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Spatiotypological Structure and Organization of Communities of Amphibians and Reptiles on the Cis-Altai Plain

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Abstract—Spatial changes in the population density and species diversity of amphibians and reptiles are described on the basis of material collected in 1998, 2002, and 2014–2016. The spatial and typological structures of their populations were identified and analyzed, and the strength of the connection between the heterogeneity of their communities and the main structure-forming factors of the environment was assessed. Three species of amphibians have been identified on the territory of the cis-Altai Plain during the research, common toad (*Bufo bufo* (Linnaeus 1758)), moor frog (*Rana arvalis* Nilsson 1842), and lake frog (*Pelophilax ridibundus* (Pallas 1771)), as well as four species of reptiles, sand lizard (*Lacerta agilis* Linnaeus 1758), viviparous lizard (*Zootoca vivipara* Jacquin 1787), common snake (*Natrix natrix* (Linnaeus 1758)), and common viper (*Vipera berus* (Linnaeus 1758)). The moor frog absolutely predominates in the population of amphibians (93%), the share of the common toad and lake frog is significantly lower, and the sand and viviparous lizards predominate in the communities of reptiles (48 and 46%). It is shown that amphibians and reptiles are unevenly distributed over the territory, and their greatest abundance and species diversity are typical for the forest–steppe part of the cis-Altai Plain. With an increase in the area of steppe and plowed landscapes and a decrease in the proportion of forests in the central and western parts of the cis-Altai Plain, the locality of their distribution over the territory increases. The population density of amphibians, taking into account the underyearlings, reaches the highest values near the breeding water bodies and does not depend on the landscape specifics of the environment. Excluding underyearlings, the highest total abundance of amphibians is characteristic of lowland bogs, floodplain habitats, and relatively moist small-leaved forests. The majority of reptiles live in forested habitats, while the highest abundance rates are typical for small-leaved and humid birch–pine forests and significantly lower for other habitats. The spatial heterogeneity of the amphibian population is determined, first of all, by differences in the moisture content and food supply of habitats, and anthropogenic transformation of the environment in the form of grazing, which leads to trampling of the vegetation cover and compaction of the topsoil, the degree of afforestation, and the composition of forest-forming species, moisture, and food supply have a significant impact on reptiles.

Keywords: amphibians, reptiles, distribution, abundance, spatial heterogeneity, structural graph, environmental factors, cis-Altai plain, Altai mountain region

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INTRODUCTION

To date, the communities of birds and small mammals among terrestrial vertebrates in the cis-Altai Plain, as well as in the adjacent plains and mountains, have been studied to the greatest extent (Vozniychuk et al., 2002, 2006; Ravkin, 2002; Ravkin et al., 2003a; Dolgovykh, 2006; Vartapetov et al., 2008; Litvinov and Pozhidaeva, 2008; Bochkareva and Irisova, 2009; Toropov and Grazhdan, 2010; Bochkareva et al., 2010; Bochkareva and Volokitina, 2012; Bochkareva and Livanov, 2013). Detailed ornithological and theriogeographic maps have been compiled for these groups of animals within the plain territories of the Upper Ob region and the cis-Altai Plain (*Atlas Altaiskogo kraya*, 1978; Tsybulin, 2009). Ideas about the heterogeneity of the population of these groups were formed, classifications of their communities were compiled, and the strength of the relationship between environmental factors and the spatial variability of their communities was estimated (Makarov, 2017; Makarov et al., 2018, 2018a). At the same time, there is much less information on amphibians and reptiles in the territories bordering the cis-Altai Plain. For the West Siberian Plain as a whole, these are publications by Ravkin et al. (2003, 2005, 2007), which describe interzonal changes in the species diversity and total abundance of

amphibians and reptiles, compile the spatial and typological structures of their populations, and evaluate the role of environmental factors that correlate with the heterogeneity of their communities. In addition, works on species diversity and modern distribution of amphibians and reptiles were carried out in the forest–steppe and steppe regions of the southeast of Western Siberia within the Upper Ob region and in the mountainous provinces of Altai (Yakovlev, 1999; Grazhdan et al., 1999; Borisovich et al., 2002; Ravkin et al., 2003b, 2008; Vozniychuk and Kuranova, 2008; Kuranova et al., 2010, 2016).

Until recently, there was not enough complete information on the abundance and distribution of these groups of animals in the cis-Altai Plain; no classification of their populations has been made, and the relationship between the heterogeneity of communities and environmental factors had not been quantified. The almost universal agricultural development of the territory of the cis-Altai Plain significantly changed the conditions for the existence of animals, including amphibians and reptiles, and caused significant changes in their fauna and population. Therefore, information about the current appearance of the communities of the studied groups of animals, due to their mass character and, to some extent, visibility, can serve as a starting point for predicting changes in their numbers, as well as for assessing the consequences of anthropogenic transformation of landscapes. Based on this, the purpose of this work is to study the spatial heterogeneity and organization of the population of amphibians and reptiles of the cis-Altai Plain. To achieve this goal, the following tasks were set:

– to assess the spatial heterogeneity of the abundance and distribution of all encountered species of the indicated groups of animals; and

– to identify the spatial and typological structure and organization of their communities, as well as to assess the significance of the main environmental factors that determine the heterogeneity of their distribution across the territory.

MATERIALS AND METHODS

According to physical-geographical zoning, the cis-Altai Plain is part of the Altai Mountain Region as a separate North cis-Altai province. It borders the Altai Mountains from the northwest and north with a narrow foothill strip with a total area of about 21000 km^2. In the north, the Cis-Altai Plain borders on the orographic units of the southeast of the West Siberian Plain: on the Ob Plateau in the northwest and on the Bie-Chumysh Upland in the northeast. The mountainous provinces of Northwestern, Northern, and Northeastern Altai adjoin the cis-Altai Plain in the south, and it gradually passes into the foothills of the Salair in the east. The cis-Altai Plain is a slightly undulating, ridged region with meadow grass–cereal steppes. The forest areas are represented by pine forests growing on the sandy terraces of the lower reaches of the Biya and the upper reaches of the Ob. In some places, small birch groves bordered in depressions by thickets of willow, bird cherry, viburnum, and currant bushes are common. Otherwise, the territory is almost treeless and heavily plowed under grain crops, from which buckwheat, wheat, and oats are mainly cultivated (*Atlas Altaiskogo kraya*, 1978).

