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THE ROLE OF THE STEPPE MARMOT IN MAINTAINING THE SPECIES AND STRUCTURAL DIVERSITY OF INTRAFOREST MEADOWS

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Abstract. Marmots weren't part of the ecosystems of Bryansk regions for a long time, because they disappeared under the pressure of the plow and uncontrolled hunting. In this area, the first colony of marmot was noticed in 2013 on the gentle slopes of the southern exposure. The aim of the work is to estimate the role of *Marmota bobak* activity for intraforest steppe meadows in the east of the Bryansk region. Route survey showed that plants communities transformed under their activity. Based on geobotanical relevés and statistical analysis, two groups of vegetation were identified in the study area: short-grass and tall-grass meadows. Tall-grass meadows are characterized by low biodiversity indices, because highly competitive grasses dominate the community (*Bromus inermis, Calamagrostis epigeios, Elytrigia repens* etc.). Small-grass meadows are associated with marmot settlements and are sustained by animal activity. Due to the grazing of dominant grasses, less competitive species can occupy more advantageous positions in the grass stand. The activity of marmots allows plant species of different ecological-coenotic groups to coexist in the meadows. To maintain structural and species diversity of the vegetation cover of intraforest meadows, the following features of marmots' behaviour are important: formation of burrows with fresh throwings, which are characterized by an exposed substrate necessary for seed and vegetative propagation of plants; creation and maintenance of pasture or forage areas near the burrows. The above determines the development of vegetation patches (micro-groupings) in meadows and their spatial redistribution in communities.

Keywords: steppe marmot, marmot's settlement, floristic diversity, small-grass meadow, tall-grass meadow

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РОЛЬ СТЕПНОГО СУРКА В ПОДДЕРЖАНИИ ВИДОВОГО И СТРУКТУРНОГО РАЗНООБРАЗИЯ ВНУТРИЛЕСНЫХ ЛУГОВ

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Аннотация. Сурки долгое время не входили в экосистемы Брянской области, поскольку исчезли под давлением распашки и неконтролируемой охоты. На этой территории первая колония сурков была отмечена в 2013 г. на пологих склонах южной экспозиции. Цель работы – оценить роль байбака для внутрилесных степных лугов на востоке Брянской области. Маршрутное обследование показало, что под влиянием байбака происходит трансформация растительных сообществ. На основании геоботанических описаний и статистического анализа на исследуемой территории выделены две группы растительности: низкотравные и высокотравные луга. Высокотравные луга характеризуются низкими показателями биоразнообразия, поскольку в сообществе доминируют высококонкурентные злаки (*Bromus inermis, Calamagrostis epigeios, Elytrigia repens* и др.). Мелкотравные луга связаны с поселениями сурков и поддерживаются деятельностью животных. За счет выедания доминирующих злаков менее конкурентные виды могут занимать более выгодные позиции в травостое. Активность сурков позволяет видам растений разных эколого-ценотических групп сосуществовать на лугах.

Для поддержания структурного и видового разнообразия растительного покрова внутрилесных лугов важны следующие особенности поведения сурков: формирование нор со свежими выбросами, которые характеризуются обнаженным субстратом, необходимым для семенного и вегетативного размножения растений; создание и поддержание вблизи нор пастбищных или кормовых участков. Все это определяет развитие на лугах участков растительности (микрогруппировок) и их пространственное перераспределение в сообществах.

Ключевые слова: степной сурок, поселение сурка, флористическое разнообразие, мелкотравный луг, высокотравный луг

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Introduction

The steppe marmot (*Marmota bobak* Müll.), or baibak is one of the powerful ecosystem engineers (environmental changers) of steppes and steppe meadows [1–3]. Previously, the species was widely spread in the pastureland ecosystems of the Russian Plain. However, under the pressure of the plow and uncontrolled hunting by the beginning of the twentieth century, the small animal had begun to massively disappear [4–6]. As a result, programs for the reintroduction of the marmot have been developed [7, 8]. The scale of the settlement of the baibak in 1977–1990 of the previous century seems to be impressive: only in Russia about 42,000 animals were settled in more than 375 geographical locations [9]. Owing to that and their natural distribution, the animals have reappeared in some regions [5, 10, 11]. Within natural ecosystems, the activity of the baibak reveals itself in two ways: on the one hand, it belongs to the main consumers of plant products [12–14], but on the other hand, it refers to the ecological group of fossorial animals [15–17]. By consuming plants as food, marmots extract part of the biomass of grass communities. By burrowing and renewing the burrows, baibaks mix and throw soil material onto the surface. In this regard, the aim of the work is to show the role of the marmot in the formation and sustenance of structural and species diversity of the vegetational cover of steppe meadows.

Materials and methods

The material was collected in 2018–2023 in the east of the Bryansk region in the Karachevsky physiographic area (Fig. 1). Here, in 2013, a settlement of marmots was discovered in the steppe intraforest meadows [18].

