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Influence of Fires on Desert Plant Communities at the Chernye Zemli (SW Russia)

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Abstract: Understanding the rate and direction of pyrogenic succession in arid ecosystems, which depends on many factors, including the intensity of grazing and the frequency of pyrogenic expo-sure, will allow for more accurate predictions of the consequences of fire onplant communities, and will assist with better fire management. We studied the vegetation on 55 sites in and near the "Chernye Zemli" Natural Biosphere Reserve that burned at different times or were not affected by fires over the past 35 years and characterized the changes in vegetation cover associated with the impact of wildfire and grazing. The descriptions were grouped into chronological stages according to the time elapsed since the last fire, or into groups according to the frequency of fires. In pairwise comparison of the projective cover of plant species between chronological stages, it correlated most strongly between successive initial stages (for stages 1 and 2, $p = 0.003$, $r = 0.73$; for stages 2 and 3, $p < 0.001$, $r = 0.78$). Species with an initially higher projective cover were more likely to grow on plots in the first year after the fire: $p < 0.03$. Plots with rare and frequent fires had similar projective cover of individual species ($r = 0.64$, $p < 0.001$). We conclude that in the course of pyrogenic succession, communities are gradually replaced over at least ten years. At the same time, the composition of a plant community at the initial point of succession depends on the prevalence of species in the community before the fire. No fundamental effect of the frequency of fires on the composition of plant communities has been revealed.

Keywords: arid ecosystems; chronoseries; environmental filtering; Landsat images; natural revegetation; pyrogenic succession; spatiotemporal replacement; vicinism; xerophyte-grass communities

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1. Introduction

Pyrogenic dynamics are an integral element of the functioning of treeless arid ecosystems in southern Russia. Steppe fires are characterized by lower fire intensities than crown fires in boreal forests. Probably for this reason, pyrogenic successions in treeless arid ecosystems have been poorly studied [1]. In the Republic of Kalmykia, the territory most affected by fires is the State's Natural Biosphere Reserve "Chernye Zemli" [1], where the largest fires among all specially protected natural areas in the southeast of the European part of Russia were recorded. Over the period 1987–2022, 88% of the area of the "Chernye Zemli" Reserve and adjacent territories has been burned 4–7 times, which is significantly more than in Central Kazakhstan [2]. Up to 90% of fires from the five-kilometer zone adjacent to the "Chernye Zemli" Reserve, and all fires from its protective zone, spread to the reserve core. However, since 2018, the number of fires on the territory of the "Chernye Zemli" Nature Reserve has decreased to almost zero [3].

Periodic exposure to certain environmental factors can considerably change ecosystems. This is especially true for fires in arid ecosystems in recent decades [4–6]. Burning of sagebrush communities significantly reduces the cover of dwarf shrubs and (sub)shrubs, that die due to the elimination of renewal buds located above the soil [7–9]. As a result, in the first few years after fires, previously dominant (sub)shrubs are found only as single individuals that survived the fire. On the other hand, the projective cover of cespitose grasses increases after fires. In the Chernye Zemli, these are primarily small-turf *Poa bulbosa* L. and large-turf species of the genera *Stipa* and *Agropyron*. Thus, pyrogenic communities are primarily characterized by the predominance of cespitose grasses and a small participation of (sub)shrubs. During further succession, the cover of (sub)shrubs is restored via seed propagation from soil seed bank and intake from outer territories, primarily under the strong influence of ungulates, which primarily eat grasses and contribute to the restoration of sagebrush community [9,10]. However, excessive grazing pressure prevents the restoration of (sub)shrubs and leads to the formation of communities with a predominance of *Poa bulbosa* and annual species [11]. There is an opinion that the predominance of (sub)shrub vegetation on the territory of Kalmykia is the result of many years of overgrazing, and steppe phytocenoses with a predominance of *Stipa* and *Agropyron* should be considered as climax communities [12].

Despite the fact that the structure and dynamics of desert communities in the "Chernye Zemli" Nature Reserve have been studied previously [13–15], there are many aspects that have not been well studied, including pyrogenic succession changes in the composition of plant communities in Kalmykia. There is a lack of understanding of the effects of frequent burning of the same area on vegetation composition. The reason is that only recently, thanks to the gradual accumulation of a homogeneous array of Landsat images covering the entire territory of the Earth over several decades, has it become possible to accurately determine the frequency of burning and the age of the last fire. Free and easy access to Landsat images has become available in 2008 (https://www.usgs.gov/news/free-open-landsat-data-unleashed-power-remote-sensing-decade-ago) (accessed on 23 January 2024).