Amphibians and reptiles were counted in three key areas of the cis-Altai Plain (Fig. 1). The first of them is located in the eastern part of the North cis-Altai province on the territory of the Nizhnebiysk physical-geographical region within the moderately humid meadow-steppe and forest–steppe landscapes (Biysk and Krasnogorsk regions of Altai krai). Here, counts were conducted in 2014 in the vicinity of the towns of Svetloozerskoe, Usyatskoe, and Krasnogorskoe. In addition, materials from K.V. Toropov and K.V. Grazhdan for 1998 and S.M. Tsybulin for 2002 stored in the data bank of the Zoological Monitoring Laboratory of the Institute of Animal Systematics and Ecology, Siberian Branch, Russian Academy of Sciences (Data Bank: Information, Rules for Contributors, 2012). The second and third sites are located in the central and western parts on the territory of the Nizhneanuy and Verkhnealey physical-geographic regions. Mostly arid and moderately arid steppe landscapes are widespread here (Petropavlovsky and Kuryinsky districts of Altai krai). The material was collected at the Nizhneanuy site in 2015 in the vicinity of the towns of Petropavlovskoe and Antonievka and at the Verkhnealey site in 2016 in the vicinity of the towns of Kurya and Ivanovka. The distribution of the population was analyzed for 25 variants of amphibians' population and for 23 variants of reptiles' population. The population variant means data averaged over the first or second half of summer on the species composition and abundance of all amphibian and reptile species recorded in one habitat. Reptiles were counted in the period before the formation of a high grass stand (from May 16 to July 1), and amphibians were counted in the second half of summer (from July 16 to August 31).

Reptiles were counted by the route method, since they can overcome trapping grooves (Ravkin and Livanov, 2008). At least five kilometers were covered in each habitat for a 2-week period. Reptiles were counted on constant, but not strictly fixed, routes without limiting the width of the transect, with subsequent recalculation per unit area according to the average distances from the counter to the animal at the time of detection. Due to the fact that reptiles are poorly visible after the grass stand was raised, their count was carried out only in the first half of summer. For comparability of the data obtained with the data on amphibians, a correction was made for the result of reproduction (the abundance of each species was multiplied by 1.5). The abundance of reptiles was esti-

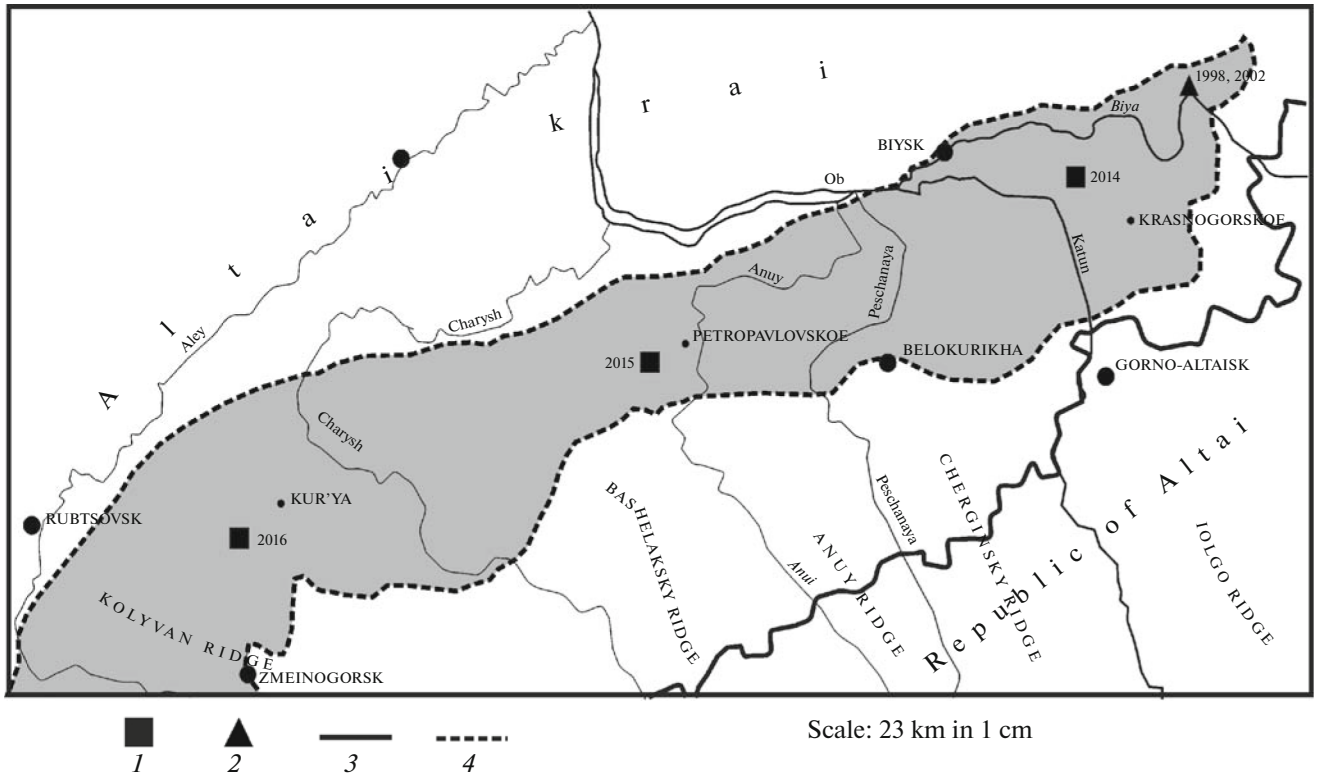

Fig. 1. Places and dates of censuses of amphibians and reptiles in the cis-Altai Plain: (*1*) author's data; (*2*) materials of K.V. Grazhdan, K.V. Toropov, and S.M. Tsybulin; (*3*) border between Altai krai and the Republic of Altai; and (*4*) border of the cis-Altai Plain.

mated as the number of individuals per 1 km^2 (Ravkin and Livanov, 2008).

Amphibians were caught using trapping ditches 50 m long, in which cones were placed every 10 m (Ravkin and Livanov, 2008). Plastic 5-L cone-shaped bottles with a cut-off bottom, which were filled to a quarter of the height with a 4% formalin solution, were used as cones. The catches of amphibians in terms of 100 cone-days (hereinafter, 100 c/d) are taken as the accounting unit. Conversion factors were used to convert relative accounting indicators into absolute ones (per 1 km^2) and to compare the obtained data with information on reptiles. To do this, the indicators of the abundance of amphibians were multiplied by 300, thereby obtaining approximate indicators for 1 km^2 (Ravkin and Lukyanova, 1976). Latin names of amphibian species are given according to (Kuzmin, 2012), and names of reptiles are given according to (Ananyeva et al., 2004).