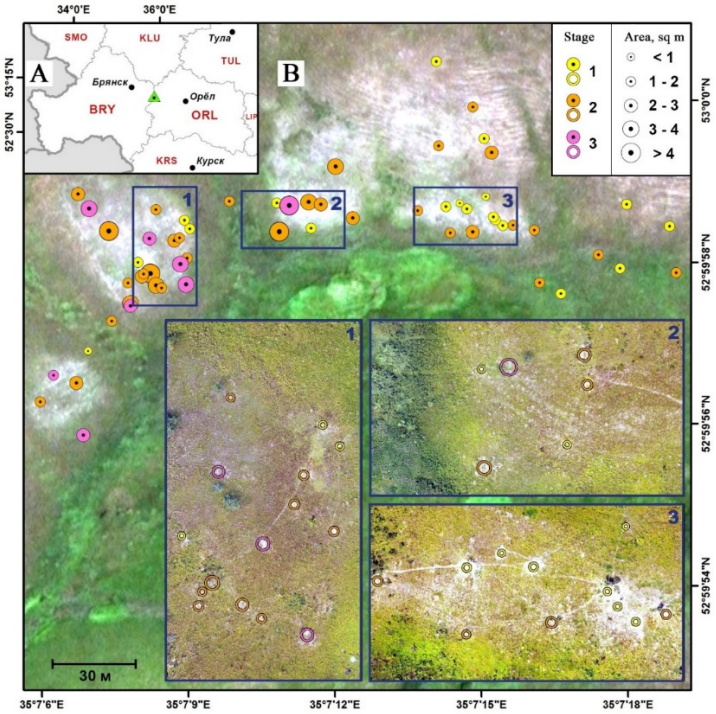

Fig. 1. Settlement of marmots in the Bryansk region:
A – spatial location; *B* – detailed cartography; *1*, *2*, *3* – marmots' burrows of different sizes and stages.
The designations of the countries and regions in the inset are given according to ISO 3166

It is located on the gentle slopes of the southern exposure. Apparently, the animals settled on the territory of the Bryansk region from the neighbouring Oryol region, where in the 1980s the restoration work on the marmot population was in progress. More than 1,000 animals were released in the region [19]. Palaeontologists indicate that the marmot was spread on the territory of the Bryansk region in the Late Pleistocene [20]. The nearest Palaeolithic site of Betovo, in the sediments of the cultured layers of which many bones and whole skeletons of baibaks were found, is located only 70 km away from the settlement under study.

The steppe marmot (Fig. 2) is one of the largest representatives of the order of rodents (*Rodentia*). There are animals weighing up to 10 kg and more. The body length of adult males reaches 70 cm, and females – 65 cm. The animals have short and strong paws well adapted to burrowing activities [21, 22].

Fig. 2. The steppe marmot, or baibak (*Marmota bobak*) in the Bryansk region.
At the top there is a drawing by Shut G.V. based on the photo by Gornov A.V.

They inhabit open landscapes, avoiding places overgrown with tall dense grass and shrubs. This is determined by several reasons. Firstly, such territories are characterized by low food attractiveness for marmots. It is known that tall-grass meadows formed on abandoned lands are characterized by low floristic diversity [23–25] and, therefore, have a narrow composition of plants suitable for food.

Secondly, it is believed that high and dense thickets impair the view and prevent the animals from seeing the approaching danger [22]. Some studies have shown that in the modern biogeocenotic cover, the most suitable conditions for marmots are created on livestock pastures [26, 27]. Animal settlements, due to the widespread ploughing of interfluve plains, are often confined to inconveniences – the slopes of ravines and gullies. In pre-agricultural landscapes, marmots apparently lived on the pastures created by large herd ungulates: mammoths, giant deer, primitive bison, woolly rhinoceroses, bison, tours, tarpans, etc. [28–30]. During excavations, palaeontologists find the bones of these animals arranged together [20, 31, 32]. The marmot was listed in the Red Book of Russia (from 1983 to 1998), but the species was excluded as having regained its numbers. Currently, the animal is protected in many regions, where it has a different status [33].

As a result of the route survey of the territory occupied by the settlement of marmots, two types of communities have been identified: meadows with a predominance of short grasses and meadows with a dominance of tall grasses. The first type of the communities is characterized by pronounced intracoenotic horizontal heterogeneity associated with trophic and burrowing activity of the animals, and the second one – by the absence of zoogenic microsites. Geobotanical studies of the communities of the marmot settlement have been carried out. In each type of the community, 8 relevés have been made at the sites of 25 square meters in size, a total of 16 relevés. The names of the plants are given according to the database Plants of the World Online [34]. The abundance of species in the communities has been assessed on the scale by J. Broun-Blanquet [35]. Based on the descriptions, the occurrence of species, species richness of vascular plants, species density, distribution of plants by ecological-coenotic groups and life forms have been defined. Species richness has been defined as the total number of species at all the sites that belong to the same type of communities. Species density is the arithmetic average number of species at the sites of a fixed size obtained from all the relevés of one variant of the communities [36]. Ecological-coenotic groups (ECGs), in accordance with the ideas of A.A. Nitsenko [37], are considered to be large groups of ecologically close species that in their genesis are associated with certain types of communities. At the same time, the classification of species according to ECGs developed for European Russia has been used [38]. The ecological and morphological classification of I.G. Serebryakov [39] has been used in the analysis of plant life forms. The ratio of species in microgroups by ECGs and life forms has been determined from the general list of plants found at all the sites of the same type of communities. Additionally, the features of the marmots' activity were assessed by observing the animals with field binoculars and the data from "ScoutGuard" camera traps installed at residential burrows.