The purpose of our work was to evaluate the effects of time since the last fire and fire frequency on phytocenoses at the "Chernye Zemli" Reserve and adjacent areas. The study investigated three issues: (1) assessing the degree of differences in the composition of communities in and beyond the "Chernye Zemli" Nature Reserve, (2) identifying changes in plant communities during pyrogenic succession, and (3) estimating the impact of fire frequency on the state of plant communities.

2. Materials and Methods

2.1. Characteristics of the Study Area

The "Chernye Zemli" Reserve (Republic of Kalmykia, SW Russia; Figure 1) is located in the northwestern part of the accumulative, weakly dissected Caspian lowland, inclined from west to east and corresponding to the late Pleistocene–Quaternary tectonic structure of the Caspian depression, which continues to descend [16]. The absolute altitude of the area ranges from −5 to −20 m below sea level. The climate of the region according to the Köppen classification [17] is moderately warm (Cfb). The sum of positive temperatures reaches 3950–4100 °C. The average annual precipitation is 210–220 mm. The hydrothermal coefficient is 0.3–0.45. The frost-free period lasts 180–200 days [18]. The area is in a transition zone between sandy-loamy Kastanozems and winnowed sandy Gypsisols and Regosols. The vegetation cover of the Chernye Zemli has been greatly changed due to overgrazing and haymaking. Intact plant communities are practically absent. Most often, the indigenous vegetation of the region is considered to be plant communities with a predominance of (sub)shrubs [19–21]. In terms of the area occupied, (sub)shrub communities are dominated by *Artemisia lercheana* Weber ex Stechm. In some places, feather grasses (*Stipa sareptana*

A.K.Becker, *S. lessingiana* Trin. and Rupr., etc.) are abundant, giving the landscapes a steppe appearance [22].