The communities of amphibians and reptiles were classified according to (Trofimov, 1976; Trofimov and Ravkin, 1980). Its essence is reduced to subdividing the set of population variants into an unspecified number of groups according to the degree of similarity of each sample with all the others. The Jaccard coefficient (Jaccard, 1902) for quantitative traits was used as a measure of similarity (Naumov, 1964). The spatial and typological structures of amphibian and reptile communities were constructed according to (Terentyev, 1959) using matrices of average similarity coefficients at the level of population type. The strength and generality of the relationship between environmental factors and their inseparable combinations (natural–anthropogenic regimes) with the spatial heterogeneity of the population of amphibians and reptiles was assessed using a linear qualitative approximation for the selected gradations of factors (Ravkin et al., 1978).

RESULTS

Quantitative Characteristics of the Population of Amphibians

Three species of amphibians were found on the territory of the cis-Altai Plain: common toad (*Bufo bufo* (Linnaeus 1758)), moor frog (*Rana arvalis* Nilsson 1842), and lake frog (*Pelophilax ridibundus* (Pallas 1771)). In addition, the borders of the ranges of the Siberian salamander (*Salamandrella keyserlingii* Dybowski 1870) and the Siberian frog (*Rana amurensis* Boulenger 1886) lie within the study area (Kuzmin, 2012). Perhaps, the absence of these two species in the counts is explained by the locality of their distribution in the forest–steppe and steppe regions.

The highest population density of amphibians was found in low-lying swamps of the forest–steppe Nizhnebiysky physical-geographical region of the cis-Altai Plain. There are five and seven times fewer amphibians in small-leaved forests, in floodplain meadows, and in residential landscapes. The abundance of amphibians is the lowest in the forest–field and pine–pine forest landscapes (Table 1). The change in the quantitative indicators of amphibians in individual habitats has the same direction, with the only exception in large settlements, where a relatively high abundance of underyearlings was found due to the proximity of the trapping groove to the breeding pond. At the same time, a higher population density of amphibians in birch forests and large settlements, compared to this indicator in floodplains, is associated with the close proximity of trapping grooves to breeding reservoirs: river oxbow lakes with warm and stagnant water, where underyearlings breed in mass numbers and from where they later settle. Large puddles with well-heated water in pine forests, in contrast to birch–pine forests, remain in clearings throughout the summer, which also attracts frogs here. Thus, a gradual decrease in the total abundance of amphibians correlates with the degree of remoteness from breeding sites. Without taking into account the underyearlings, the quantitative characteristic of the distribution of amphibians acquires the following form. The population density is maximum in floodplain meadows and lowland bogs (6300 and 6000), and it is slightly lower in small-leaved forests (5700). It is three times lower in settlements (2100) and minimal in forest–field and pine–pine forest landscapes (700–900). Almost all landscape tracts are dominated by the moor frog, which accounts for 82 to 99% of the population. The common toad predominates only in floodplain meadows with willows (64%), as well as in nonfloodplain meadows with copses (66%).

Amphibians are most numerous in the residential landscape of the steppe Nizhneanuy key area, and there are about half as many in the floodplain landscape. This is explained by the fact that the trapping groove in large settlements was located not far from floodplain meadows in close proximity to the oxbow reservoir, where conditions are favorable for the breeding of underyearlings, as well as for the existence of adult and young frogs. If we do not take into account the clearly overestimated abundance indicators for large settlements, the population density of amphibians decreases from floodplain meadows with shrubs and willows to forest zones among buckwheat and rye fields and reaches minimum values in open fields, steppe pasture meadows, and small settlements. The nature of the change in the total population density of amphibians, excluding underyearlings, is the same. The moor frog dominates in abundance in large settlements (95%), floodplain meadows (97%), and in all open habitats (100%). In small settlements, it shares the first place with the common toad (50% each) in terms of the share in the community. The lake frog is in second place (2–5%) in the floodplains and large settlements, while the share of the common toad is insignificant (0.1–0.8%).

In the west of the cis-Altai Plain, Amphibians are most numerous in the floodplain and steppe landscape on the territory of the Verkhnealey steppe physiographic region and six times less in the field landscape (Table 1). According to habitats, the population density of amphibians decreases from forb-meadow steppes, in combination with wet swampy groves, and floodplain meadows with shrubs and willows, and reaches relatively low values in forest zones among fields and, finally, minimum values in feather grass steppes. Excluding underyearlings, more than half of the total population of amphibians in the key area was found in floodplain meadows with shrubs and willows (11 100), and significantly lower amounts were found in other stows (420–1290). The moor frog, whose share in almost all habitats is 100%, is the basis of the population of amphibians in this key area, and the share of the common toad is significant only in the fields of forage grasses (43%).

So, amphibians are most evenly distributed on the territory of the eastern forest–steppe part of the cis-Altai Plain. The locality of their distribution over the territory increases with an increase in the area of steppe and plowed landscapes and a decrease in the proportion of forests in the central and western parts of the cis-Altai province. Excluding underyearlings, the distribution of which is closely related to the reservoirs of breeding and, therefore, is of a local nature, the highest population density of amphibians on average in the cis-Altai Plain was found in floodplain meadows (8100), and there are fewer amphibians in lowland swamps and in small-leaved forests (5700–6000). There are significantly fewer amphibians (2100) in the open habitats of the field landscape, and their minimum number is typical for pine forest, forest field, and steppe tracts (700–1100). The abundance of amphibians is also low (1800) in settlements where censuses were carried out far from breeding reservoirs. Thus, the decrease in the total abundance of amphibians coincides with a decrease in the moisture content and food supply of biotopes, as well as with an increase in anthropogenic transformation of landscapes: plowing and built-up area. The main contribution to the total abundance of amphibians is made by the moor frog, whose share in the population is 93%. The participation of the common toad and lake frog in amphibian communities is significantly lower (5 and 2%, respectively).

