

CLIMATE-RELATED GRADIENTS ON VEGETATION DIVERSITY OF THE ALTAI-SAYAN OROBIOME (SOUTHERN SIBERIA)

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ABSTRACT. An analysis of the spatial organization of vegetation cover has been carried out for the Altai-Sayan orobiome in connection with climatic conditions in the Southern Siberian mountains based on original relevés of plant communities at the 4 altitudinal spectra. Basic bioclimatic parameters on the altitudinal spectra of vegetation have been determined according to latitudinal and longitudinal differentiation of climate. Correlation and discriminate analyses allowed to identify the regional features of altitudinal gradients in species diversity of the spectra as well as the role of parameters in the structure of typological diversity of vegetation for belts of high-mountain tundra, alpine and subalpine meadows and sparse forests, dark coniferous mountain taiga forests, chern-taiga forests, small leave – light coniferous subtaiga forests, forest-steppe. A compiled bioclimatic scheme characterizes the spatial organization of orobiome's vegetation by basic bioclimatic parameters on the regional level (continentality index, average temperature of January). This scheme shows regional features of the diversity of vegetation in Southern Siberia, in adjacent plain and mountain regions according to climatic conditions. Identified patterns determine unity of the Altai-Sayan orobiome as well as regional differentiation that reflected on the development of types of vegetation zonality. They can be used to analysis of vegetation forming in different mountain systems.

KEYWORDS: ecosystem, biodiversity, bioclimate, altitudinal zonality, mountain territories, ordination

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INTRODUCTION

Ecological gradients in the structure of biodiversity is one of the fundamental problems of biogeography. The spatial differentiation of ecosystems and their components is influenced by external factors, and climate is one of the main factors. Climatic justification of vegetation diversity is a traditional direction of botanical and geographical investigations at different spatial levels with thermic and moisture parameters (Francis and Currie 2003; Rivas-Martinez et al. 2004; Whittaker et al. 2001). The variety of functional parameters of plant species (Yang et al. 2019), key phytocoenotic characteristics (Dolezal and Srutek 2002), and also biodiversity indices have connections with climatic gradients at different levels of biota spatial structure (Shao and Halpin 1995; Qian et al. 2007). The spatial organization of large zonal and altitudinal-belt subdivisions of vegetation is determined on a global scale (Holdridge 1967; Tuhkanen 1984). The structure of typological diversity (types of vegetation, vegetation

formations) can be explained by climate on a regional scale (Grebenshchikov 1974; Nakamura et al. 2007; Bocharnikov 2019).

There are more opportunities for strong analysis in connection with new environmental data. They are represented by spatial models of ecological and geographical conditions. Such climatic models allow using a wide spectrum of key bioclimatic parameters and indices to reveal vegetation-climate patterns. The examples of these models are global model Bioclim created by interpolation of data of meteorological stations, altitude, and MODIS data (Fick and Hijmans 2017), and global model CHELSA created by orographic predictors among others (wind fields, valley exposition) (Karger et al. 2017). They can be used in medium- and small-scale investigations all over the world according to global coverage of the models (spatial resolution is about 1 km and below). The relevance of the work is increasing in connection with vegetation reactions on climate change in the past (Otto-Bliesner et al. 2006), and potential forecast scenarios in the future (De Dios et al. 2007; Navarro-Racines et al. 2020).

The concept of biome diversity describes biomes as basic ecosystem complexes on a regional spatial level. The development of ecosystems in the contemporary period connects to climatic conditions on certain amplitudes of key bioclimatic parameters. They determine compositions, spatial structure, and functions of ecosystems. Altitudinal-belts spectra of vegetation as a strong ecosystem complex in mountains have the name «orobiome» (Walter and Breckle 1991; Ogureeva and Bocharnikov 2017). The differences in relations of species and vegetation communities to environmental factors in the various parts of spatial distribution and a variation of coenotic role of plant communities in vegetation cover (Alberto et al. 2013; Svenning et al. 2014; Bocharnikov et al. 2018) determine regional level as a basis for biogeographical researches. They find integral reflection in the diversity of altitudinal-belt spectra with the specific composition of belts for each spectrum (Ogureeva 1991). Regional differentiation on spectra with different levels of biodiversity can be identified by climatic conditions (del Rio and Penas 2006). This characterizes the advantage of the biome concept in research of vegetation-climate relations.

The main purpose of the investigation is the evaluation of climate as a factor of the spatial organization of vegetation for the Altai-Sayan orobiome. The determination of the key bioclimatic parameters connected to the vegetation and regional patterns of its distribution is the basic task of research. Types of vegetation, classes, and groups of formations are used as basic typological units that are the background for altitudinal belts. At a higher level, altitudinal belts and spectra are considered to determine of types of altitudinal zonation within the Altai-Sayan group of zonation that characterizes the orobiome (Ogureeva and Bocharnikov 2017). Types of altitudinal zonation are described as basic units of the comparative regional analysis. Chosen key areas for climatic interpretation of the spatial structure of vegetation diversity in the South Siberian mountains correspond to these types.

MATERIAL AND METHODS

Reveiling of the diversity of vegetation in connection with climatic conditions is based on the analysis of original geobotanical and model climatic data. Relevés of vegetation communities, completed from 2008 to 2015 in different regions of Southern Siberia on key areas, cover full altitudinal spectra on ranges (Fig. 1). They characterize the diversity of the Altai-Sayan orobiome and its 4 geographical variants with specific types of altitudinal zonation. All relevés have been completed according to traditional methods of phytocoenosis analysis (Sukachov and Zonn 1964). Species composition of vascular plants, ground mosses and lichens with an evaluation of projective cover, mean altitude, and phenophases for each species have been described on key plots by 100 m² (non-forest communities) и 400 m² (forest communities). Tree, shrub, and herb layers' density (by percent) have been described. Geographical coordinates, as well as altitude, have been measured by GPS.

Choosing of key areas has been determined by tasks of investigations connected with spatial patterns in the structure of vegetation in different ranges by climatic conditions and altitudinal gradients of temperature and moisture parameters. It is reflected in the development of different types of altitudinal zonation which relate to the Altai-Sayan group of boreal class with a prevalence of mountain taiga belt (Ogureeva 1991). Cyclonic provinces, shown on the scheme of forest regionalization (Polikarpov et al. 1986), are characterized by a low level of continentality. Dark coniferous forests (*Abies sibirica*, *Pinus sibirica*) and small-leaved (*Populus tremula*, *Betula pendula*) – dark coniferous («chern-taiga») forests develop in these regions (Nazimova et al. 2014). In regions with a higher level of continentality larch (*Larix sibirica*) forests are typical. High-mountain vegetation of boreal class relates to alpine type (Tolmachev 1948).

Relevés of vegetation communities have been completed on different levels of catena and slopes according to tasks of revealing spatial patterns of diversity with the main role

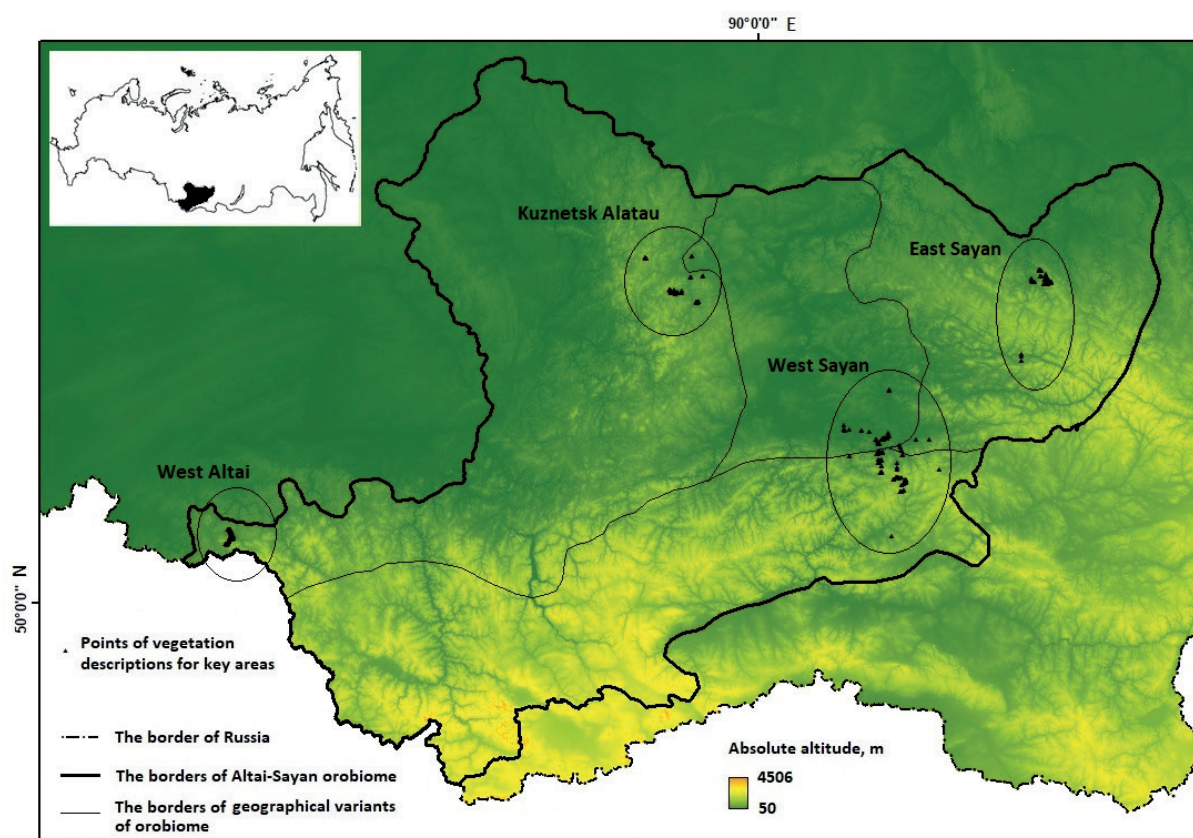


Fig. 1. Points of relevés on key areas

of climate. It is known a significant influence of ecological conditions through slope gradients which are reflected on vegetation (Ogureeva 1997; Namzalov 2020). Generally, they are associated with the middle parts of drained slopes of the ranges (transit positions of catena). The analysis has been performed by 396 relevés on 4 general profiles (Table 1). Relevés are included in groups (general profiles) presented by altitudinal-belt spectra of 4 types of altitudinal zonality (basic types for orobiome).