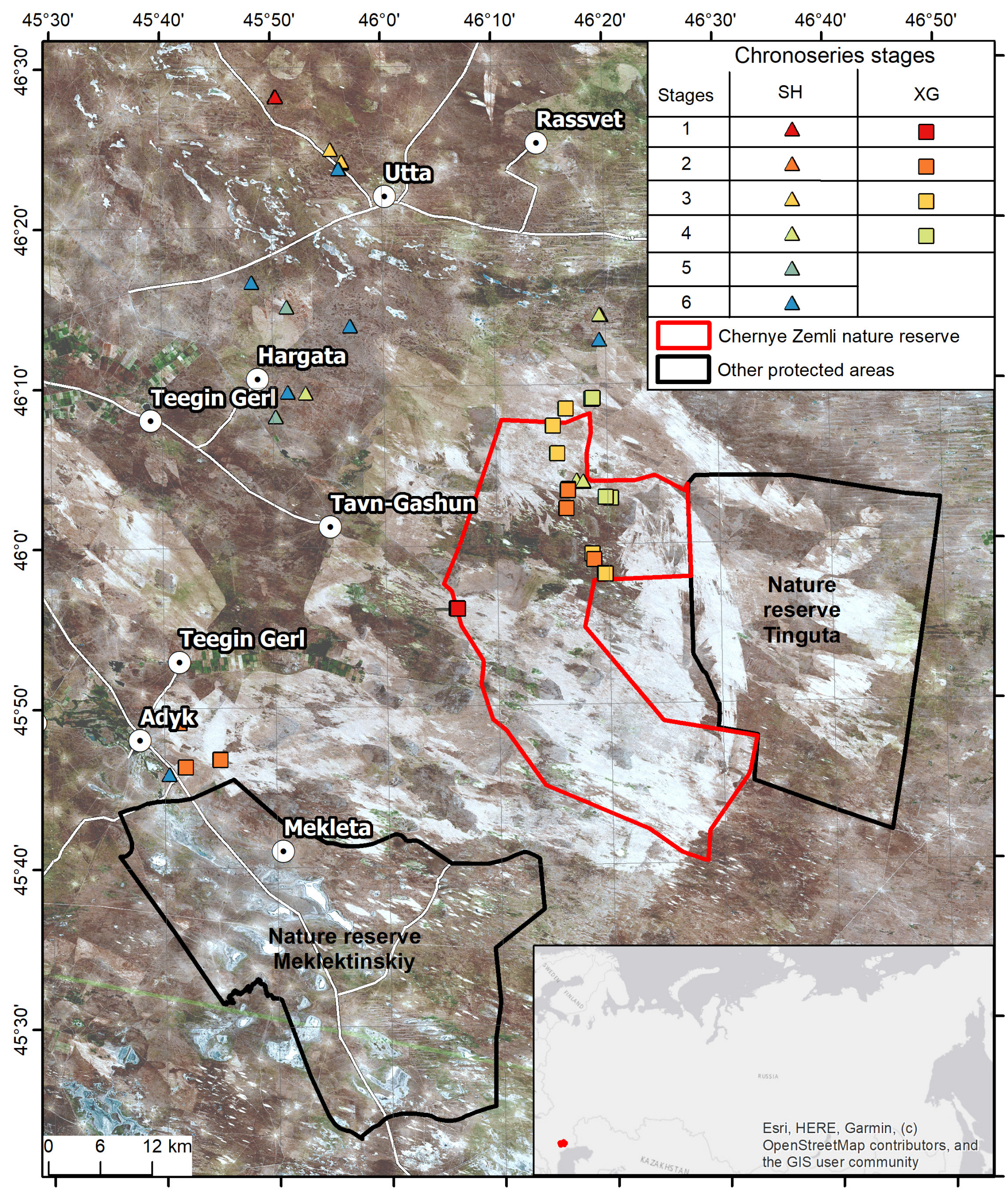

Figure 1. Map of location of key plots of two studied chronosequences in the "Chernye Zemli" reserve and near it (triangles—(sub-)shrub, SH; squares, xerophyte-grass, XG).

2.2. Selection of Key Sites for Field Work

Information about fires in the study area was obtained from satellite images from the Landsat program satellites, shooting in the visible and near-infrared range with a spatial resolution of 30 m. The difference in brightness of the resulting images in the ranges of 1.56–1.66 and 2.1–2.3 µm perfectly emphasizes recently burned territory and is described by the NBR2 index image [23], constructed for each image for the spring and autumn period, starting from 1987. Normalization of the resulting index image by a similar image of the same area for the pre-fire period allows for the most contrasting separation of fires from other objects and shooting or image processing artifacts [2,24]. Based on a normalized index image in the ArcGIS package, the boundaries of all fires for each growing season were identified using automated methods. To determine the frequency of fires, layers with fires for each year were superimposed on each other using the overlay operation, as a result of which information on the frequency of fires for 1987–2021 was obtained for each area of the terrain.

2.3. Field Work

Based on a predetermined pattern of distribution of different-aged areas of burning on the leveled surfaces of elevated mesorelief elements, possible locations for carrying out the descriptions within the "Chernye Zemli" Nature Reserve and in its vicinity were determined. To form the most homogeneous data set, we excluded rare depressions from consideration. Geobotanical descriptions with characteristics of the total projective cover (TPC) of vascular plants, species composition of the community, and projective cover of each vascular plant species were made on flat areas within burned and unburned territories, taking into account the prevailing vegetation, on 55 plots 10 m × 10 m each at the end of April–beginning of May 2021. The projective cover was estimated visually in increments of 10%. For values less than 10%, smaller gradations were used (5, 3, 1, and <1%). All plant names are from the Plants of the World Online database [25].