Spatial-Typological Structure and Organization of the Amphibian Population

The structural graph of the similarity of the population of amphibians, taking into account the underyearlings, is a vertical row formed by six classes and

Table 1. Population density of amphibians in the cis-Altai Plain (1998, 2002, 2014–2016, ind./km^2)

Key site, landscape, landscape tract	Total	*Bufo bufo*	*Rana arvalis*	*Pelophylax ridibundus*
Nizhnebiyski forest–steppe	**14865**	**1755**	**13110**	**0**
Pine forest	**3825**	**75**	**3750**	**0**
Pine forests	7350	150	7200	0
Birch–pine forests	300	0	300	0
Small-leaved forests	**13200**	**1050**	**12150**	**0**
Birch forests	23100	1500	21600	0
Birch–aspen forests	3300	600	2700	0
Forest field	**8700**	**3600**	**5100**	**0**
Meadows with copses	9600	6300	3300	0
Buckwheat fields	7800	900	6900	0
Floodplain meadows with shrubs and willows	**10800**	**6900**	**3900**	**0**
Lowland swamps	**66000**	**600**	**65400**	**0**
Residential	**10200**	**300**	**9900**	**0**
Small settlements	2100	0	2100	0
Large settlements	18300	600	17700	0
Nizhneanuy steppe	**27420**	**165**	**26130**	**1125**
Steppe grasslands	**2400**	**0**	**2400**	**0**
Field	**2985**	**0**	**2985**	**0**
Forest zones among fields of:				
buckwheat	6900	0	6900	0
rye	3300	0	3300	0
Forage grass fields	1500	0	1500	0
Deposit fields	240	0	240	0
Floodplain meadows with shrubs and willows	**35670**	**270**	**34800**	**600**
Residential	**84675**	**525**	**79950**	**4200**
Small settlements	1800	900	900	0
Large settlements	167550	150	159000	8400
Verkhnealy steppe	**5528**	**128**	**5400**	**0**
Steppe	**10650**	**0**	**10650**	**0**
Forb–meadow steppes	21000	0	21000	0
Feather-grass steppes	300	0	300	0
Field	**1500**	**225**	**1275**	**0**
Forest zones among fields of:				
sunflower	1500	0	1500	0
maize and buckwheat	1500	0	1500	0
fodder grasses	2100	900	1200	0
deposits	900	0	900	0
Floodplain meadows with shrubs and willows	**11400**	**0**	**11400**	**0**

Table 2. Strength and generality of the association between environmental factors and the heterogeneity of the amphibian population of the cis-Altai Plain (1998, 2002, 2014–2016, with and without taking into account underyearlings)

Factor, mode	Accounted variance, %	
	including underyearlings	excluding underyearlings
Proximity to breeding ponds	27	–
Composition of forest-forming species	14	5
Humidity	12	8
Food supply	12	7
Afforestation	7	2
Anthropogenic influence, including	5	4
plowing	4	4
built-up area	0.9	0.4
Zoning (provinciality)	0.8	6
Relief (floodplain—not floodplain)	0.7	1
All factors	40	28
Regimes by classification	60	17
by structure	65	16
All regimes	65	30
All factors and regimes	74	48

reflecting the degree of proximity to the reservoirs of the offspring. Therefore, the maximum total abundance of amphibians and the proportion of underyearlings gradually decrease with distance from these water bodies (from lowland bogs and large settlements near floodplain meadows, through communities of small-leaved forests, floodplain meadows, and mixed herb–meadow steppes with waterlogged pegs to predominantly open steppe and plowed habitats, as well as birch–pine forests). The distribution of underyearlings largely depends on the location of the breeding reservoirs, and thus, it levels out the dependence of the distribution of amphibians on other environmental factors to some extent. Therefore, we constructed a similarity graph without taking into account underyearlings (Fig. 2).

The vertical trend in the diagram illustrates changes in the amphibian population depending on differences in optimal habitat conditions in terms of moisture and food supply. In this series, there is a decrease in the indicators of total abundance and species diversity from the most humid tracts through moderately humid and unplowed to predominantly dry habitats. The basis of the communities here is made up of the moor frog, the abundance of which gradually decreases from the first to the third type of population. Deviation from the main series associated with plowing leads to a decrease in the number of amphibians and the number of species encountered compared to wet and moderately wet unplowed habitats. The informativeness of structural ideas about the population of amphibians with and without taking into account underyearlings is 65 and 16% of the considered variance.

The strength and generality of the relationship between the heterogeneity of the environment and the variability of the amphibian population was assessed with and without taking into account underyearlings (Table 2). Taking into account the underyearlings, the most significant effect on the distribution of amphibians is exerted by the degree of proximity to the hatching water bodies (27% of the accounted variance). The influence of the composition of forest-forming species (14%), as well as moisture and nutrition (12% each) is approximately two times lower. The relationship between population heterogeneity and afforestation and anthropogenic influence is much less significant (5–7%).

The spatial heterogeneity of amphibian communities without taking into account underyearlings primarily depends on the moisture content and food supply of habitats (8 and 7%). The influence of zoning significantly increases (6%) compared with the results of the analysis carried out for all age groups, and the significance of the composition of forest-forming species decreases slightly (5%). This is explained by the differences between the forest–steppe and steppe landscapes where the studies were carried out. Young and adult amphibians are more evenly distributed over the territory of the forest–steppe part of the cis-Altai Plain than in the steppe regions, where they are localized in the most favorable habitats, due to greater moisture and the number of suitable biotopes. All this increases the role of zoning in the distribution of amphibians. At the same time, the occurrence of