The statistical analysis of differences in the species composition of communities was performed based on Random forests [40]. We built a statistical model, where species abundance values were treated as independent variables, to classify the collected relevés into two respective communities. Overall classification accuracy (the sum of the diagonal values of the error matrix divided by the total sample size) and Cohen's kappa [41], both estimated on out-of-bag model predictions, were utilized as the integral separability measures. We used *ranger* package [42] in the R environment [43] as a fast and versatile Random forests program realization.

The mapping of the marmot settlement has been carried out based on combination of in-field and remote sensing data. Ground mapping being used, elements of horizontal heterogeneity of the settlement under study were recorded using the Garmin GPSMAP navigator. The coordinates and sizes of marmots' burrows were noted. Additionally, aerial photography of the settlement was carried out from a height of 30 meters using unmanned aerial vehicle (UAV) DJI Phantom. Based on the UAV images, Agisoft Photoscan specialized software being used, an orthophotoplan of a marmot colony with a spatial resolution of 2.5 cm was obtained. Using the overlay of the ground data on the orthophotoplan, a detailed map-scheme of the settlement under study was compiled (Fig. 1).

Results

Two types of communities have been identified on the territory of the marmot settlement under study: tall-grass and short-grass meadows. The first type of communities develops in the areas with minimal impact of baibaks and is characterized by the absence of zoogenic microsites. The second type of coenoses is formed in the areas where animals graze, dig and renew burrows. It is characterized by pronounced intra-coenotic horizontal heterogeneity – mosaicism. The analysis of the measurement proximity matrix, obtained during the training of the Random forest classification model, has revealed a perfect separability in terms of species abundance for the communities under study (Fig. 3,*A*). Hence, the overall classification accuracy was 100 % (with kappa equals to 1.0). Moreover, the abundance indicators of only nine species ensured complete separability of classes (Fig. 3,*B*).