Depending on the dominant composition of vegetation, we assigned plots to xerophytic-grass and (sub)shrub pyrogenic chronoserie (Table 1). In the communities of the xerophytic-grass chronoserie, large-turf (*Stipa sareptana, S. lessingiana*) and small-turf (*Poa bulbosa*) grasses predominate, and the participation of (sub)shrubs is minimal (projective cover less than 1%). In the communities of the (sub)shrub chronoserie, there is a considerable (>1%) proportion of (sub)shrubs and dwarf shrubs (*Artemisia lercheana, A. pauciflora* Weber ex Stechmann, *Anabasis aphylla* L., *Krascheninnikovia ceratoides* (L.) Gueldenst., etc.). Based on the time that has passed since the last fire (1, 4–6, 9–13, 15–17, 20–35, and >35 years ago) and the corresponding different-age areas within the territory under consideration, 6 chronological stages in the (sub)shrub chronoserie and 4 chronological stages in xerophytic-grass chronoserie were designated. During the field work, it was planned to characterize each age stage with at least four replicates (if possible, the number of replicates was increased up to 10). However, the collection of additional material (the fifth and subsequent descriptions to characterize one age stage) was limited by the fact that there were few distant areas of the same age within the territory under consideration, because it was subjected to large fires several times, which pushed back pyrogenic succession to the beginning.

Table 1. Projective cover of plant species (in %) in communities of two chronosequences studied in the "Chernye Zemli" Reserve and near it at the different stages of a pyrogenic succession.

Plant Species	**Chronoseries Stage and Time since the Last Fire**									
Chronosequence	**(sub)shrub**						**Xerophytic-Grass**			
Stage	**1**	**2**	**3**	**4**	**5**	**6**	**1**	**2**	**3**	**4**
Years	**1**	**4–6**	**9–13**	**15–17**	**20–35**	**>35**	**1**	**4–6**	**9–13**	**15–17**
Annuals										
Adonis aestivalis L.	–	–	–	–	0.1	–	–	–	–	–
Alyssum desertorum Stapf	0.5	0.5	0.5–1	0.1–0.5	0.5	0.1–0.5	–	0.1–0.5	0.5–30	0.1–0.5
Androsace maxima L.	–	–	–	–	0.5	–	–	–	–	0.1
Bromus tectorum L.	–	0.5	0.5	0.5	–	0.5	–	0.5–25	0.5–1	0.5
Buglossoides arvensis (L.) I.M.Johnst.	–	–	–	–	–	–	–	0.5	–	0.1–0.5
Ceratocarpus arenarius L.	–	0.5	–	0.1–0.5	–	–	–	–	0.1–1	0.1–0.5
Chorispora tenella (Pall.) DC	–	–	–	0.1–0.5	–	–	–	–	–	–
Crepis sancta (L.) Bornm.	–	–	–	–	0.1	–	–	0.1–0.5	0.1–3	–
Delphinium consolida subsp. *divaricatum* (Ledeb.) A.Nyár.	–	–	–	–	–	–	–	0.5	–	–
Descurainia sophia L.	–	–	–	0.5	–	–	–	0.5	0.1–0.5	0.1–0.5
Eremopyrum orientale (L.) Jaub. and Spach	–	–	–	0.5	0.5	0.5	–	0.5	–	0.1
Eremopyrum triticeum (Gaertn.) Nevski	–	–	–	–	–	1	–	–	–	0.5
Erodium cicutarium (L.) L'Hér.	–	–	–	–	–	0.5	–	0.1–0.5	–	0.1
Filago arvensis L.	–	–	–	–	–	0.1	–	0.5	0.5–1	0.1
Holosteum umbellatum L.	–	0.5	0.5	0.5	0.5	0.5	–	0.1–0.5	0.1–0.5	0.5–1
Lappula patula (Lehm.) Menyh.	–	–	–	0.5	–	0.5	–	–	0.5	–
Lepidium perfoliatum L.	0.5	0.5	0.1–0.5	0.5	0.5	0.5–5	–	0.1	–	0.1
Medicago orthoceras (Kar. and Kir.) Trautv.	–	0.5–1	0.1	0.1–0.5	0.1	0.5–1	–	0.1–0.5	0.1–10	0.5
Meniocus linifolius (Stephan ex Willd.) DC.	–	0.1	–	0.5	–	–	–	0.5	0.5	–
Myosotis stricta Link ex Roem. and Schult.	–	–	–	–	–	0.5	–	0.5	0.1–0.5	0.1–10