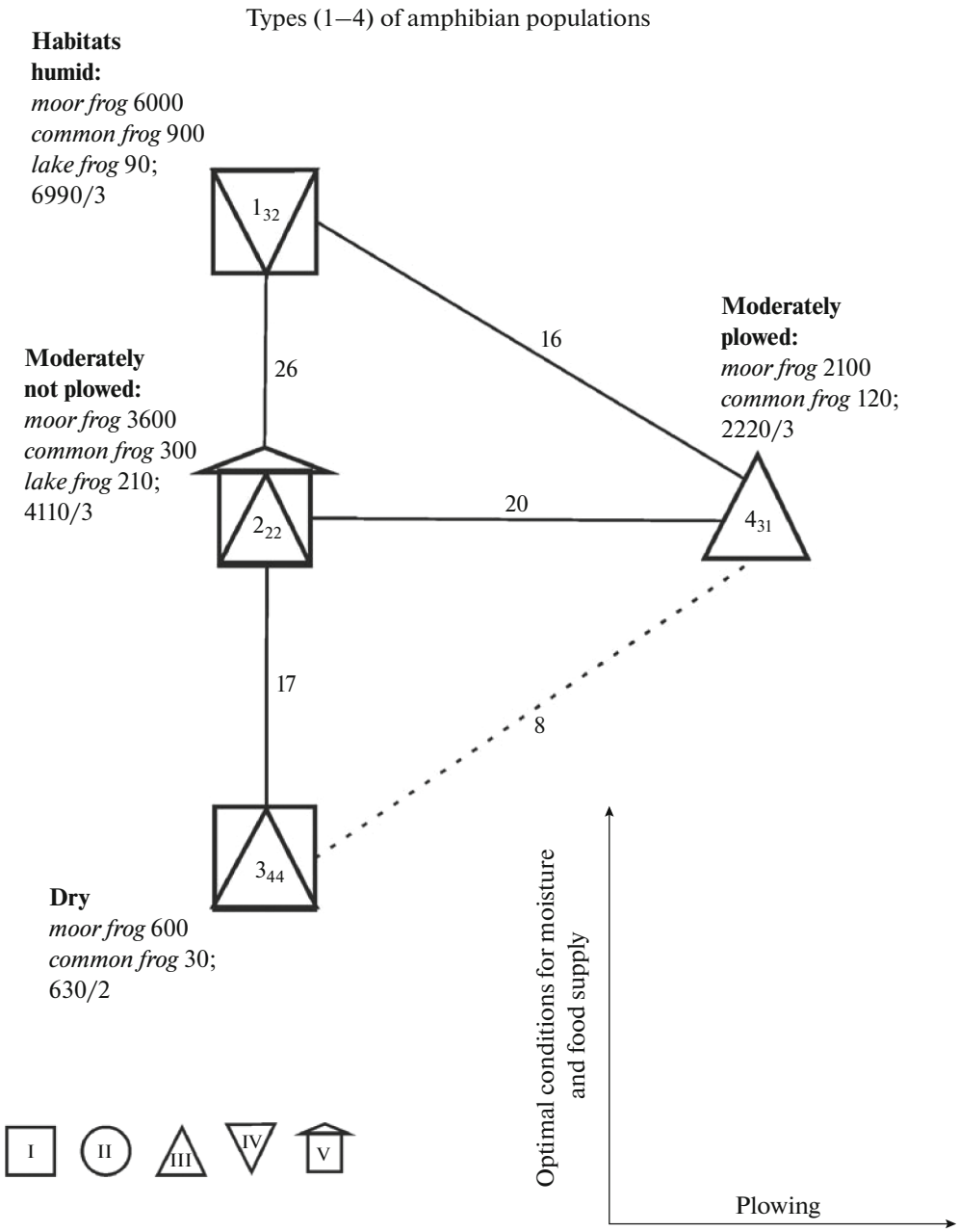

Fig. 2. Spatial and typological structure of the amphibian population of the cis-Altai Plain, excluding underyearlings (1998, 2002, 2014–2016). Types of population: (1) birch and birch–aspen forests, floodplain meadows with shrubs and willows of forest–steppe and steppe regions, low-lying swamps; (2) nonfloodplain meadows with copses, steppe pasture meadows, small and large settlements in forest–steppe and steppe regions; (3) relatively dry pine and birch–pine forests, fallows of steppe regions, forb-meadow, and feather-grass steppes; and (4) fields. Designations for Figs. 2 and 3: I—forest landscapes; II—habitats where areas of forests and open spaces alternate; III—open spaces depleted in productivity; IV—open spaces rich in productivity; V—built-up areas. Subscript shows intra-class similarity, and links between icons show inter-class similarity. Solid lines show significant inter-class relationships; dotted line, links below the threshold value given as additional information. The names of encountered species and their abundance (ind. /km^2) are given next to the icons, and their total abundance/number of species is shown at the end of the list. Arrows in the direction of increasing influence of factors indicate the main trends in the population and the environmental factors that determine them.

underyearlings is highest near the breeding water bodies, and zonal differences fade into the background. The strength of the relationship between anthropogenic factors, mainly plowing (4%), has hardly changed, but its significance is now higher than the influence of forestation (2%). Differences in relief through flooding during high water have a minimal impact on the heterogeneity of the amphibian popula-

tion (1%), which is associated with the absence of extensive annually flooded low floodplains in the study area.

Quantitative Characteristics of the Population of Reptiles

During our work on the territory of the cis-Altai Plain, we have recorded four species of reptiles: sand lizard (*Lacerta agilis* Linnaeus 1758), viviparous lizard (*Zootoca vivipara* Jacquin 1787), common snake (*Natrix natrix* (Linnaeus 1758)), and common viper (*Vipera berus* (Linnaeus 1758)).

On the territory of the Nizhnebiysk physical-geographical region, reptiles are most numerous in small-leaved, pine, and mixed forests. Their number in the tracts of the forest field landscape and floodplains is six times lower, and it is the lowest in the meadow–marsh landscape (Table 3). In some habitats, the population density decreases from birch forests to moist birch–pine and birch–aspen forests. At the same time, the high total abundance is associated mainly with the abundance of the sand lizard in birch forests (87%) and the viviparous lizard in the humid birch–pine and birch–aspen forests (82 and 92%). There are even fewer reptiles in the habitats of the forest and field landscape: meadows with copses, fields and pasture meadows, where the sand lizard predominates (93–100%), as well as in floodplain meadows and lowland bogs, where the viviparous lizard dominates (71–80%). The latter species determines some decrease in the total abundance of reptiles in pine and relatively dry birch–pine forests. The minimum indicators were noted in fallows and meadows among swamps. So, 94% of the population of reptiles (average for the key area) falls on sand (45%) and viviparous (49%) lizards. Common snake and viper make up an insignificant part of reptile communities: 5 and 0.6%, respectively.

Only two species—the sand lizard and the common viper—have been found in the steppe Nizhneanuy and Verkhnealey key areas of the cis-Altai Plain. In these areas, the highest indicators of the abundance of reptiles were noted in the floodplain landscape, they were twice as low in the steppe landscape and the lowest in the field. For individual habitats, this figure decreases from floodplain meadows with shrubs and willows to well-heated mixed-grass–meadow and feather-grass steppes. There are significantly fewer reptiles in steppe pasture meadows and in annually plowed fields of forage grasses, as well as in fields of buckwheat, rye, sunflower, and corn, and least of all in fallows. All the changes in the indicators of the abundance of reptiles are determined, first of all, by the sand lizard, whose share in general in both steppe key areas is 99%.

Thus, the population density of reptiles on the cis-Altai Plain is maximum in forested and relatively humid habitats, while there are more reptiles in small-leaved forests than in pine and birch–pine forests. A decrease in afforestation and moisture and an increase in bogging lead to a decrease in the total abundance of reptiles in open field tracts and lowland bogs. There are an order of magnitude fewer reptiles in the steppes due to the dryness of the climate, while such moisture-loving species as the viviparous lizard, common snake, and common viper are not found here at all. The decrease in the number of reptiles is influenced especially strongly by such factors as plowing and grazing: the abundance indicators are reduced to a minimum.