Climatic data have been derived from the global model CHELSA (Karger et al. 2017). It contains data on 19 bioclimatic parameters with 30'' spatial resolution averaged on period 1979-2013. There are temperature and moisture parameters and their ratio (average values for the year, each quarter of the year,

July and January). Basic parameters have been used to calculate bioclimatic indices which apply to the analysis of vegetation and climate (del Rio and Penas 2006; Rivas-Martinez et al. 2011; Bocharnikov 2019). The values of bioclimatic variables for each vegetation community have been determined by extraction of these in points of relevés based on the climatic model. Altitude has been used as an integral parameter that characterizes gradients of climatic conditions in the mountains. 25 bioclimatic parameters including 8 bioclimatic indices have been used (Table 2).

Nonmetric multidimensional scaling (NMS-ordination) (Clarke 1993) allowed to identify the character of vegetation communities' variation in the system of ecological and geographical factors. This method is one of the most used for

Table 1. Relevés in the Southern Siberian mountains

Region	Geographical location	Number of relevés	Years of investigations	Types of altitudinal zonality of vegetation	Geographical variant of Altai-Sayan orobiome
West Sayan	Kulumys, Kedranskiy, Oiskiy, Ergaki ridges	147	2008, 2009, 2010	Alpine-subalpine-mountain taiga-chern-taiga	Central Altai
West Altai	Tigirek ridges	143	2015	Alpine-subalpine-mountain taiga-chern-taiga-shrub-forest-steppe-steppe	North Altai
East Sayan	Sayan ridges	52	2012	Alpine-subalpine-mountain taiga	Sayan
Kuznetsk Alatau	Profile the Black Lake – Ivanovskie lakes	54	2008	Alpine-subalpine-mountain taiga-forest-steppe-steppe	North Altai, Minusinsk depression

Table 2. Bioclimatic parameters for ordination analysis of vegetation

Parameters	Symbol
Average annual temperature	Bio1
Average temperature of summer	Bio10
Average temperature of winter	Bio11
Average annual precipitation	Bio12
Average precipitation of summer	Bio18
Average precipitation of winter	Bio19
Average temperature of January	T_January
Average temperature of April	T_april
Average temperature of July	T_July
Average temperature of October	T_october
Average maximum temperature of January	T_max_January
Average maximum temperature of July	T_max_July
Average minimum temperature of January	T_min_January
Average minimum temperature of July	T_min_July
Average precipitation of January	P_January
Average precipitation of July	P_July
Continental index	Ic
Thermicity index	It
Aridity index	Ia
Ombrothermic index of summer	los_summer

Ombrothermic index of July	los_July
Oceanity index	OCE
Pluviothermic quotient	Q_pluv
Evapotranspiration estimate	Pet
Altitude above sea level	Alt_gps

the ordination of species and communities (Aynekulu et al. 2012; Rahman et al. 2020). Interpretation of spatial structure of vegetation cover has been carried out in connection with bioclimatic parameters. Euclidian metric has been used as a measure of similarity. The evaluation of conjugacy of vegetation and climate has been carried out based on a correlation between values of communities on ordination scheme and bioclimatic parameters. We used 3 axes to interpretation of ordination. Linkage and reliability of each axis and each parameter have been determined by Spearman's nonparametric coefficient of linear correlation (p -value < 0.001).

The analysis of climate patterns in vegetation has been carried out on the different levels of its spatial organization. **Complete altitudinal spectra of types of altitudinal zonation** describe a high level. The vegetation cover of key areas is formed as a part of altitudinal spectra of the Altai-Sayan group of boreal class (Ogureeva 1991; Ogureeva et al. 1999). It belongs to West Altai, West-East Sayan, and Salair-Kuznetsk types of altitudinal zonation. The dominant position of dark and light coniferous forests in the mountain taiga belt, the alpine type of high-mountain vegetation with alpine and subalpine belts character this group. Regional specificity finds expression in the typological diversity of different vegetation belts. West Altai and West-East Sayan types are developed in the very wet climate of the rain-barrier ranges (Polikarpov et al. 1986). They are characterized by the basic participation of dark coniferous forests and unique relict chern-taiga forests in the warmest and humid conditions of low mountains with a high level of botanical diversity (Nazimova 1975; Nazimova et al. 2005, 2014; Stepanov 2012). The basis of chern-taiga forests is consisted by small-leave – dark coniferous communities. The lower part of altitudinal spectra is occupied by the forest-steppe belt with a high level of shrub communities in West Altai (Ogureeva 1980). High mountains are characterized by a high level of typological diversity and relatively low amplitudes of ecological conditions suitable for the development of alpine and subalpine meadows and high-mountains tundra. Salair-

Kuznetsk type of altitudinal zonation is connected with the east macroslope of the Kuznetsky Alatau with lower humidity. The dominance of larch forests in the forest-steppe belt, Siberian fir, and Siberian pine forests in the mountain taiga and subalpine belts describe the diversity of this type.

The next level of the spatial organization of vegetation relates to **altitudinal belts**. Types of altitudinal zonation for key areas are described by forest-steppe, sub-taiga, mountain taiga (with chern-taiga forests), subalpine and alpine-tundra belts. The altitudinal amplitude, development of sub-belts, different phytocoenotic optimum of basic communities characterize each type. The most important regional patterns are connected with vegetation of the low part of altitudinal spectra. Chern-taiga forests dominate in warm and wet conditions in the low parts of West Altai and West Sayan. Forest-steppe belt with exposure combinations of larch forests and grass steppes is developed in the low parts of Kuznetsk Alatau and West Altai.

The third level of the spatial organization of vegetation is determined by the **typological composition of vegetation**. It can be evaluated through basic formations and types of vegetation according to geographical-genetic classification (Sochava 1980). Vegetation communities are presented by three phratries of formations: Altai-Sayan alpine, Ural-South Siberian boreal, and Transvolga-Kazakhstan steppe. Following V.B. Sochava, a «phratry» are described as a complex of plant formations with genetic and geographic unity of formations. Altai-Sayan phratry is presented by alpine and subalpine meadows, sparse forests. Dark coniferous (*Abies sibirica*, *Pinus sibirica*) and light coniferous (*Larix sibirica*) forests of Ural-South Siberian form the mountain taiga belt. Larch and pine (*Pinus sylvestris*) forests and grass steppes (*Stipa pennata*, *Helictotrichon altaicum*, *Koeleria cristata*) of Transvolga-Kazakhstan phratry form the forest-steppe belt. The basic typological units of vegetation are associated with the general structure of diversity of altitudinal belts for key areas (Table 3). Each type of altitudinal zonation has common features and also regional specifics in diversity (Table 4).

Table 3. Typological diversity of vegetation communities of Altai-Sayan orobiome

	Altitudinal belts	Typological diversity of vegetation			
		Geographic-genetic complexes			
		Altai-Sayan		Ural-South Siberia	Transvolga-Kazakhstan
I	Alpine-tundra	1. Alpine meadows	2. High-mountain tundra		
II	Subalpine	1. Subalpine meadows	2. Subalpine sparse forests		
III	Mountain taiga			III.1. Siberian pine-fir forests	
IIIa	Chern-taiga			IIIa.1. Birch and aspen-Siberian pine-fir forests	
IV	Subtaiga			IV.1. Birch-pine forests	IV.2. Birch-larch forests
V	Forest-steppe			1. Birch-larch forests	2. Herb-grass steppes, shrubs, steppe meadows

The role of climate as a factor of vegetation diversity has been determined at different levels of its organization (for complete altitudinal spectra of vegetation, altitudinal belts, and typological units of vegetation). The significance of differentiation of altitudinal belts and typological units by bioclimatic parameters has been determined based on discriminant analysis (F-statistic and p-value have been used).

The relations between vegetation and climate are presented on the integral bioclimatic scheme of the Altai-Sayan orobiome. The experience of creating such schemes determines the opportunity of explanation of the spatial organization of vegetation cover at the regional level (Nakamura et al. 2007; Bocharnikov 2019). Key bioclimatic parameters on the integral axes of ordination have been used to create a scheme. The scheme is presented by a matrix with cells containing typological units of vegetation of different types of altitudinal zonality for the Altai-Sayan orobiome. Additional interpretation of vegetation-climate connections has been reflected in the picture.

The analysis of species diversity distribution correlated with key bioclimatic parameters has become one of the ways of revealing vegetation-climate relations. Two indicators have been used: species richness per area (alpha-diversity) and gradient differentiation between altitudinal belts (Whittaker beta-diversity index). Beta-diversity has been determined to groups of communities into 100-m stages on the spectrum (before 1700 m a.s.l.). Gradients of diversity have been analyzed by each key area and by complete data. Altitude above sea level has been used as an integral factor of the spatial structure of species diversity in the mountains (Odland 2009; Mokarram and Sathyamoorthy 2015). The relation patterns between diversity and ecological factors have been given based on correlation analysis.

The spatial analysis of data has been completed using Saga 2.1.4, ArcGIS Pro Advanced 10.8.1, and Statistica 12.5.192.5.

RESULTS

The conjugation of vegetation and climate along altitudinal gradients in different types of altitudinal zonality

The altitude above sea level as an integral parameter characterizes the differentiation of vegetation diversity on the spectrum for each type of altitudinal zonality (Table 5). The strongest connection is marked for the West Sayan type (correlation coefficient 0.65). Axes 1 and 3 of ordination schemes have the main contribution in connection with climate. This is confirmed by maximum significant values of correlation with bioclimatic parameters (Table 5). There are 2 main gradients determined by bioclimatic parameters. The first includes temperature parameters with the highest values of correlation. The second is connected with altitude and humidity. Moisture parameters in every type of altitudinal zonality have more close connections. Ombrothermic indices based on the ratio of temperature and moisture parameters in the warmest quarter of the year have the maximum values among these.