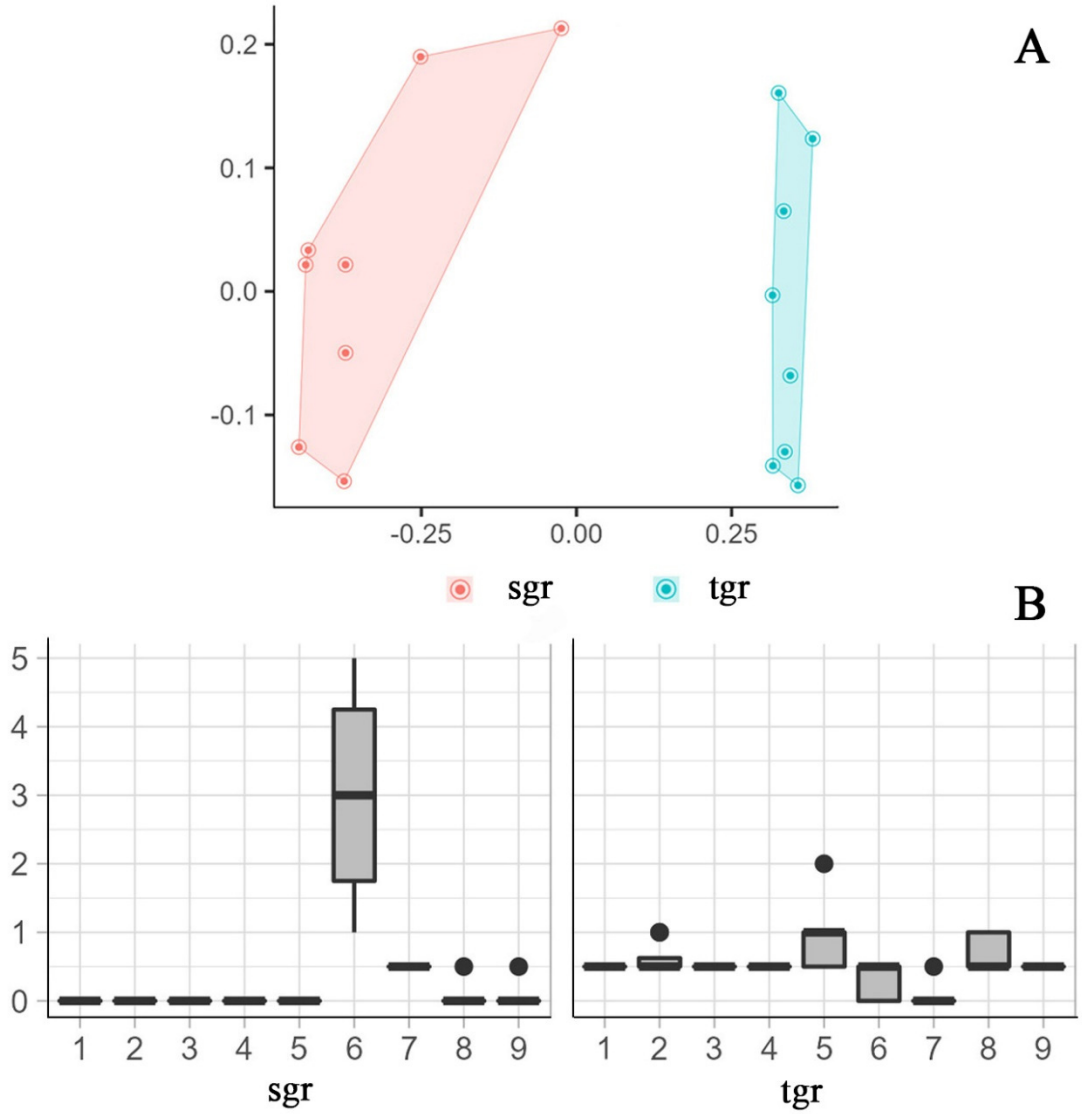

Fig. 3. Diagrams of the statistical analysis of plant communities of the marmot settlement. Communities: sgr – short-grass meadows; tgr – tall-grass meadows: *A* – diagram of separability of plant communities of the marmot settlement (2D-projection of Random forest proximity matrix). The dots indicate the initial belonging of the descriptions to the communities, the circles indicate the results of classification; *B* – diagrams of the distribution of abundance indicators of the most significant plant species in the communities of the marmot settlement. Species are marked on the abscissa axis, and species abundance values on the scale by J. Broun-Blanquet are marked on the ordinate axis. Plant species: *1 – Knautia arvensis*; *2 – Medicago lupulina*; *3 – Allium oleraceum*; *4 – Polygala comosa*; *5 – Nonea pulla*; *6 – Bromus inermis*; *7 – Vicia cracca*; *8 – Leucanthemum vulgare*; *9 – Euphorbia esula*

Short-grass meadows, or short grass. In the meadows where marmots graze, dig and renew their burrows, herbs and small grasses co-dominate: *Agrimonia eupatoria, Fragaria viridis* Weston, *Pilosella officinarum* F.W. Schultz & Sch.Bip., *Poa angustifolia, Salvia pratensis* L., etc. (Fig. 4,*A*,*B*). These communities are characterized by pronounced horizontal heterogeneity, relatively sparse and low grass cover, as well as significant indicators of floristic diversity. Species density reaches 42 species of vascular plants per area of 25 square meters, 38–47 species on each site, and species richness is 80 species. At the same time, in the ecological-coenotic structure of the meadow, there are species of contrasting groups: dry-meadow (*Cichorium intybus*, *Fragaria viridis*, *Poa angustifolia*, etc.), wet-meadow (*Dactylis glomerata*, *Galium mollugo*, *Vicia cracca* L., etc.), nemoral (*Fraxinus excelsior* L., *Malus sylvestris* (L.) Mill., *Platanthera bifolia* (L.) Rich., etc.), nitrophilous (*Arctium lappa* L., *Solanum dulcamara* L., *Urtica dioica* L.) and piny group (*Pinus sylvestris* L.).

Tall-grass meadows, or tall grass. In the areas where marmots have no impact or it is minimum, grasses (*Arrhenatherum elatius* (L.) P. Beauv. ex J. Presl & C. Presl, *Bromus inermis* Leyss., *Dactylis glomerata* L., *Poa angustifolia* L., etc.) and some species of herbs (*Agrimonia eupatoria* L.,

Cichorium intybus L., *Galium mollugo* L., etc.) co-dominate. These plants develop their competitive properties without regular grazing and burrowing activity of baibaks and reach maximum sizes (Fig. 5,*A*,*B*; Table 1). The species density is only 26 species of vascular plants per area of 25 square meters, 22–29 species on each site, and the species richness is 53 species. In the ecological-coenotic structure of tall grass, dry-meadow grasses of different life forms predominate. Among them, the most common grasses are short-rhizome (*Centaurea jacea* L., *Cirsium vulgare* (Savi) Ten., *Hieracium umbellatum* L., *Jacobaea vulgaris* Gaertn., *Leontodon hispidus* L., etc.) and taproot grasses (*Artemisia vulgaris* L., *Cichorium intybus, Picris hieracioides* L., *Pimpinella saxifraga* L., etc.) (Table 1). Most of the listed types are characterized by low indicators of projective coverage.