Spatial-Typological Structure and Organization of the Population of Reptiles

The similarity graph is constructed at the level of the population type with a significance threshold of nine units (Fig. 3). The main spatial trends in the reptile communities of the cis-Altai Plain correlate with changes in afforestation and moisture content, as well as swampiness and floodplain. The vertical row on the graph reflects changes in the total abundance and species diversity of reptiles depending on the degree of afforestation and moisture content of biotopes. A decrease in the number of reptiles was found in this series, as the afforestation and moisture decrease (from small-leaved and light-coniferous small-leaved forests to meadows, fields, and steppes of the steppe regions). At the same time, the greatest decrease in the total abundance was traced during the transition from relatively dry forests to open habitats of the forest–steppe regions, as well as from the latter to similar tracts of the steppe regions. A gradual decrease in the proportion of the viviparous lizard and an increase in the occurrence of the sand lizard was found from the first to the fourth types of the population. So, the viviparous lizard absolutely predominates in the population of reptiles in humid forests, while the sand lizard moves to first place in relatively dry forests and in open habitats of the forest field, field, and steppe landscapes, and the share of the first one in meadows, fields, and steppes is reduced to a minimum. Deviation from the main series is associated with communities of floodplain meadows with shrubs and oxbow lakes, as well as with communities of nonfloodplain lowland bogs. The population density of reptiles is much lower here than in forest communities, but it is higher than in the meadows and fields located in the steppe regions of the cis-Altai Plain. The natural conditions of such biotopes are equally favorable for viviparous and sand lizards, the proportions of which are almost the same here. The informativeness of structural representations is 24% of the considered variance.

The spatial heterogeneity of the population of reptiles of the cis-Altai Plain is determined, first of all, by the anthropogenic transformation of the environment and, in particular, by cattle grazing (21 and 20%). Differences in the food supply of habitats, composition of forest-forming species, moisture content, and afforestation (14–19%) have a lesser effect, while zoning

Table 3. Population density of reptiles in the cis-Altai Plain (1998, 2002, 2014–2016, ind./km^2)

Key site, landscape, landscape tract	Total	*Lacerta agilis*	*Zootoca vivipara*	*Natrix natrix*	*Vipera berus*
Nizhnebiyski forest–steppe	**3556**	**1586**	**1752**	**196**	**21**
Pine forest	**4749**	**94**	**3967**	**612**	**76**
Pine forests	1215	160	1055	0	0
Birch–pine forests	1321	121	1200	0	0
Moistened birch–pine forests	11712	0	9646	1837	229
Small-leaved forests	**9496**	**6000**	**3236**	**260**	**0**
Birch forests	13848	12000	1756	92	0
Birch–aspen forests	5143	0	4715	428	0
Forest field	**1569**	**1488**	**75**	**0**	**6**
Meadows with copses	2404	2231	149	0	24
Pasture meadows	1500	1500	0	0	0
Deposit fields	191	191	0	0	0
Fields of buckwheat and rye	2181	2030	151	0	0
Floodplain meadows with shrubs and willows	**1559**	**312**	**1247**	**0**	**0**
Meadow–marsh	**800**	**244**	**556**	**0**	**0**
Lowland swamps	1555	444	1111	0	0
Meadows among swamps	43	43	0	0	0
Nizhneanuy and Verkhnealey steppe	**462**	**458**	**0**	**0**	**4**
Steppe	**523**	**523**	**0**	**0**	**0**
Steppe grasslands	343	343	0	0	0
Forb-meadow steppes	682	682	0	0	0
Feather-grass steppes	545	545	0	0	0
Field	**179**	**169**	**0**	**0**	**10**
Deposit fields	98	68	0	0	30
Forage-grass fields	272	272	0	0	0
Fields of buckwheat, rye, corn and sunflower	167	167	0	0	0
Floodplain meadows with shrubs and willows	**1126**	**1126**	**0**	**0**	**0**

and differences in relief have the least effect on the distribution of reptiles (Table 4).

DISCUSSION

According to the results of our studies, the batracho- and herpetofauna of the cis-Altai Plain contains seven species, which is 58 and 64% of all encountered species of amphibians and reptiles in the territory of Altai krai and the mountainous provinces of Altai, respectively. In addition to the representatives listed above, five more species were found in the flat territories of Altai krai adjacent to the cis-Altai province. Of amphibians, the common newt (*Lissotriton vulgaris* (Linnaeus 1758)) is relatively widespread throughout the region, and the Siberian salamander (*Salamandrella keyserlingii* Dybowski 1870) was found in humid places of the Kulunda steppe and the Ob pine forest. The findings of the sunwatcher toadhead agam (*Phrynocephalus helioscopus* (Pallas 1771)) and steppe runner (*Eremias arguta* (Pallas 1773)) in steppe ribbon pine forests, where these species adhere to sand dunes and dead cover areas, as well as the steppe viper (*Vipera renardi* (Christoph 1861)) found in the southwest of Altai krai near Zmeinogorsk (*Krasnaya kniga Altaiskogo kraya*, 2006, 2016) are of particular interest. In addition to the steppe viper, the steppe ratsnake (*Elaphe dione* (Pallas 1773)) and the Siberian pit viper (*Gloydius halys* Pallas 1776), as well as the green toad (*Bufo viridis* Laurenti 1768), the occurrence of which was noted in the steppe valleys of Karagem and Argut and in the Kurai steppe, are relatively common in the mountainous provinces of Altai (Yakovlev, 1999; Vozniychuk and Kuranova, 2008).

The main structural changes in the amphibian population on the cis-Altai Plain, taking into account all age groups, depend, first of all, on the proximity to the breeding water bodies, and the distribution of