Comparison of ordination schemes in different types of altitudinal zonality determines a differentiation in connections between the vegetation and bioclimatic parameters. Maximum values of correlation coefficients are identified on general profiles on key areas in West Sayan and West Altai. They have maximum diversity of altitudinal subdivisions with the development of chern-taiga sub-belt. Fewer strong connections are determined to East Sayan. It is characterized by a simpler structure of altitudinal zonality including a sub-taiga belt of pine forests, a mountain taiga

Table 4. Typological diversity of vegetation of altitudinal zonality types for Altai-Sayan orobiome

Typological subdivisions of altitudinal belts	Types of altitudinal zonality			
	West Sayan	East Sayan	West Altai	Salair-Kuznetsk
I.1. Alpine meadows	1		2	
I.2. High-mountain tundra	3	4	5	6
II.1. Subalpine meadows	7	8	9	10
II.2. Subalpine sparse forests	11	12	13	14
III.1. Siberian pine-fir forests	15	16	17	18
IIIa.1. Birch and aspen-Siberian pine-fir forests	19		20	
IV.1. Birch-pine forests	21	22		23
IV.2. Birch-larch forests		24		
V.1. Birch-larch forests and steppes			25	26
V.2. Herb-grass steppes, shrubs, steppe meadows			27	28

Vegetation of altitudinal belts: 1-2 – alpine meadows (*Schulzia crinita*, *Viola altaica*, *Carex aterrima*, *Festuca sphagnicola*, *Bupleurum triradiatum*); 3-6 – high-mountain tundra (*Betula rotundifolia*, *Rhododendron aureum*, *Dryas oxyodonta*, *Sibbaldia procumbens*, *Omalotheca norvegica*, *Empetrum nigrum*, *Cladina rangiferina*); 7-10 – subalpine meadows (*Veratrum lobelianum*, *Heracleum dissectum*, *Geranium albiflorum*, *Euphorbia lutescens*, *Delphinium elatum*); 11-14 – subalpine sparse forests (*Pinus sibirica*, *Abies sibirica*); 15-18 – Siberian pine-fir forests (*Abies sibirica*, *Pinus sibirica*); 19-20 – birch and aspen-Siberian pine-fir forests (*Abies sibirica*, *Pinus sibirica*, *Betula pendula*, *Populus tremula*); 21-23 – birch-pine forests (*Pinus sylvestris*, *Betula pendula*); 24 – birch-larch forests (*Larix sibirica*, *Betula pendula*); 25-26 – birch-larch forests and steppes (*Larix sibirica*, *Betula pendula*, *Stipa capillata*, *Carex pediformis*, *Cleistogenes squarrosa*, *Bupleurum scorzoniferifolium*); 27-28 – herb-grass steppes, shrubs, steppe meadows (*Stipa capillata*, *Poa attenuata*, *Carex pediformis*, *Artemisia santolinifolia*, *Phleum phleoides*, *Pulsatilla flavescens*).

Table 5. Correlation between species diversity of the altitudinal spectra and bioclimatic parameters (Spearman's rank correlation coefficient; reliable values at $p < 0.001$ are bold font)

Bioclimatic parameters	Correlation coefficients for types of altitudinal zonality									
	Altai-Sayan group of types of zonality		West-Sayan		East-Sayan		West-Altai		Salair-Kuznetsk	
	Axis 1	Axis 3	Axis 1	Axis 3	Axis 1	Axis 3	Axis 1	Axis 3	Axis 1	Axis 3
Alt_gps	-0.054	-0.420	0.648	-0.083	0.304	-0.520	-0.522	-0.238	0.485	-0.247
Bio1	0.232	0.262	-0.661	0.083	-0.232	0.371	0.532	0.244	-0.462	0.248
Bio10	0.106	0.411	-0.659	0.079	-0.237	0.382	0.530	0.241	-0.465	0.238
Bio11	0.390	-0.032	-0.681	0.085	-0.199	0.324	0.536	0.244	-0.456	0.248
Bio12	0.121	0.034	0.272	0.076	0.232	-0.283	-0.639	-0.224	0.479	-0.276
Bio18	-0.241	0.123	0.200	0.278	0.233	-0.372	-0.479	-0.267	0.367	-0.383
Bio19	0.255	0.080	0.350	-0.186	0.153	-0.052	-0.631	-0.197	0.504	-0.265
T_January	0.393	-0.045	-0.679	0.086	-0.120	0.329	0.541	0.242	-0.459	0.248
T_april	0.209	0.268	-0.657	0.082	-0.233	0.379	0.529	0.243	-0.463	0.261
T_July	0.090	0.423	-0.654	0.079	-0.236	0.379	0.531	0.243	-0.463	0.237
T_october	0.253	0.241	-0.661	0.080	-0.228	0.364	0.527	0.244	-0.461	0.240
T_max_January	0.399	-0.060	-0.682	0.086	-0.189	0.312	0.534	0.243	-0.461	0.265
T_max_July	0.155	0.355	-0.657	0.078	-0.236	0.375	0.526	0.243	-0.467	0.239
T_min_January	0.386	-0.025	-0.680	0.086	-0.213	0.343	0.542	0.246	-0.445	0.241
T_min_July	0.028	0.484	-0.653	0.079	-0.243	0.383	0.528	0.243	-0.464	0.242
P_January	0.276	0.077	0.346	-0.194	0.146	-0.047	-0.629	-0.195	0.506	-0.269
P_July	-0.264	0.143	0.218	0.278	0.226	-0.381	-0.441	-0.270	0.349	-0.408
Ic	-0.360	0.519	-0.050	-0.026	-0.321	0.490	0.499	0.245	-0.469	0.208
It	0.358	0.051	-0.675	0.085	-0.213	0.344	0.536	0.244	-0.457	0.252
Ia	-0.061	-0.053	0.476	-0.082	0.132	-0.315	-0.590	-0.240	0.427	-0.304
los_summer	-0.229	-0.104	0.468	0.080	0.168	-0.368	-0.520	-0.256	0.395	-0.350
los_July	-0.249	-0.084	0.467	0.090	0.167	-0.371	-0.507	-0.260	0.388	-0.363
OCE	0.224	-0.230	0.383	-0.120	0.223	-0.518	-0.435	-0.121	0.359	-0.513
Q_pluv	0.202	-0.100	0.294	0.067	0.234	-0.303	-0.635	-0.231	0.476	-0.276
Pet	0.155	0.050	0.208	0.113	0.265	-0.268	-0.643	-0.221	0.483	-0.270

Bioclimatic parameters – see table 2. Axes 1, 3 – according to NMS-ordination data.

belt of dark coniferous forests, and high-altitudinal belts with less diversity of alpine and subalpine meadows and mountain tundra.

The conjugation of vegetation and climate along altitudinal gradients in a general altitudinal gradient of types of altitudinal zonality

The strongest connection has been detected with a temperature of January and winter months, and also thermicity index (correlation coefficient with axis 1 is about 0.4) (Table 5). They limit the position of the upper level of distribution of key vegetation communities according to the integral altitudinal gradient. Moisture parameters, and also

bioclimatic indices have fewer clear connections but with statistical confidence ($p < 0.001$). The ordination scheme on a general set of communities is similar to schemes for each type of altitudinal zonality. Differentiation of humidity (annual precipitation of year, July and January) reflects the spatial structure of types of altitudinal zonality with forest-steppe belt (West Altai, Kuznetsk Alatau). The development of hemiboreal forests (the subtaiga and chern-taiga belts) is determined by a high level of temperature and moisture supply. The development of the forest-steppe belt is connected with a relatively low level of humidity (annual precipitation – 600-800 mm, ombrothermic index of summer – 130-160).

The conjugation of the key typological divisions of vegetation and climate in the different types of altitudinal zonation

The main formation complexes of vegetation determine each type of altitudinal zonation (Table 3). The correlation of climatic parameters with vegetation on the ordination scheme characterizes the close connection of spatial structure of climate and vegetation. The bioclimatic parameters with maximum correlation connections with vegetation communities have been determined for the axes of NMS-ordination. They are mean annual temperature and continentality index (Rivas-Martinez et al. 2004). The reliability of differences in altitudinal belts of vegetation in each type of altitudinal zonation and between types has been determined by choosing bioclimatic parameters using the Kruskal-Wallis test.

The confidence intervals for each altitudinal belt in different types of altitudinal zonation on the ordination scheme characterize differences between vegetation communities (Fig. 2). They are significantly different on the ordination scheme by the first and the third axes (Wilks' Lambda = 0.06286, $F = 40.623$, $p < 0.000$). Based on the proximity of areas of altitudinal belts determined by the confidence intervals different types of altitudinal zonation have a high level of phytocoenotic similarity. The alpine and subalpine belts are the closest in different regions. The similarity of these communities can be determined by development in a cold climate with typical conditions for high mountains (Kolomyts 1966). The regional differentiation of the lower-lying belts is clearer. For example, the area of the mountain taiga belt of the East Sayan is located within the area formed by the subalpine sparse forests of the West Sayan without intersecting with its mountain taiga belt. This characterizes the warmer conditions for the mountain taiga of the West Sayan, which is distinguished by a high level of floristic and coenotic diversity with the development of large-herb, large-fern (*Dryopteris expansa*, *Athyrium distentifolium*) forest types. A similar position in the scheme is occupied by the area of the chern-taiga of the West Altai, which partially overlaps with the area of subalpine sparse forests of this region. The most differences between key areas are noted in the lower parts of

the altitudinal-belt spectra. A separate position in the diagram is occupied by birch-pine subtaiga forests of the West Sayan. They belong to the most moisture variant of the subtaiga of the mountains of Southern Siberia with dominance of bracken and large-herb types of forest communities with the participation of nemoral elements (Drobyshevskaya and Nazimova 2007). Subtaiga forests in other regions form intersecting areas under conditions of increasing continentality of the climate. Areas of forest-steppe complexes in all types of altitudinal zonation in the scheme are superimposed on each other in the conditions of high heat supply.