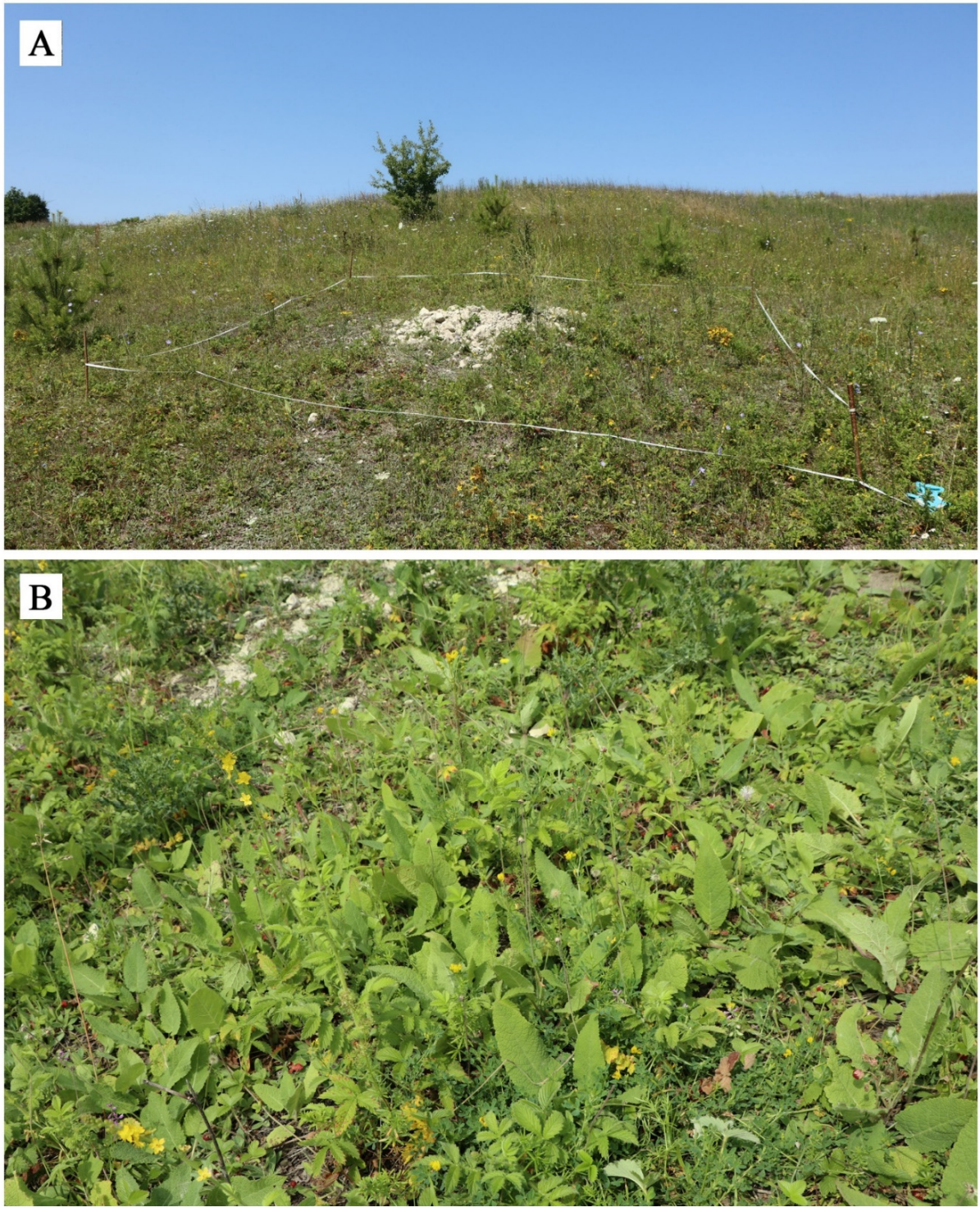

Fig. 4. Short-grass meadows of the marmot settlement:
A – general view of a short-grass meadow with a laid geobotanical site;
B – plot with *Agrimonia eupatoria*, *Fragaria viridis*, *Salvia pratensis*, etc.