Table 1. *Cont.*

Plant Species	Chronoseries Stage and Time since the Last Fire									
Chronosequence	**(sub)shrub**						**Xerophytic-Grass**			
Stage	**1**	**2**	**3**	**4**	**5**	**6**	**1**	**2**	**3**	**4**
Years	**1**	**4–6**	**9–13**	**15–17**	**20–35**	**>35**	**1**	**4–6**	**9–13**	**15–17**
Ranunculus falcatus L.	0.5	0.5	–	0.5–1	0.5	0.1–0.5	0.1–0.5	0.5–1	0.1–0.5	0.5–1
Ranunculus testiculatus Crantz	0.5	–	–	–	–	0.1–0.5	–	0.5	–	–
Salsola tragus L.	–	–	–	0.5	–	–	–	–	0.5	0.5
Senecio vernalis Waldst. and Kit.	–	–	–	–	–	–	–	–	0.5	–
Veronica triphyllos L.	–	–	–	0.5	–	0.5	0.5	0.5–2	0.5	0.1–0.5
Veronica verna L.	–	0.5	0.5	–	0.5–1	0.5–1	–	0.1–0.5	–	–
Annuals or biennials										
Sisymbrium altissimum L.	–	–	–	–	–	–	–	–	0.5	–
Sisymbrium loeselii L.	–	–	–	–	–	0.5	–	–	0.5	–
Biennials										
Falcaria vulgaris Bernh.	–	–	–	–	–	0.5	–	–	–	–
Perennials										
Agropyron fragile (Roth) P.Candargy	–	–	–	0.5–3	–	1	–	0.5	0.1	–
Anabasis aphylla L.	–	0.5	–	0.5	–	0.1–0.5	–	–	–	0.5–5
Artemisia lercheana Weber ex Stechm.	0.1	–	–	2–40	2–5	1–20	–	0.5	–	–
Artemisia pauciflora Weber ex Stechmann	–	–	–	–	0.5	1–3	–	–	–	–
Artemisia santonicum L.	–	1–5	1–5	–	5	–	–	–	–	–
Astragalus dolichophyllus Pall.	–	0.5	–	0.1–0.5	0.1–1	–	–	–	–	–
Astragalus longipetalus Chater	–	–	–	0.1–0.5	–	–	–	–	–	–
Astragalus varius S.G.Gmel.	–	–	–	0.5	–	0.5	–	–	–	–
Bassia prostrata (L.) Beck	–	–	0.1	1	–	0.5	–	–	–	–
Carduus uncinatus M.Bieb.	–	–	–	–	–	–	–	0.5	0.5–1	–
Carex stenophylla Wahlenb.	0.5–1	0.5–1	0.5–3	0.5	10–15	0.5–1	3–5	1–10	0.5–1	0.5–3
Convolvulus arvensis L.	–	–	–	0.5	–	–	–	–	–	–
Elymus repens (L.) Gould	0.5	0.5	0.5	–	0.1–0.5	0.5	–	0.5	1	0.5
Gypsophila paniculata L.	–	–	–	–	–	–	–	0.5	0.1	–
Krascheninnikovia ceratoides (L.) Gueldenst.	–	–	–	–	–	–	–	–	–	0.5
Peganum harmala L.	–	–	–	0.1	–	–	–	–	–	–
Phlomis herba-venti L.	–	–	–	–	–	0.5	–	0.1	–	–
Poa bulbosa L.	5–10	10–20	20–35	15–35	20–45	3–40	1–10	0.1–20	1–50	1–50
Prangos odontalgica (Pall.) Herrnst. and Heyn	0.5	0.5	0.1–0.5	0.5	0.5	0.1–1	0.1–0.5	0.5	0.1	0.1–0.5
Ranunculus oxyspermus Willd.	0.5–1	0.5	0.5–1	0.5–0.1	0.1–1	0.1–0.5	0.5–2	0.5–2	0.5–1	0.1–3
Stipa lessingiana Trin. and Rupr.	–	–	–	–	–	–	–	–	0.5–5	–
Stipa sareptana A.K.Becker	–	0.5–1	0.1–1	1	0.5	0.5	0.5–1	0.5–10	0.1–10	1–10
Tanacetum achilleifolium (M.Bieb.) Sch.Bip.	0.5–1	–	0.5–1	0.5	0.5–1	0.5	–	–	–	–
Tulipa biflora Pall.	0.1–0.5	0.5	–	–	–	0.5	–	–	–	–
Tulipa sylvestris subsp. *australis* (Link) Pamp.	–	0.5	–	0.5	–	–	0.5–2	–	–	–
n	4	3	4	7	4	7	4	10	7	5

Note. The identified scatter of species projective cover values for communities in which this species was found is presented. Dash—the species is not found in any plot at this stage.