The horizontal axis of NMS-ordination, in general, characterizes the change of communities of different altitudinal subdivisions according to the change in the temperature supply of the cold season. By these parameters, the altitudinal change of the complexes of basic forest-steppe, subtaiga, mountain-taiga, and high-mountain communities is expressed. The values on the vertical axis are closely related to the climate continentality index, heat supply indicators for the summer period and July, as well as altitude above sea level.

The conjugation of species diversity of vegetation communities with climate

The altitudinal gradient is expressed in the change in the relative species diversity of communities in all types of altitudinal zonation. This parameter decreases with an increase of altitude. It is described by a linear model for every mountain profile (Fig. 3–6). The range of values of parameters is large at each altitudinal level for every profile. The degree of conjugation of changes in the species diversity of communities with climatic conditions along altitudinal gradient is varied in different types of zonation. The closest relationship is observed on the profile on the northern macroslope of West Sayan ($R^2 = 0.52$). It is characterized by the participation of subtaiga and chern-taiga forests with the high level of diversity (Ermakov 2003). The high abundance of communities of the forest-steppe belt on the profile in the Kuznetsk Alatau and its sharp decrease in the mountain-taiga belt and high-mountain belts

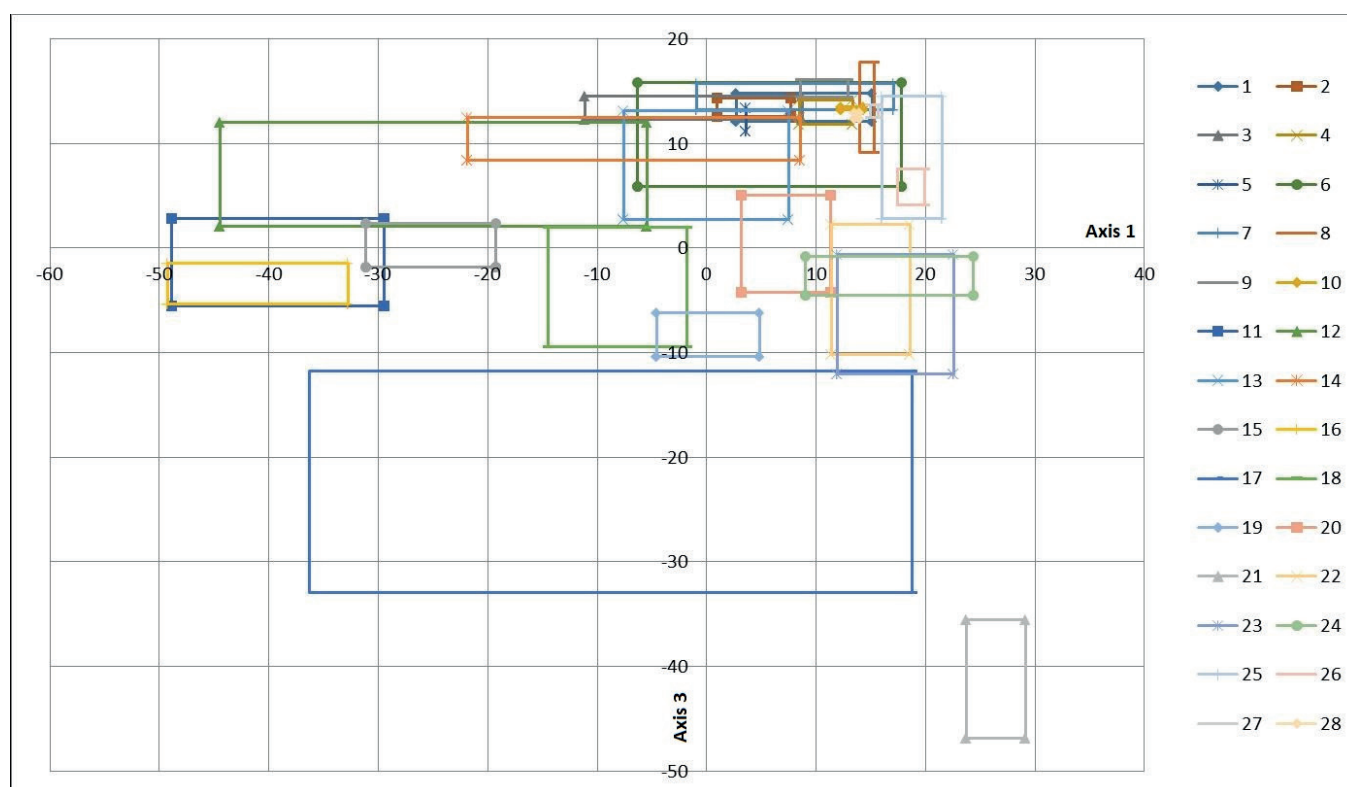


Fig. 2. Confidence intervals of typological subdivisions of vegetation on the first and third axes of the NMS-ordination
Typological subdivisions of vegetation of altitudinal belts – see table 4.

determine a rather high degree of correlation of this parameter with the altitude ($R^2 = 0.37$). A more even distribution of species diversity is expressed in conditions of high floristic richness for every altitudinal belt (West Altai) and in a lower level of diversity (East Sayan).

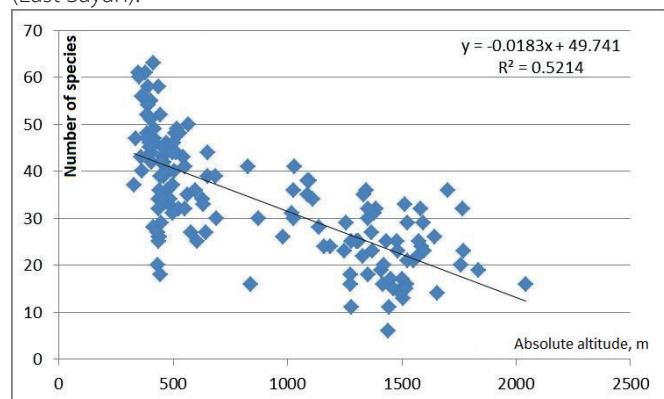


Fig. 3. Changing of relative species richness of communities on altitudinal profile in West Sayan type of zonation

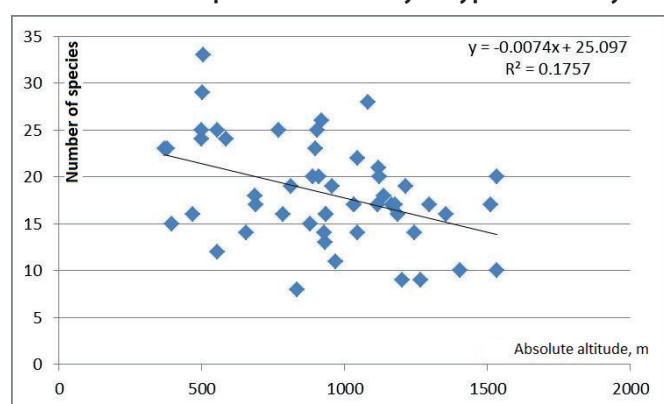


Fig. 4. Changing of relative species richness of communities on altitudinal profile in East Sayan type of zonation

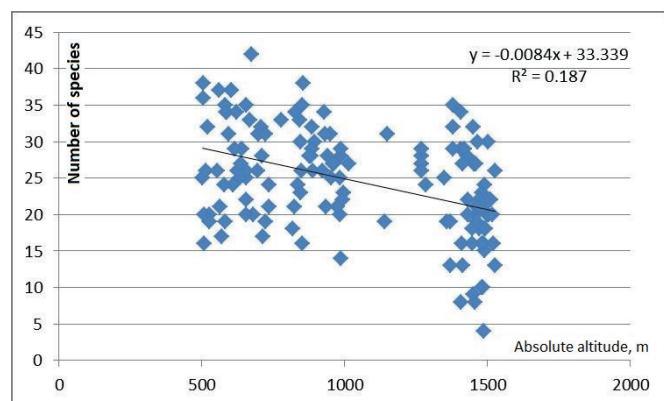


Fig. 5. Changing of relative species richness of communities on altitudinal profile in West Altai type of zonation

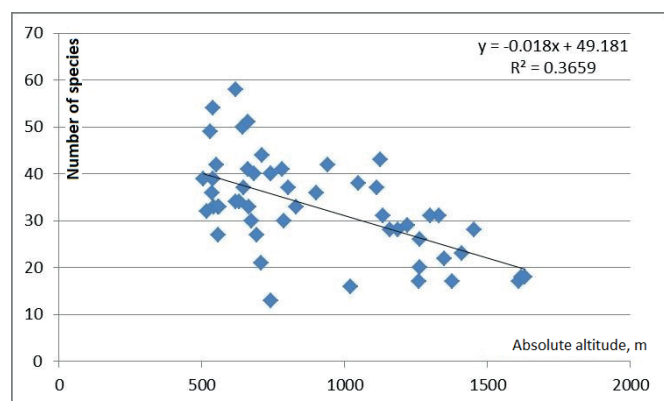


Fig. 6. Changing of relative species richness of communities on altitudinal profile in Salair-Kuznetsk type of zonation

There is a tendency to a decreasing the relative species richness (species abundance) of vegetation communities with an increase of altitude for the mountains of Southern Siberia in general (Fig. 7). The communities with the largest floristic diversity connect with the lower part of the altitudinal spectrum in conditions of increased temperature supply.