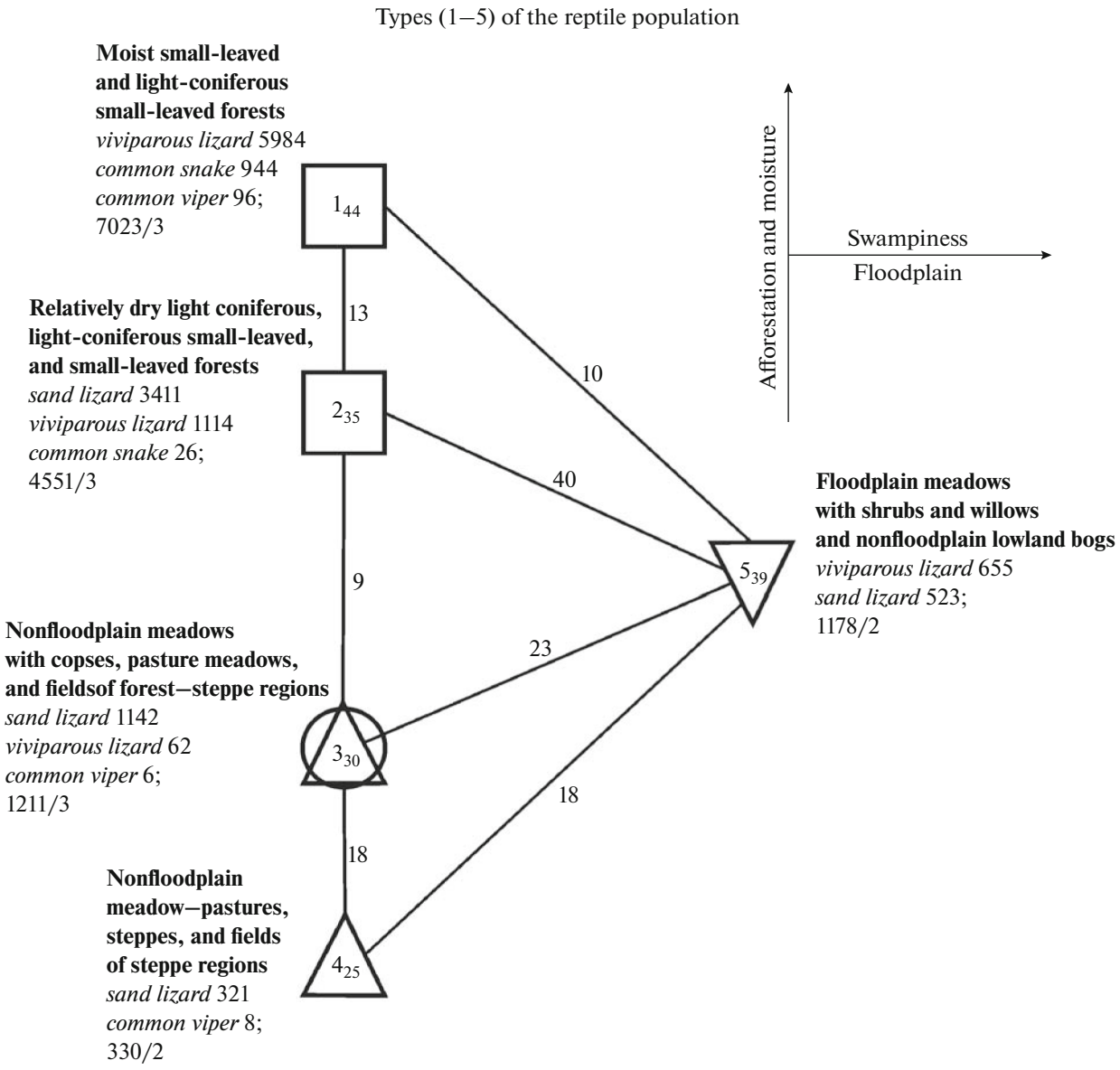

Fig. 3. Spatial and typological structure of the reptile population of the cis-Altai Plain (1998, 2002, 2014–2016). For designations, see Fig. 2.

adults and young individuals without taking into account the underyearlings is explained by the differences in moisture content, food supply, and plowing of the territory. The spatial trends of the amphibian population in similar schemes made for the West Siberian Plain and Altai as a whole, as well as for its individual Northeastern and Central provinces have a common direction with the cis-Altai Plain (Ravkin et al., 2003, 2003a; *Severo-Vostochnyi Altai*, 2009; Vozniychuk, 2013). The changes taking place in the population of amphibians in these territories are associated with the optimal ratio of heat and moisture supply and food supply of habitats, which manifest through latitudinal zonality or absolute heights of the area. That is, a decrease in the population density and species diversity of amphibians occurs with a decrease in moisture, heat supply, and food supply of biotopes, as well as with increased shading, plowing, and building. In addition, the abundance of amphibians in the floodplains of large rivers in the West Siberian Plain can be adversely affected by the influence of floods, leading to the washout of eggs or tadpoles.

Humidity and food supply of habitats are the most significant factors influencing the formation of the amphibian population on the cis-Altai Plain. The distribution of amphibians, taking into account the underyearlings, primarily depends on the proximity to the breeding water bodies, and the heterogeneity in the

Table 4. Assessment of the strength and generality of the association between environmental factors and the heterogeneity of the reptile population of the cis-Altai Plain (1998, 2002, 2014–2016)

Factor, regime	Accounted variance, %
Anthropogenic influence,	21
including	
grazing	20
plowing	1
built-up area*	–
Food supply	19
Composition of forest-forming species	16
Humidity	15
Afforestation	14
Zoning (provinciality)	6
Relief (floodplain—not floodplain)	0.2
All factors	43
Regimes by classification	10
by structure	24
All regimes	24
All factors and regimes	51

* Reptile accounting was not carried out in settlements.

distribution of amphibians without taking into account the underyearlings correlates to a greater extent with zonality (provinciality). In addition to moisture and food supply, amphibian populations in the taiga and forest–steppe subzones of the West Siberian Plain are most affected by zonal differences in heat supply, as well as floodplain and anthropogenic influence (plowing and built-up area), afforestation, and composition of forest-forming species in the forest–steppe landscapes of the upper Ob region (Borisovich et al., 2002; Ravkin et al., 2003, 2003b). The most significant factors affecting the distribution of amphibians in Central Altai, as well as in all the mountainous provinces of this region as a whole include heat supply and moisture, the values of which depend on the absolute height of the area (Ravkin et al., 2003a; Vozniychuk, 2013). In addition, significant factors in the Central Altai province include differences in relief (flood land), the composition of forest-forming species and afforestation, and provinciality (in general, throughout Altai). So, the heterogeneity of the amphibian population in the compared territories is primarily explained by the influence of moisture, food supply, and heat supply, determined by the absolute heights of the area or latitudinal zonality, as well as provinciality. Depending on the provincial specifics, the impact of differences in relief, the composition of forest-forming species, afforestation and anthropogenic transformation of landscapes was also traced.