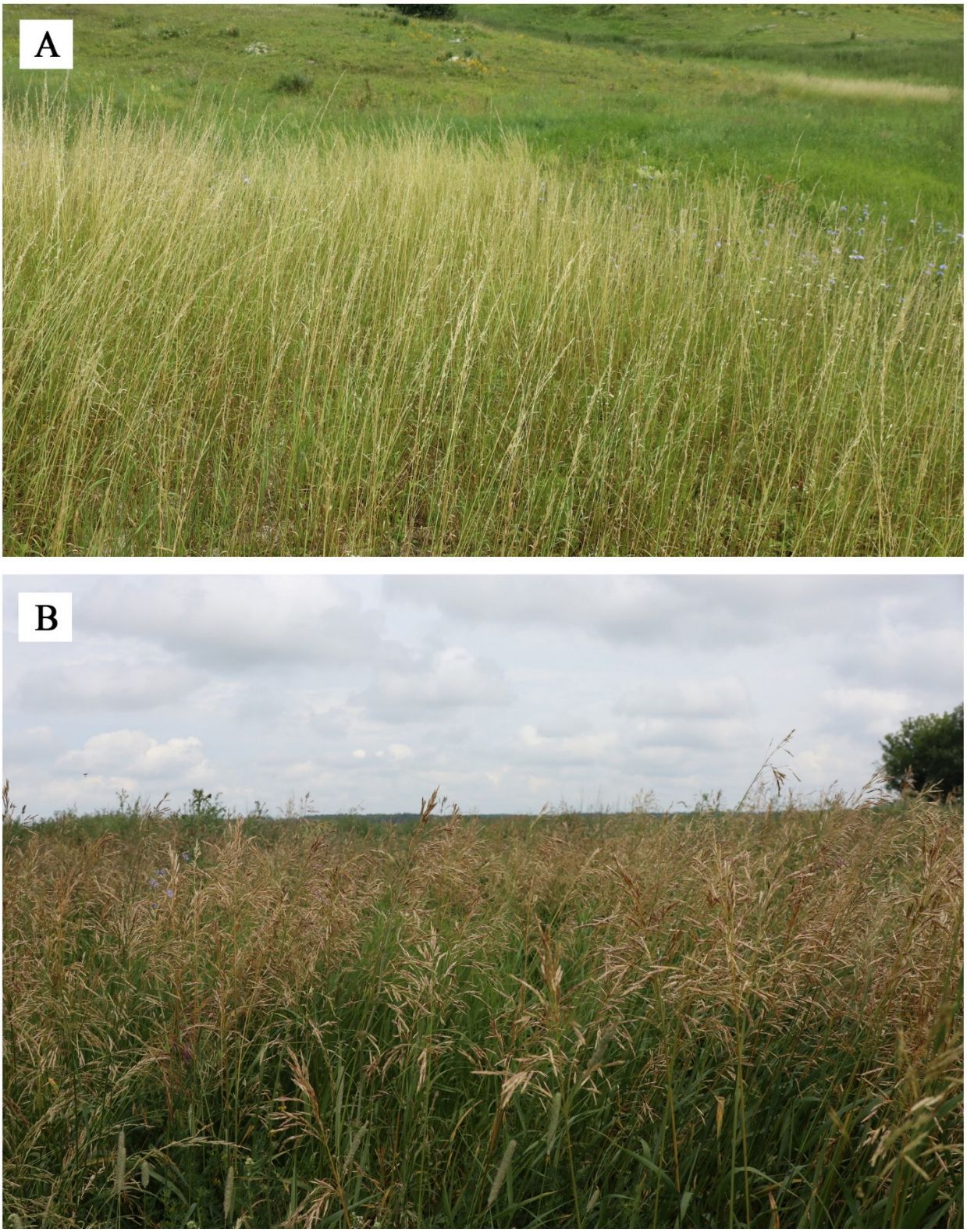

Fig. 5. Tall-grass areas of the meadow with a predominance of *Arrhenatherum elatius* (*A*) and *Bromus inermis* (*B*)

Table 1

Characteristics of the marmot settlement grass cover

Characteristics	Short-grass meadows	Tall-grass meadows
1	2	3
Grass layer coverage, %	70–75	90–100
Grass stand height 1, cm	10–20	40–60
Grass stand height 2, cm	80–120	130–160

End of Table 1

1	2	3
Number of species (and percentage) of different ecological-coenotic groups		
Piny	1 (1)	–
Wet-meadow	9 (11)	6 (11)
Nemoral	5 (6)	–
Dry-meadow	62 (78)	47 (89)
Nitrophilous*	3 (4)	–
Number of species (and percentage) of different life forms according to I. G. Serebryakov		
Tree, shrub	7 (9)	–
Long-rhizome	15 (19)	9 (17)
Root sucker	3 (4)	4 (8)
Short-rhizome	18 (23)	15 (28)
Bulbous	2 (3)	–
Caespitose	6 (8)	6 (11)
Taproot	29 (36)	19 (36)
Number of species (and percentage) of plants considering a specimen's lifespan		
Perennial	65 (81)	44 (83)
Annual, biennial	15 (19)	9 (17)

N o t e: * species of black-alder forest and black-alder forest-fringe groups are combined into nitrophilous.

On the other hand, *Bromus inermis* as one of the dominate species in tall-grasses meadows, rapidly loses positions in short-grass meadows. It makes cover and abundance of *Bromus inermis* the most informative variable for statistical classification.

Discussion

Observation of grazing marmots showed that the basis of the animals' diet consists of fresh, the most moisture-retaining vegetative parts of herbs. Most researchers pay attention to the fact that the species composition of grasses eaten by baibaks is diverse and determined by the flora of their habitats [44–46]. In the meadows studied at the beginning of the season, marmots massively eat young shoots of graminoids (*Arrhenatherum elatius, Bromus inermis, Dactylis glomerata, Phleum pratense* L., *Poa angustifolia*, etc.) and sedges (*Carex hirta* L., *C. spicata* subsp. *spicata*). It is known that spring grazing promotes enhanced shoot formation in graminoids and sedges. It is carried out due to the outflow of nutrients from the underground organs of plants [47]. Therefore, regular early alienation of green parts of grasses leads to a decrease in their productivity, size and projective coverage in the community. Among the listed grasses, only *Poa angustifolia* co-dominates in the grass stand, since it is the most resistant to pasture load and has a high renewable ability. *Poa angustifolia* withstands grazing well because the growth zone of its generative shoots (a panicle hidden in a tube from the sheaths of leaves) is located relatively low [48], and marmots bite off the upper parts of plants. After grazing, the growth zone of generative shoots, as a rule, is not damaged, and they continue to grow. As a result, the grass does not have to spend plastic substances on the formation of new shoots instead of the cut ones, and it does not reduce productivity. At the same time, the high competitive power of *Poa angustifolia* coenopopulations is achieved due to a significant renewable capacity: several axillary buds are formed in the tillering zone of one vegetative shoot, from which new orthotropic and plagiotropic shoots develop. As a result, a close mesh is created, consisting of partial bushes (fixing centres) and communications in the form of rhizomes. Over time, in the meadows under study, actively vegetating grasses are included in the diet of marmots: *Cichorium intybus, Daucus carota* L., *Fragaria viridis, Leucanthemum vulgare* Lam., *Plantago lanceolata* L., *Pilosella officinarum, Salvia pratensis*, etc. In addition to vegetative organs, baibaks willingly eat the upper parts of generative shoots with flowers, unripe fruits and seeds. This reduces the height of plants and gives a competitive advantage to those species that have well-developed basal leaves: *Fragaria viridis, Pilosella officinarum, Salvia pratensis*, etc. It is not without reason that they have the maximum values of projective coverage and occurrence in the feeding areas. Later than other plants, with the beginning of blooming, marmots begin to feed on legumes: *Chamaecytisus ruthenicus* (Fisch. ex Woł.) Klásk., *Genista tinctoria* L., *Medicago lupulina* L., *Trifolium pratense* L., *Vicia cracca*, etc. In the settlement of baibaks, there are areas dominated by *Chamaecytisus ruthenicus*. While grazing, the animals do not eat the plants entirely, but consume only parts of them. At the same time, grazing marmots are not at the same place, cutting off all the plants in a row, but all the time they move around the feeding area in search of suitable food. Such feeding behaviour of the animals was also noted by other authors [21]. Selective feeding of marmots preserves part of the plants from grazing, and changing the diet during the vegetation