Differential diversity, calculated using the Whittaker index for elevation segments on the generalized profile for key areas in the aggregate, has a non-linear character of variation along the elevation gradient (Fig. 8). There are several peaks of diversity. The maximum values are connected with an altitude of 500-600 m (the optimum development of chern-taiga forests in West Sayan and West Altai, the forest-steppe belt of the Kuznetsk Alatau and subtaiga forests of East Sayan). The high level of floristic diversity corresponds to an increased level of differential diversity under the large temperature supply conditions in the low part of altitudinal-belt spectra of mountain ranges. A decrease in the diversity index is observed in the mountain-taiga belt. It is increased again near the upper limit of the distribution of forests at the contact with subalpine sparse forests (900-1000 m). The third extremum is connected with an altitude of 1500-1600 m (the optimum development of the subalpine meadows on contact with the alpine-tundra belt). An increased level of phytocoenotic diversity of the subalpine belt is typical for different mountain systems (Molozhnikov 1986; Sedel'nikov 1988). Based on the identified trends in the change of diversity, it is determined its increasing at the contact of altitudinal-belt divisions, characterized by the mixing of communities at different altitudinal levels.

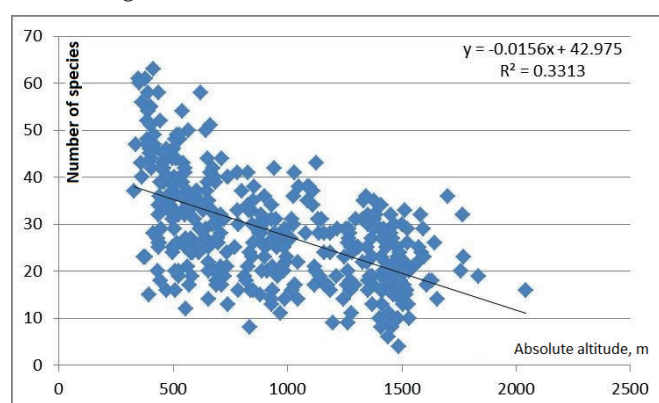


Fig. 7. Changing of relative species richness of communities on complex altitudinal profile in Altai-Sayan group of zonation types

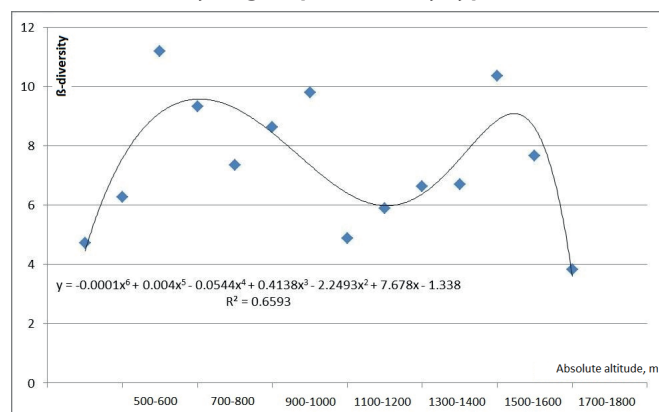


Fig. 8. Changing β -diversity of communities (Whittaker index) on complex altitudinal profile in Altai-Sayan group of zonation types

Moisture characteristics (average precipitation of July and summer) have significant correlations among the bioclimatic parameters (Table 6). The diversity is increased with moisture decreasing in the lower part of the altitudinal spectrum. A deviation from the linear dependence is observed in the subalpine belt, where the level of diversity increases with increasing moisture. January temperatures also have high positive relationships with the level of diversity. It confirms the general pattern according to which an increase in temperature supply contributes to an increase in the diversity of biota at different spatial levels (Currie and Paquin 1987; Shao and Halpin 1995; Morozova 2011).

The revealed gradients of temperature and moisture supply are summarized on the bioclimatic matrix of the vegetation of the Altai-Sayan orobiome (Table 7). The compiled scheme makes it possible to determine the patterns of vegetation diversity at the regional spatial level. The horizontal and vertical rows of the matrix are characterized by differences in conditions along

the integral vectors of bioclimatic parameters through temperature and moisture indicators. Data on the key climatic conditions, which are basic in the differentiation of typological subdivisions of vegetation, are given for the most closely related bioclimatic variables. The continentality index and the average temperature of January are taken as a basis. In addition, the indicators of the average annual temperature, the average temperature of July, the average precipitation of July, and the thermicity index are given.

Vegetation diversity of the Altai-Sayan orobiome is formed under climatic conditions, which determine the development of altitudinal-belt units within the climatic sectors (Fig. 9). The average temperature of January and the continentality index characterize the spatial structure of vegetation through basic complexes of altitudinal belts of different types of zonality.

Table 6. Correlations between β -diversity (Whittaker index) with bioclimatic parameters (Spearman's rank correlation coefficient; reliable values at $p < 0.001$ are bold font)

Bioclimatic parameters	Correlation coefficient
Bio1	0.328
Bio10	0.206
Bio11	0.533
Bio12	-0.437
Bio18	-0.597
Bio19	-0.394
T_January	0.540
T_april	0.314
T_July	0.195
T_october	0.349
T_max_January	0.558
T_max_July	0.258
T_min_January	0.525
T_min_July	0.132
P_January	-0.388
P_July	-0.608
Ic	-0.565
It	0.477
Ia	-0.431
los_summer	-0.459
los_July	-0.463
OCE	0.161
Q_pluv	-0.367
Pet	-0.439

Bioclimatic parameters – see table 2.

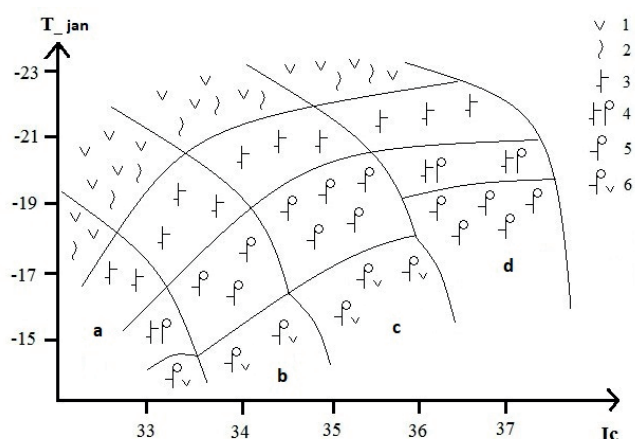


Fig. 9. Bioclimatic scheme of altitudinal belts of vegetation for Altai-Sayan orobiome

Vegetation: 1 – high-mountain tundra; 2 – alpine and subalpine meadows and sparse forests; 3 – dark coniferous mountain taiga forests; 4 – chern-taiga forests; 5 – small leaf – light coniferous subtaiga forests; 6 – forest-steppe. Types of altitudinal zonality: a – West-Altai; b – Salair-Kuznetsk; c – East-Sayan; d – West-Sayan.

Axes: Ic – continentality index, T_{jan} – the average temperature of January.

DISCUSSION

According to the classification of continentality types of climate (Rivas-Martinez et al. 2004), the vegetation cover of considering types of altitudinal zonality are developed in the continental sector (Ic = 31–37). It connects with boreal macrobioclimate and a low level of temperature supply (Table 7). There are significant differences between altitudinal divisions in the level of continentality (the parameter of Ic varies from 31 to 37, the parameter of It varies from 33 to 47) and in the temperature supply (the average temperature of January varies from –14 °C to –24 °C, the average temperature of July varies from +12 °C to +20 °C). Bioclimatic parameters allow determining the patterns, which characterize the changing of belts within types of altitudinal zonality and between spectra in the

The area of the increased temperature supply is occupied by the vegetation of the low part of altitudinal spectra (forest-steppe, sub-taiga, and chern-taiga belts). They are developed by an average temperature of about 0 °C. Regional features are expressed in the level of continentality and moisture supply. The sub-taiga forests are the most moisture ecosystems (the average precipitation of July is above 120–130 mm). Low mountains of the West Sayan are characterized by maximum amplitudes of temperature that reflect on maximum values of continentality index and minimum values of thermicity index. The vegetation cover of this region belongs to the humid geographical variant of sub-taiga birch-pine forests

Table 7. The vegetation of the Altai-Sayan orobiome in the system of bioclimatic parameters

Bioclimatic parameters			Ic	31±0.04	31.4±0.07	32±0.0	32.5±0.22	33±0.0	33.4±0.3	34±0.2	34.6±0.2	37.2±0.2
			P _{July}	102.5±2.3	102.5±0.9	95±0.0	112.5±10.2	147.3±1.2	90.3±12.4	114.7±13	90±18.6	141±18.7
			It	-39.2±0.2	-37.7±1.1	-32.9±0.0	-36.2±1.6	-47.4±0.3	-37.7±2.5	-40.1±1.9	-35.4±3.9	-45.6±2.3
T _{January}	T _{July}	T _{year}										
-23.8±0.8	13.3±1.1	-3.9±0.9										3 7 11
-23.1±0.3	13.9±0.5	-3.3±0.4										1
-22.1±1.5	15.2±1.6	-2.1±1.5										15
-21.4±0.1	11.9±0.1	-4.5±0.1						4				
-20.3±0.3	12.9±0.4	-3.2±0.4				6 10				8 12		
-19.7±0.3	13.2±0.3	-3.1±0.3				14						
-19±0.6	15±0.8	-1.8±0.7								16		
-18.3±2.1	15.2±1.1	-1.3±1	2 5 9	13					18		22 24	19
-17.5±0.5	19.7±0.4	2.2±0.4										21
-17.3±0.7	16.7±1	-0.1±0.9								23		
-16.6±0.2	17.6±0.1	0.7±0.1			17						26 28	
-15.3±0.6	17.2±0.8	1.5±0.7				25 27						
-14.6±0.7	17.9±0.9	2.2±0.8				20						

Vegetation typological subdivisions of altitudinal belts – see table 4.