Relatively moist forested habitats, mainly small-leaved and light-coniferous forests are the most favorable habitats for reptiles on the cis-Altai Plain. The same order in their distribution is typical for the Northeastern province of Altai, in which reptiles are most common in the foothill and low-mountain small-leaved, pine-birch, and black forests, as well as in the West Siberian Plain as a whole, where their maximum total abundance is typical for the southern taiga and subtaiga pine forests (Grazhdan et al., 1999; *Severo-Vostochnyi Altai*, 2009; Ravkin et al., 2007). The exception is the territory of the Central Altai, where reptiles are more abundant in well-moistened and less shaded, compared to forests, subalpine woodlands (Vozniychuk and Kuranova, 2008). A decrease in the total abundance of reptiles occurs in all compared territories with a decrease in moisture and afforestation, as well as with an increase in swampiness and floodplain. Thus, the total abundance of reptiles is an order of magnitude greater in the forest–steppe habitats of the forest–field landscape on the cis-Altai Plain than in open steppes, fields, and meadows from the steppe regions of this province, and it is comparable only with floodplain meadows and lowland bogs. In contrast to the mountainous provinces of Altai, where the viviparous lizard predominates in the reptile population, the share of the sand lizard on the cis-Altai Plain is slightly higher (48%) than the share of the viviparous lizard (46%). This is probably explained by the larger area of open forest–steppe and steppe areas and the fragmentation of forest tracts, which are more favorable for viviparous lizards. Judging by the schemes of the spatial heterogeneity of the population of reptiles, moisture and afforestation can be attributed to factors common for the cis-Altai Plain

and the Central Altai, and trends associated with waterlogging and floodplain are common in the scheme for the West Siberian Plain as a whole, as well as for the cis-Altai Plain. In addition, the main trends of community change in the mountains are associated with heat supply and absolute heights of the terrain, and with latitudinal zonality in the plains. In addition, a trend associated with shading is expressed in the scheme of the Northeastern province of Altai, a trend associated with anthropogenic influence is expressed in the Central province, and a trend associated with the composition of forest-forming species, meadows, salinity, and plowing is expressed in the West Siberian Plain.

A similar set and hierarchy of environmental factors in the formation of reptile communities in the cis-Altai Province were found in the Ob pine forests and adjacent plain landscapes of Altai krai (Borisovich et al., 2002). There is also the most significant anthropogenic influence, but plowing and a built-up area come to first place here, unlike in the cis-Altai Plain. The significant factors that form the heterogeneity of the reptile population in the Central Province of Altai include zonality, moisture content, composition of forest-forming species, and afforestation. However, the anthropogenic impact is insignificant because of a lower anthropogenic transformation of landscapes (Vozniychuk, 2013). The spatial distribution of reptiles on the West Siberian Plain as a whole primarily depends on zonality. The effect of the composition of forest-forming species, meadows and soil salinity was noted to a much lesser extent, and the effect of moisture was noted to a minimal extent (Ravkin et al., 2007).

Thus, the formation of the reptile population in the considered territories depends on a similar set of environmental factors: moisture content, food supply, afforestation, and the composition of forest-forming species. The significant factors include: anthropogenic influence in the lowland forest–steppe and steppe regions, zonality in the mountains, and zonality in the West Siberian Plain as a whole, which is associated with significant changes in heat supply when moving from north to south.

CONCLUSIONS

Three species of amphibians (common toad, moor frog, and lake frog) and four species of reptiles (sand lizard, viviparous lizard, common snake, and common viper) were found during the study on the territory of the cis-Altai Plain. The highest values of the abundance and number of amphibian and reptile species were found in the forest–steppe part of the cis-Altai Plain. The local distribution of these animals over the territory increases and the species diversity decreases with an increase in the area of steppe and plowed landscapes and a decrease in the proportion of forests in the steppe part of the cis-Altai province. The lake frog was recorded only on the territory of the Nizhneanuy steppe site, where it adheres to water bodies located in floodplains and in large settlements. The viviparous lizard and the common snake are found only in the forest–steppe Nizhnebiya area, where they mainly inhabit pine, mixed, and small-leaved forests. The remaining species are found everywhere: the moor frog tends to lowland swamps, floodplain meadows, and small-leaved forests, while the common toad tends to floodplains and nonfloodplain meadows with copses. Small-leaved forests and open tracts of forest–field and steppe landscapes are most favorable for the sand lizard, and the common viper adheres mainly to the pine-forest landscape.

The population density of amphibians, taking into account the underyearlings, reaches the highest values near breeding water bodies and does not depend on the landscape specifics of the environment. The highest total abundance of amphibians, excluding underyearlings, is typical for lowland bogs, floodplain habitats, and relatively moist small-leaved forests. The decrease in these indicators coincides with a decrease in moisture and forage, as well as with an increase in the anthropogenic transformation of landscapes: plowing and building. The main contribution to the total abundance of amphibians is made by the moor frog, the share of which in the population is 93%. The participation of the common toad and lake frog in amphibian communities is significantly lower (5 and 2%, respectively).

The population density of reptiles is maximum in forested habitats, while most of them are in moist small-leaved and birch–pine forests and less in other tracts. A decrease in afforestation, an increase in swampiness, and flooding during floods lead to a decrease in their total abundance in cleft field habitats, in lowland bogs, and in floodplains. There are an order of magnitude fewer reptiles in the steppes due to higher indicators of dryness, despite the fact that three of the four species (viviparous lizard, common snake, and viper) are relatively moisture-loving. When plowing, the total abundance is reduced to a minimum. On average, over the territory, the reptile population is dominated by sand and viviparous lizards (48 and 46%).

The spatial and typological structures of the population of amphibians and reptiles are quite similar to each other, and the heterogeneity in their distribution is determined primarily by the optimal conditions for moisture and food supply. At the same time, the structure of amphibians is simpler, and all variants of the population are divided into four types according to the degree of habitat moisture and the presence of waterlogging and plowing. The structure for reptiles, in comparison with that for amphibians, is distinguished by a more fractional division due to the division of fields, steppes, and meadows beyond the floodplain into two types by provinciality, represented by reptile communities from forest–steppe and steppe regions.

In addition to differences in moisture content, the structural graph for reptiles shows the influence of afforestation and the negative impact of differences in relief, which are not shown in the structure for amphibians.

The hierarchies of the strength of links between environmental factors that affect the heterogeneity of communities of amphibians (excluding underyearlings) and reptiles differ significantly from each other. The heterogeneity of the amphibian population is more influenced by such factors as moisture, food supply, and zoning, while their significance for reptiles is somewhat lower. The distribution of the latter is most affected by the anthropogenic factor, including grazing, and, in addition, the role of afforestation and the composition of forest-forming species is noticeably increasing. At the same time, the role of these factors in the heterogeneity of their distribution is of secondary importance for amphibians, taking into account all age groups, due to the dependence of the abundance of underyearlings on the proximity to breeding water bodies.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest. The authors declare that they have no conflicts of interest.

Statement on the welfare of animals. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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