period enables bitten shoots to grow, in which the growth zone is not damaged, and to form new ones from dormant buds. The ability to grow or give new generations of shoots after mowing or grazing during the same vegetation period is called regrow capacity of plants [49]. According to some researchers, the animals can take from 2 to 8 % of the harvest of the aboveground phytomass of the community which they inhabit [50]. However, when converted to the area of the feeding plots, the value increases to 40 % [44].

The marmot also belongs to the ecological group of burrowing animals [13, 15]. The animals spend a significant part of their lives in their underground shelters – nesting and protective burrows [16]. When digging and renewing burrows, baibaks throw soil material onto the surface. As a result, flat-topped mounds are formed – burrows (Fig. 6,*A*,*B*), which are characterized by special ecological conditions.

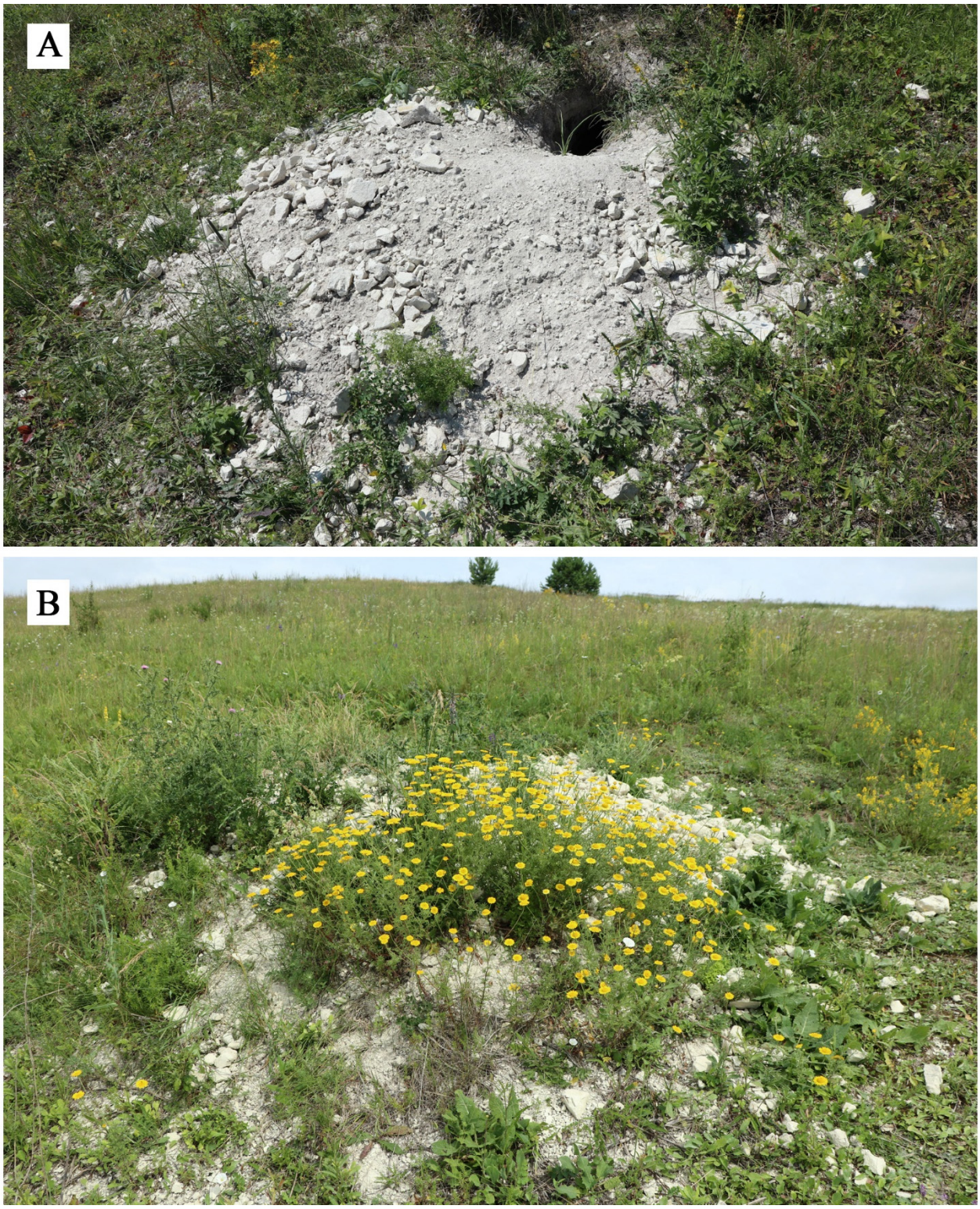

Fig. 6. Burrows with fresh (*A*) and partially overgrown (*B*) throwings

The free space of fresh throwings contributes to the active root take of grasses propagating by seeds. Therefore, there is a high participation of annual and biennial plants (*Arenaria serpyllifolia* L., *Carduus nutans* L., *Carlina biebersteinii* Bernh. ex Hornem., *Clinopodium acinos* (L.) Kuntze, *Daucus carota, Erigeron canadensis* L., *Myosotis arvensis* (L.) Hill, etc.), most of which belong to the group of field-weed plants. Such grasses in natural ecosystems can carry out their life cycle due to zoogenic disturbances of the ground cover. M. S. Gilyarov was one of the first to note this feature [51, 52]. He showed that field-weed grasses are permanent components of the virgin steppe, confined to soil throwings near the holes of rodent burrows. Diaspores of plants get to a burrow in different ways: anemochoric and zoochoric. The soil towering above the surface, exposed and mixed by marmots, dries up quickly. This determines the absolute dominance of dry-meadow taproot grasses at the burrows: *Artemisia campestris* L., *Carduus nutans, Cichorium intybus, Pimpinella saxifraga, Salvia pratensis*, etc. They form a well-developed, lifelong, often storing main root, which can penetrate deeply into loose aerated soil and provide plants with moisture. Vegetative-mobile species are also widely represented at the burrows: *Achillea millefolium* L., *Campanula rapunculoides* L., *Convolvulus arvensis* L., *Euphorbia esula* L., *Pilosella officinarum, Poa angustifolia*, etc. These plants appear at the burrows in two ways. Firstly, long-rhizome and root sucker grasses buried by soil material make their way through a burrow, and secondly, they are actively introduced to burrows from the surrounding grass stand. Besides, baibaks create small digs (holes) in the ground cover of meadows. Plants propagating by seeds can take root in them. For instance, juvenile and immature specimens of *Fraxinus excelsior* and *Pinus sylvestris* were found in the old holes.