Bioclimatic parameters (mean ± standard deviation) – see table 2.

of South Siberia (Drobushhevskaya and Nazimova 2007). Shrub (*Caragana arborescens*, *Spiraea chamaedrifolia*), bracken (*Pteridium pinetorum* ssp. *sibiricum*), herb (*Lathyrus humilis*, *L. frolovii*, *Vicia sepium*, *Cruciata glabra* ssp. *krylovii*) and grass (*Calamagrostis arundinacea*, *Brachypodium pinnatum*) forests are the basis of these vegetation diversity. These communities have a high species abundance (about 40 species of vascular plants on a key area of 400 m²). Forest-steppe vegetation complexes are formed in the low part of the altitudinal spectra of West Altai and Kuznetsk Alatau. Forest-steppe belt is an example of the complicated spatial organization of vegetation cover with a combination of forest, steppe, meadow, and shrub communities on the slopes of different temperature and moisture supply (Chytry et al. 2007; Ogureeva 1980). The conditions of moisture favor the development of meadow steppes (*Stipa pennata*, *Helictotrichon altaicum*), shrub communities (*Caragana arborescens*, *Spiraea trilobata*, *Rosa acicularis*) in the West Altai type of zonality (Ogureeva 1980). They develop in combination with larch and birch-pine herb-grass forests. The least humid geographical variant of the forest-steppe, associated with the eastern macroslope of the Kuznetsk Alatau, is distinguished by the predominance of herb-sod-bunch-grass steppes, (*Stipa pennata*, *Helictotrichon altaicum*, *Iris ruthenica*, *Filipendula stepposa*, *Schizonepeta multifida*) and larch forests. The sub-taiga forests of the East Sayan are developed in conditions of the lowest temperature supply (the average annual temperature is negative; the average temperature of July does not exceed +15...+16 °C). Sedge (*Carex macroura*) – grass (*Calamagrostis arundinacea*) and herb-grass birch-pine forests are characterized. They are distinguished by a relatively low typological diversity and lower floristic diversity in comparison with their analogs in other types of the Altai-Sayan group (Nazimova et al. 1987).

The mountain taiga belt is formed under conditions of a decreasing heat supply with a high level of moisture. Differences in the types of altitudinal zonality are well expressed. In West Altai, mountain taiga forests are formed at the highest temperatures (the average temperature of July is +16...+17 °C). In West Sayan, mountain taiga is developed in conditions of high humidity. Differentiation of the belt into two sub-belts characterize West Altai and West Sayan types of altitudinal zonality. The diversity is based on large-herb birch-aspen-Siberian pine-fir large-herb (*Cacalia hastata*, *Verathrum lobelianum*, *Senecio nemorensis*) and large-fern (*Athyrium filix-femina*, *Dryopteris filix-mas*, *Matteucia struthiopteris*) communities. The chern-taiga complexes, which are characterized by the development of nemoral relict species of the Neogene age and a high level of biota diversity (Ermakov 2003; Kuminova 1960; Nazimova 1967), are determined by modern climatic conditions, primarily high moisture with increased temperature supply (the average precipitation of July exceeds 110 mm, and the average temperature of July exceeds +15 °C). The increased moisture of the winter period also contributes to the preservation of relict complexes. At the same time, the chern-taiga of West Sayan is formed under conditions of slightly higher moisture and lower temperature supply compared to West Altai (Table 7).

The purely mountain-taiga belt in the humid climate of the middle mountains of the Altai-Sayan group of types of altitudinal zonality is represented by dark-coniferous Siberian pine-fir fern (*Dryopteris expansa*), large-herb, herb-green moss forests. The lowest level of moisture supply is observed in larch (*Larix sibirica*) forests on altitudinal profiles in West Altai and Kuznetsk Alatau (average precipitation of July is less than 100 mm). Here these communities are

distributed at a narrow altitude amplitude (about 500 m). In East Sayan, the increased moisture of the mountain taiga belt does not contribute to an increase in its species diversity due to the low heat supply (the average temperature of January is –19 °C).

The high altitudinal belts of all key areas are characterized by a significant amplitude of the values of climate conditions. At the same time, within the types of altitudinal zonality for high mountain communities, there are no significant differences between the key bioclimatic indicators. It can be explained by a decrease in contrasts in the climatic conditions of high mountain regions reflected in the vegetation cover (Sedel'nikov 1988). In all types of altitudinal zonality, the subalpine belt is represented by polydominant large-herb (*Verathrum lobelianum*, *Cirsium helenioides*, *Bupleurum aureum* ssp. *longifolium*) subalpine meadows and Siberian pine and fir sparse forests. Alpine (*Schulzia crinita*, *Bistorta major*, *Myosotis krylovii*) meadows and high mountain tundra (*Rhododendron aureum*, *Festuca sphagnicola*, *Empetrum nigrum*) are characterized by a high similarity of typological diversity. In different types of altitudinal zonality, they are developed with low-temperature supply (the average temperature of January is below –13 °C) and, in general, an increased level of moisture with some regional differences (the average precipitation of July is more than 100 mm). The differences between the subalpine and alpine-tundra belts are mainly regulated by thermic conditions. The high heterogeneity of the ecotopic conditions of the highlands contributes to an increase in vegetation diversity, which is reflected in the richness of plant communities of high-mountain belts of different types of altitudinal zonality in the mountains of Southern Siberia and their close relationship with ecological factors (Molozhnikov 1986; Sedel'nikov 1988). Regional differences between high-mountain belts in relation to the complex of bioclimatic parameters are expressed to a greater extent between the types of altitudinal zonality in comparison with the differences between belts within each of the types.

The spatial structure of vegetation of the Altai-Sayan orobiome is characterized by the altitudinal gradient of climatic conditions. Temperature parameters are most closely related to gradients (especially, temperatures of the cold season) (Fig. 9). The climatic areas of the basic vegetation types of the altitudinal belts, determined by a set of key parameters (average temperature of January, continentality index), do not intersect, which provides a climatic identification for the distinguished types of altitudinal zonality.

Differences in the temperature supply and climate continentality, which characterize the zonal structure of the vegetation cover in large territories, for example, in Northern Eurasia (Nazimova et al. 2004), find similar patterns of influence for the altitudinal spectra. At the same time, the contrast of the vegetation cover increases significantly. The continentality of the climate in the mountains of Southern Siberia marks the altitudinal-belt spectra of vegetation, which are formed under a certain ecological and geographical specificity of mountain ranges. By the prevailing Atlantic transport of air masses, the spatial structure is dependent on the relative position of the ranges, their latitudinal position, and orientation. The entire altitudinal spectrum of the West Sayan type of altitudinal zonality is developed within the same sector of continentality with the maximum values for the group of zonality types, which do not have significant differences between the belts (Table 7). Temperature parameters play a key role in regulating the change of altitudinal belts. The

remaining types of altitudinal zonality are differentiated according to the degree of continentality, reflecting changes in moisture along the altitudinal gradient. The largest amplitude of the parameter has been noted for the West Altai and Salair-Kuznetsk types with forest-steppe belts in the lower part of the spectra. The climatic areas of the corresponding belts in different spectra are partially intersected but do not completely correspond to each other. It is expressed in different aspects of the diversity of vegetation (the level of absolute and relative floristic richness, the ratio of basic and associated types of communities, etc.).

Traditionally the analysis of vegetation cover in relation to climate altitudinal gradient is based on the warm season parameters mainly (Nakamura et al. 2007). The average temperature of January has been used to characterize the thermic conditions. The role of the cold season parameters is not given sufficient attention, while they determine the functioning of ecosystems in different belts during a long frosty period. Extreme temperatures and their annual amplitudes are limiting in the distribution of individual plant species and communities (Bocharnikov 2021). Under the conditions of the development of the Altai-Sayan group of types of altitudinal zonality, the lowest temperatures occur in January. The greatest variation in vegetation diversity is associated with their change.

The conditions for the development of belts of different types of altitudinal zonality are not identical and can differ quite significantly due to a change in the continental climate. The basis of each spectrum is the mountain-taiga belt of dark-coniferous forests. Regional differences in the mountain-taiga belt are clearly expressed in the formation of the chern-taiga sub-belt in the West Altai and the West Sayan types. Despite the increased values of the continentality index, the development of the chern-taiga in West Sayan is determined by a high level of moisture, including a large amount of precipitation of summer. It contributes to forming relict nemoral complexes, which are possible even under low negative average annual temperatures.

The species diversity patterns in the orobiome find some particularities in comparison with mountain gradients of biodiversity. The maximum diversity relates to the lowest part of the spectra (about 400-600 m). The position of maximum in the world is changed in the wide range with gravitation to middle mountains (about 1500 m at 50-60° of North latitude) (Sang 2009; Guo et al. 2013). The orobiome has a similar species diversity pattern in different types of altitudinal zonality that characterizes its unity.

Each type has a specific spread of diversity values with a general trend. The differentiation of beta-diversity confirms a complicated character of mountain diversity (Zhu et al. 2009; Bueno et al. 2021). It can not describe by linear models on the basis of certain bioclimatic parameters. The explanation of diversity trend is in changing of vegetation belts as the basic ecosystems in mountains.

The unity of the groups of types of altitudinal zonality connects with a certain amplitude of bioclimatic parameters (Ogureeva 1991). Changes between types concern the altitudinal limits of belts, the development of individual sub-belts, the variations in the level of absolute and relative species richness of communities founded in each type of altitudinal zonality. At the regional level of the evaluation of the spatial structure of vegetation in connection with climatic conditions, it corresponds to the first level of bioclimatic organization, characterizing the group of types of zonality (Table 8). At the second level, the diversity of climatic conditions determines the development of certain types of zonality, differing in the level of temperature and moisture supply and the degree of continentality. The third level of bioclimatic organization characterizes the conditions of the formation of individual altitudinal vegetation belts, contributing to their development in the composition of the spectra. The amplitude of the values of bioclimatic parameters that determine the unity of its typological subdivisions decreases with a decrease in the hierarchical level of the bioclimatic organization of the vegetation cover. At the same time, different parameters respond to this to a different extent. The level of moisture and continentality of the climate vary rather weakly within individual types of zonality, while temperature supply marks the change of individual belts. It is especially expressed in the lower part of the altitudinal spectra.

