Western Caucasus. *Ecologica Montenegrina*, 87: 77–89. <https://doi.org/10.37828/em.2025.87.3>
- SHIT, P.K., POURGHASEMI, H.R., DAS, P., BHUNIA, G.S., 2021. *Spatial modeling in forest resources management: rural livelihood and sustainable development*. Charm: Springer Nature. 675 p.
- SOCHAVA, V.B., 1949. O proiskhozhdenii bukovykh lesov Kavkaza [On the origin of beech forests of the Caucasus]. *Izvestiya of the USSR Academy of Sciences. Biological Series*, 2: 224–236. (In Russian).
- SOKOLOVA, T.A., 2022. Validizatsiya sintaksonov lesnoy rastitelnosti basseyna r. Belaya (Severo-Zapadnyy Kavkaz) [Validation of syntaxa of forest vegetation of the Belaya River basin (North-Western Caucasus)]. *Diversity of Plant World*, 2 (13): 60–64. (In Russian with English summary).
- Soó, R., 1964. Die regionalen Fagion-Verbände und Gesellschaften Südosteuropas [Regional beech communities and alliances in the South-Eastern Europe]. *Studia Biologica Academiae Scientiarum Hungaricae*, 1: 5–104. (In German).
- TUAN, N.T., PHU, N.T., HAI, N.H., RODRÍGUEZ-HERNÁNDEZ, D.I., SUBEDI, M.R., 2026. Climate change impacts on the distribution of deciduous forests in the Central Highlands of Vietnam. *Folia Oecologica*, 53 (2): 88–107. <https://doi.org/10.2478/foecol-2026-0009>
- TZONEV, R., DIMITROV, M., CHYTRÝ, M., ROUSSAKOVA, V., DIMOVA, D., GUSSEV, C., PAVLOV, D., VULCHEV, V., VITKOVA, A., GOGUSHEV, G., NIKOLOV, I., BORISOVA, D., GANEVA, A., 2006. Beech forest communities in Bulgaria. *Phytocoenologia*, 36 (2): 247–279. <https://doi.org/10.1127/0340-269X/2006/0036-0247>
- WARREN, D.L., GLOR, R.E., TURELLI, M., 2010. ENMTools: a toolbox for comparative studies of environmental niche

- models. *Ecography*, 33: 607–611. <https://doi.org/10.1111/j.1600-0587.2009.06142.x>
- WILLNER, W., JIMÉNEZ-ALFARO, B., AGRILLO, E., BIURRUN, I., CAMPOS, J.A., ČARNI, A., CASELLA, L., CSIKY, J., ČUŠTEREVSKA, R., DIDUKH, YA.P., EWALD, J., JANDT, U., JANSEN F., KĄCKI, Z., KAVGACI, A., LENOIR, J., MARINŠEK, A., ONYSHCHENKO, V., RODWELL, J.S., SCHAMINÉE, J.H.J., ŠIBÍK, J., ŠKVORC, Ž., SVENNING, J.-C., TSIRIPIDIS, I., TURTUREANU, P.D., TZONEV, R., VASSILEV, K., VENANZONI, R., WOHLGEMUTH, T., CHYTRÝ, M., 2017. Classification of European beech forests: a Gordian Knot? *Applied Vegetation Science*, 20 (3): 494–512. <https://doi.org/10.1111/avsc.12299>
- ZAURBEKOV, SH.SH., 2012. *Sovremennye klimaticheskie izmeneniya i ikh vliyanie na landshafinuyu strukturu regiona (na primere Severnogo Kavkaza)* [Modern climatic changes and their impact on the landscape structure of the region (using the example of the North Caucasus)]. Dissertation for the degree of Doctor of Geographical Sciences. Krasnodar: Kuban State University. 306 p. (In Russian).
- ZERNOV, A.S., 2006. *Flora Severo-Zapadnogo Kavkaza* [Flora of the North-Western Caucasus]. A.G. Elenevsky (ed). Moscow: KMK Scientific Publications Association. 664 p. (In Russian).

Received May 9, 2026
Accepted August 3, 2026