Short-grass meadows supported by marmots attract animals of different systematic and functional groups. Thus, the pastures of baibaks with green after-grass are visited by ungulates, and the burrows – by carnivorous mammals and birds. These animals supply diaspores of plants from surrounding communities to the meadow. So, ungulates could have brought to the meadow *Malus sylvestris, Pyrus communis* L., *Urtica dioica*, etc., carnivorous mammals – *Solanum dulcamara*, and birds – *Frangula alnus* Mill. In addition, owing to the grazing of marmots, meadows do not accumulate litter and dry grass, which are known to lead to a high fire danger of unused land [53, 54]. During the research (2018–2023), no traces of fire have been recorded in the marmot settlement. However, in the surrounding abandoned meadows overgrown with tall grass, fires occur regularly.

Large grasses *Arrhenatherum elatius, Bromus inermis, Dactylis glomerata* form numerous tall and foliated aboveground vegetative and generative shoots in the absence or minimal activity of marmots. In addition, the *Bromus inermis* develops long creeping rhizomes with numerous roots and a large supply of buds in the tillering nodes, and *Arrhenatherum elatius* and *Dactylis glomerata* – loose caespitose with a powerful root system. Due to the significant photosynthetic surface, the above-mentioned grasses accumulate a sufficient supply of plastic substances in underground organs. This gives them a competitive advantage: they begin vegetation faster than many plants in early spring and actively occupy a dominant position in communities. Overgrown grasses form closed coenotic groupings, the high grass stand of which deprives lower plants of the light, and heavy sod reduces soil aeration and absorbs precipitation before it reaches the deep roots of various grasses. The above leads to the gradual displacement of weakly competitive heliophilous meadow plants from the community. For example, by the time of the research, many plant species (*Allium oleraceum* L., *Knautia arvensis* (L.) Coult., *Medicago lupulina, Nonea pulla* (L.) DC., *Polygala comosa* Schkuhr, etc.), which have relatively high rates of occurrence in short-grass communities, were not noted in tall-grass meadows. In this regard, tall-grass meadows are characterized by low indicators of floristic diversity.

Conclusion

As a result of trophic and burrowing activities, the common marmot, or baibak, turns tall-grass thickets into short-grass meadows, maintains a rich floristic and structural diversity, determines the mixed nature of the flora of communities (species of different ECG grow together), and also restrains destructive fires. To maintain structural and species diversity of the vegetation cover of meadows, the following features of marmots' behaviour are important: formation of burrows with fresh throwings, which are characterized by an exposed substrate necessary for seed and vegetative propagation of plants; creation and maintenance of pasture or forage areas near the burrows. The above determines the development of vegetation patches (micro-groupings) in meadows and their spatial redistribution in communities. Unfortunately, under the onslaught of the plow and uncontrolled hunting, the baibak has become extremely rare in most regions, and the surviving populations are often small. Therefore, protection and restoration of baibak populations should be systemic in nature. First of all, it is necessary to prevent plowing of land with marmot settlements and create regional specially protected natural territories there, as well as to prevent destructive poaching.

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