Belts in different types of altitudinal zonality have differences in their climatic conditions, depending on the development in the certain type for the particular profile. These differences are reflected not only in the occupied altitudes on the profiles but also in the most important features of vegetation diversity. The predominance of formations and the indicators of the diversity of their communities determine the differences in the spectra by preserving basic formational complexes of vegetation for all the spectra. In the warmest conditions, vegetation belts of West Altai are formed. High-mountain vegetation receives limited development, and relict chern-taiga forests develop in the lower part of the spectrum (the West Altai sector of their distribution) (Ogureeva 1980). The optimal ratio of temperature and moisture contributes to

Table 8. Bioclimatic organization of the spatial structure of vegetation cover for the Altai-Sayan orobiome

A level of bioclimatic organization	Typological levels of altitudinal zonality				
I	Group of types of altitudinal zonality	Altai-Sayan			
II	Zonality types	West Sayan	East Sayan	West Altai	Salair-Kuznetsk
III	Altitudinal belts	I.1 I.2 II.1 II.2 III.1 IIIa.1 IV.1	I.2 II.1 II.2 III.1 IV.1 IV.2	I.1 I.2 II.1 II.2 III.1 IIIa.1 V.1 V.2	I.2 II.1 II.2 III.1 IV.1 V.1 V.2

Vegetation typological subdivisions of altitudinal belts – see table 3.

the development of a forest-steppe belt with a complex composition and structure. Shrub communities participate in the composition of the belt, characterizing the region's connections with the continental regions of Kazakhstan and Central Asia (Karamysheva and Rachkovskaya 1973). West Sayan sector of chern-taiga forests is associated with conditions of a higher amplitude of annual temperatures. However, due to the high level of moisture, including during the vegetation season, they get the opportunity for the development of typologically rich hemiboreal complexes (Nazimova et al. 1987; Ermakov 2003; Bocharnikov 2015). From the climatic point of view, the botanical and geographical specificity of the Altai-Sayan group of types of altitudinal zonation can be determined only by a set of parameters characterizing the temperature, moisture, and their ratio. Under similar conditions of temperature supply, specific altitudinal subdivisions of different spectra are developed (Fig. 9). Moreover, they are strictly separated in the space of climatic conditions.

The obtained results of the work are valuable not only as fundamental knowledge but for practical use. Understanding of regional differences in climatic prerequisites for the formation of vegetation creates the basis for identifying ecosystem problems and planning the rational use of plant resources (Zheng, Zhu 2017). In addition, the constructed bioclimatic system will serve as a basis for identifying trends in the structure of vegetation in connection with climate changes, to which the biota responds (Ramachandran et al. 2020).

CONCLUSION

The conducted bioclimatic interpretation of the vegetation characterizes the general trends in its spatial organization in the Altai-Sayan orobiome, determined by the differentiation of temperature and moisture supply. The unity of altitudinal spectra for the entire group of types of altitudinal zonation is reflected in a similar composition of belts with individual features of belts and sub-belts of vegetation (for example, chern-taiga forests). These features characterize the regional specificity of types of altitudinal zonation.

The vegetation diversity is associated with the climate at different spatial levels marked by bioclimatic parameters. The proposed system of levels of bioclimatic organization of the vegetation cover on the example of types of altitudinal zonation characterizes the differences in the role of specific parameters that determine the differentiation of different belts and different types of zonation within Altai-Sayan group. These differences are associated with a change of the conjugation between parameters and typological subdivisions of vegetation, different amplitudes

of the values of parameters that limit the distribution of individual belts and total altitudinal spectra. The conditions of temperature supply are key in the change of altitudinal belts of vegetation of individual spectra. The parameters of moisture and climate continentality have a dominant in determination of the differences in the complete spectra of different types of zonation. At the same time, within the group of types of altitudinal zonation, the unity of gradients of climatic conditions is preserved.

The thermic gradient prevails over the moisture gradient in terms of the degree of influence on the vegetation diversity within specific altitudinal spectra in the mountains of Southern Siberia. The temperatures of the vegetation season, winter period, as well as the ratio of average temperature extremes, have the most important limiting value. The moisture and continentality gradients characterize a change in altitudinal spectra. Each spectrum has a specific trend of changes in bioclimatic parameters by altitude, which determines differences in the types of vegetation zonation according to the diversity of belts from climatic positions. An increase in the typological diversity of vegetation within the altitudinal-belt spectra is associated with a large variation in the values of bioclimatic parameters differentiated by altitudinal profiles. An increase in the diversity of climatopes, as a reflection of the diversity of temperature and moisture supply conditions, contributes to the functioning of unique relict ecosystems, in particular, chern-taiga forests with an excessive level of moisture.

The increased floristic richness of vegetation complexes in the lower part of the altitudinal-belt spectra of the Altai-Sayan group of altitudinal zonation (forest-steppe, subtaiga, chern-taiga complexes) determines a clear trend in the decrease of relative species diversity of communities with the increase of altitude. It is marked by thermic parameters. A more even distribution of relative species diversity on altitudinal profile connects with a high level of diversity of high-mountain vegetation, and also with a more homogeneous altitudinal-belt structure with a few typological subdivisions. Differentiation diversity is associated with the moisture of the warm period and the temperature supply of the cold period. It has a non-linear trend by the altitudinal gradient. The maximum values of diversity are expressed in the lower part of the altitudinal spectrum and the contact of subalpine and alpine-tundra belts. The spatial structure of high-mountain vegetation forms in relative homogeneous climatic conditions with a smooth gradient of climatic parameters according to the low continentality of climate. It depends on ecotopic conditions mostly. The regional differentiation by climatic conditions of development of vegetation is in different types of altitudinal zonation of the Altai-Sayan group. ■

REFERENCES

- Alberto F.J., Aitken S.N., Alia R., Gonzalez-Martinez S.C., Hänninen H., Kremer A., Lefevre F., Lenormand T., Yeaman S., Whetten R. and Savolainen O. (2013). Potential for evolutionary responses to climate change-evidence from tree populations. *Glob. Change Biol.*, 19, 1645-1661, DOI: 10.1111/gcb.12181.
- Aynekulu E., Aerts R., Moonen P.E., Denich M., Gebrehiwot K., Vågen T., Mekuria W. and Boehmer H. J. (2012). Altitudinal variation and conservation priorities of vegetation along the Great Rift Valley escarpment, northern Ethiopia. *Biodivers. Conserv.*, 21, 2691-2707, DOI: 10.1007/s10531-012-0328-9.
- Bocharnikov M.V. (2015). Eco-ptytocoenotic structure of the forest cover on the northern macroslope of Western Sayan. *Lesovedenie*, 1, 10-19 (in Russian with English abstract).
- Bocharnikov M.V., Ogureeva G.N. and Jargalsaikhan L. (2018). Regional features of the altitudinal gradients in Northern Transbaikalia vegetation cover. *Geography, Environment, sustainability*, 11(4), 67-84, DOI: 10.24057/2071-9388-2018-11-4-67-84.
- Bocharnikov M.V. (2019). Role of climate in the spatial structure of vegetation of the Kodar-Kalar orobiome. *Contemp. Probl. Ecol.*, 12, 193-203, DOI: 10.1134/S1995425519030028.
- Bocharnikov M.V. (2021). Species distribution in cenofloras of the cryophytic steppes and cushion plants with the participation of *Stellaria pulvinata* Grub. in the Mongolian Altai. *Arid Ecosystems*, 11, 1, 52-61, DOI: 10.1134/S2079096121010042.

- Bueno M.L., Rezende V.L., De Paula L.F. A., Meira-Neto J.A.A., Pinto J.R.R., Neri A.V. and Pontara V. (2021). Understanding how environmental heterogeneity and elevation drives the distribution of woody communities across vegetation types within the campo rupestre in South America. *Journal of Mountain Science*, 18, 1192-1207, DOI: 10.1007/s11629-020-6125-0.
- Chytry M., Danihelka J., Kubešová S., Lustyk P., Ermakov N., Hájek M., Hajkovan P., Kočí M., Otypková Z., Roleček J., Řezníčková M., Šmarda P., Valachovič M., Popov D. and Pišút I. (2007). Diversity of forest vegetation across a strong gradient of climatic continentality: Western Sayan Mountains, southern Siberia. *Plant Ecology*, 196, 61-83, DOI: 10.1007/s11258-007-9335-4.
- Clarke K.R. (1993). Non-parametric multivariate analyses of changes in community structure. *Austral. J. Ecol.*, 18, 117-143, DOI: 10.1111/J.1442-9993.1993.TB00438.X.
- Currie D.J. and Paquin V. (1987). Large-scale biogeographical patterns of species richness in trees. *Nature*, 329, 32-327, DOI: 10.1038/329326A0.
- De Dios V.R., Fischer C. and Colinas C. (2007). Climate change effects on Mediterranean forests and preventive measures. *New Forests*, 33, 29-40, DOI: 10.1007/s11056-006-9011-x.
- Del Rio S. and Penas A. (2006). Potential distribution of semi-deciduous forests in Castile and Leon (Spain) in relation to climatic variations // *Plant Ecology*, 185, 269-282, DOI: 10.1007/s11258-006-9103-x.
- Dolezal J. and Srutek M. (2002). Altitudinal changes in composition and structure of mountain-temperate vegetation: a case study from the Western Carpathians. *Plant Ecology*, 158, 2, 201-221, DOI: 10.1023/A:1015564303206.
- Drobushvskaya O.V. and Nazimova D.I. (2006). Climatic variants of the light-coniferous low-mountain subtaiga in Southern Siberia. *Geography and Natural Resources*, 2, 21-27 (in Russian with English abstract).
- Ermakov N.B. (2003). Diversity of boreal vegetation in North Asia. *Hemiboreal forests. Classification and ordination*. Novosibirsk, 232. (in Russian).
- Fick S.E. and Hijmans R.J. (2017). WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas // *International Journal of Climatology*, 37, 4302-4315, DOI: 10.1002/JOC.5086.
- Francis A.P. and Currie D.J. (2003). A globally consistent richness-climate relationship for angiosperms. *American Naturalist*, 161, 523-536, DOI: 10.1086/368223.
- Grebenshchikov O.S. (1974). An essay of climatic characteristics for the main plant formations of the Caucasus. *Botanical journal*, 59, 2, 161-173 (in Russian).
- Holdridge L.R. (1967). *Life zone ecology*. San Jose: Tropical Science Center, 206.
- Karger D.N., Conrad O., Böhrer J., Kawohl T., Kreft H., Soria-Auza R. W., Zimmermann N. E., Linder H. P. and Kessler M. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, 4, 170122, DOI: 10.5061/dryad.kd1d4.
- Kolomyts E.G. (1966). Snow cover of mountain taiga landscapes of Northern Transbaikalia. *Moscow-Leningrad*, 184. (in Russian).
- Kuminova A.V. (1960). The vegetation cover of the Altai. *Novosibirsk*, 450. (in Russian).
- Mokarram M. and Sathyamoorthy D. (2015). Modeling the relationship between elevation, aspect and spatial distribution of vegetation in the Darab Mountain, Iran using remote sensing data. *Model. Earth Syst. Environ.*, 1, 30, DOI: 10.1007/s40808-015-0038-x.
- Morozova O.V. (2011). Spatial trends in the taxonomic richness of the vascular plant flora. *Biosfera* 3(2), 190-207 (in Russian with English abstract).
- Nakamura Y., Krestov P. V. and Omelko A. M. (2007). Bioclimate and vegetation complexes in Northeast Asia: first approximation to an integrated study. *Phytocoenologia*, 37, 3-4, 443-470, DOI: 10.1127/0340-269X/2007/0037-0443.
- Namzalov B.B. (2020). Extrazonal Steppe Phenomena in the Mountains of Southern Siberia: Features of Spatial Organization and Centers of the Latest Speciation and Cenogenesis. *Contemp. Probl. Ecol.*, 13, 495-504, DOI: 10.1134/S199542552005008X.
- Navarro-Racines C., Tarapues J., Thornton P., Jarvis A. and, Ramirez-Villegas J. (2020). High-resolution and bias-corrected CMIP5 projections for climate change impact assessments. *Scientific Data*, 7, 7, DOI: 10.1038/s41597-019-0343-8.
- Nazimova D.I. (1967). Relics of nemoral flora in the forests of the Western Sayan. *Lesovedeniye*, 3, 76-88 (in Russian).
- Nazimova D.I. (1975). Mountain dark coniferous forests of the Western Sayan: an experience of ecological-phytocoenotic classification. *Leningrad*, 119. (in Russian).
- Nazimova D.I., Danilina D.M. and Stepanov N.V. (2014). Biodiversity of rain-barrier forest ecosystems of the Sayan mountains // *Botanica Pacifica. A journal of plant science and conservation*, 3(1), 39-47, DOI: 10.17581/bp.2014.03104.
- Nazimova D.I., Ermakov N.B., Andreeva N.M. and Stepanov N.V. (2004). Conceptual model of structural biodiversity of zonal forests in North Eurasian forests. *Contemp. Probl. Ecol.*, 5, 745-755 (in Russian with English abstract).
- Nazimova D.I., Korotkov I.A. and Cherednikova Y.S. (1987). The main altitudinal-belt divisions of the forest cover in the mountains of Southern Siberia and their diagnostic features. *Lectures in Commemoration of V.N. Sukachev*. Moscow, 30-64 (in Russian).
- Nazimova D.I., Ponomarev E.I., Stepanov N.V. and Fedotova E.V. (2005). Chern dark coniferous forests in southern Krasnoyarsk krai and problems of their general mapping. *Lesovedeniye*, 1, 12-18 (in Russian with English abstract).
- Odland A. (2009). Interpretation of altitudinal gradients in South Central Norway based on vascular plants as environmental indicators. *Ecological Indicators*, 9(3), 409-421, DOI: 10.1016/j.ecolind.2008.05.012.
- Ogureeva G.N. (1980). *Botanical geography of Altai*. Moscow, 192. (in Russian).
- Ogureeva G.N. (1991). *Botanical and geographical zoning of the USSR*. Moscow, 78. (in Russian).
- Ogureeva G.N. (1997). Structure and dynamics of high mountain ecosystems of Mongolian Altai. *Arid ecosystems*, 3, 6-7, 119-133 (in Russian with English summary).
- Ogureeva G.N. and Bocharnikov M.V. (2017). Orobionomes as the basic units of the regional evaluation of the mountain region biodiversity. *Ecosystems: Ecology and Dynamics*, 1, 2, 52-81 (in Russian with English abstract).
- Ogureeva G.N., Miklyaeva I.M., Safronova I.N. and Yurkovskaya T.K. (1999). Zones and types of altitudinal zonation of vegetation of Russia and adjacent territories. Scale 1: 8 000 000. *Moscow*.
- Otto-Bliesner B.L., Brady E.C., Clauzet G., Tomas R., Levis S. and Kothavala Z. (2006). Last glacial maximum and Holocene climate in CCSM3. *Journal of Climate*, 19, 11, 2526-2544, DOI: 10.1175/JCLI3748.1.
- Polikarpov N.P., Chebakova N.M. and Nazimova D.I. (1986). Climate and mountain forests of Southern Siberia. *Novosibirsk*, 225. (in Russian).
- Qian H., Fridley J.D. and Palmer M.W. (2007). The latitudinal gradient of species-area relationship for vascular plants of North America // *American Naturalist*, 170, 5, 690-701.
- Guo Q., Kelt D., Sun Z., Liu H., Hu L., Ren H. and Wen J. (2013). Global variation in elevational diversity patterns // *Scientific Reports*, 8, 1-7, DOI: 10.1038/srep03007.
- Rahman I.U., Khan N., Ali K. and Ahmad S. (2020). Vegetation-environment relationship in Pinus wallichiana forests of the Swat Hindukush range of Pakistan. *J. For. Res.*, 31, 185-195, DOI: 10.1007/s11676-018-0864-6.

- Ramachandran R.M., Roy P.S., Chakravarthi V., Joshi P.K., Sanjay J. (2020). Land use and climate change impacts on distribution of plant species of conservation value in Eastern Ghats, India: a simulation study. *Environmental Monitoring and Assessment*, 192, 86, DOI: 10.1007/s10661-019-8044-5
- Rivas-Martinez S., Penas A. and Diaz T.E. (2004). Bioclimatic map of Europe, thermoclimatic belts. Cartographic Service. University of Leon, Spain.
- Rivas-Martinez S., Rivas Saenz S. and Penas A. (2011). World-wide bioclimatic classification system. *Global Geobotany*, 1(1), 1-634.
- Sang W. (2009). Plant diversity patterns and their relationships with soil and climatic factors along an altitudinal gradient in the middle Tianshan Mountain area, Xinjiang, China. *Ecological Research*, 24, 303-314, DOI: 10.1007/s11284-008-0507-z.
- Sedel'nikov V.P. (1988). High mountain vegetation of the Altai-Sayan mountainous region. Novosibirsk, 222. (in Russian).
- Shao G. and Halpin P.N. (1995). Climatic controls of Eastern North American coastal tree and shrub distributions. *Journal of Biogeography*, 22, 6, 1083-1089, DOI: 10.2307/2845837.
- Sochava V.B. (1980). Geographical aspects of the Siberian taiga. Novosibirsk, 256. (in Russian).
- Stepanov N.V. (2012). Endemism of boreal rainforest region of the Sayan mountains. Abstracts of the symposium The East Asian Flora and its role in the formation of the world's vegetation. Vladivostok, 85.
- Sukachov V.N. and Zonn S.V. (1961). Methodical instructions for the study of forest types. Moscow, 144. (in Russian).
- Svenning C., Gravel D., Holt R. D., Schurr F. M., Thuiller W., Münkemüller T., Schiffrers K.H., Dullinger S., Edwards T.C., Hickler J.T., Higgins S.I., Nabel J.E.M.S., Pagel J. and Normand S. (2014). The influence of interspecific interactions on species range expansion rates. *Ecography*, 37, 1198-1209, DOI: 10.1111/j.1600-0587.2013.00574.x.
- Tolmachev A.I. (1948). The main ways of vegetation formation in high-mountain landscapes of the northern hemisphere. *Botanical journal*, 33, 2, 161-180 (in Russian).
- Tuhkanen S. (1984). A circumboreal system of climatic-phytogeographical regions. *Acta Botanica Fennica* 127, 1-50.
- Walter H. and Breckle S.-W. (1991). *Ökologische Grundlagen in globaler Sicht*. Stuttgart: G. Fischer, 586, DOI: 10.1007/BF02902905.
- Whittaker R.J., Willis K.J. and Field R. (2001). Scale and species richness: towards a general hierarchical theory of species diversity. *Journal of Biogeography*, 28, 453-470, DOI: 10.1046/J.1365-2699.2001.00563.X.
- Yang Y., Wang H., Harrison S.P., Prentice I.C., Wright I.J., Peng C. and Lin G. (2019). Quantifying leaf-trait covariation and its controls across climates and biomes. *New Phytologist*, 221, 1, 155-168, DOI: 10.1111/nph.15422.
- Zheng X., Zhu J. (2017). A new climatic classification of afforestation in Three-North regions of China with multi-source remote sensing data. *Theoretical and Applied Climatology*. 127, 465-480, DOI: 10.1007/s00704-015-1646-0
- Zhu Y., Jiang Y., Liu Q., Kang M., Spehn E.M. and Körner C. (2009). Elevational trends of biodiversity and plant traits do not converge – a test in the Helan Range, NW China. *Plant Ecology*, 205, 273-283, DOI: 10.1007/s11258-009-9616-1.