2.4. Data Processing

The role of grazing was assessed by comparing the average projective cover of plants on sites with different total cover of sagebrush in the reserve and in the adjacent territories, considering sagebrush as an indicator of the restoration of conditionally native vegetation. The analysis was carried out independently for two groups of sites (with projective cover of sagebrush of less than 1% and 1–10%). This work was carried out due to the fact that human activity can considerably influence plant communities, which casts doubt on the legitimacy of combining data obtained in the reserve and beyond. The Mann–Whitney U-test was used to compare projective cover of individual species in and outside the reserve.

In order to assess changes in the communities after fire, the Spearman correlation coefficient (r) for the average projective cover of species was calculated for each pair of chronological stages, considering only species that were common between them.

To understand the relationship between community composition of the area before and after the fire, we used the concept of space-for-time substitution, when areas that were exposed to a factor at different times are considered as a chronoserie [26]. For each plot belonging to Stage 1 (i.e., the earliest chronological stage; "post-fire stage"), the pre-fire stage was determined in accordance with the year of the previous fire, estimated from Landsat images [2,24]. It turned out that before the most recent fire, all stage 1 sites of the xerophytic-grass chronoserie were at stage 2, and all sites of the (sub)shrub chronoserie were at stage 6. We named vascular plant species which were found on both pre-fire and post-fire stages as 'fire tolerant' species. We named species found only on pre-fire stage as 'fire intolerant' species (Table 1). The pre-fire projective cover of these two groups of species was compared with Mann–Whitney U-test.

To study the influence of fire periodicity on the state of plant communities of middle-aged fires (stages 2–4), two data subsets were formed based on the number of fires over the past 35 years: 0–2 fires (n = 15) and 4–6 fires (n = 19; Figure 2). Sites with three fires in the last 35 years were excluded from the analysis to provide a more contrasting differentiation between the two groups than would be obtained if these data were added to one of the two subsets. Projective cover of individual species in frequently and rarely burned areas was compared with the Mann–Whitney U-test. To clarify the fundamental differences between communities of frequently and rarely burned areas, we looked for indicator species for these groups of plots.

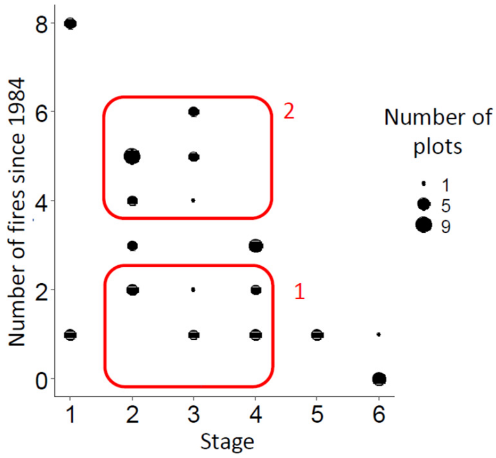

Figure 2. Number of sites with different frequency of fires at different age stages of restoration (according to the period since the last fire) in the "Chernye Zemli" Reserve and near it. The red rectangles limit the sites taken for the analysis as the rare (1) and frequent (2) fire groups.

Non-metrical multidimensional scaling (NMDS) was conducted in R with "vegan" package [27]. Significance of passive ecological vectorswas assessed using the Bonferroni correction.

In all cases of using the Mann–Whitney U-test, the significance of differences in projective cover was assessed using the Bonferroni correction for multiple testing. Calculations were conducted using the basic commands of the R language [28]. A search for indicator species was carried out based on the IndVal value using the "multipatt" function of the "indicspecies" package for R [29].

3. Results

For 1987–2022, the territory under consideration (Figure 1) was exposed to fire 20 times. The first major fire was recorded in 1991 (0.04% of the territory), and the last was recorded in 2015 (48%). There were no large fires in 1986–1990, 1996–1997, 2009, 2012 and 2016–2022. In 2006 and 2002, very large fires affected more than 96% and 57% of the territory, respectively. In 1998, 2001, 2004, 2007, 2011, 2014, 2015, fire affected about 30% of the area of the "Chernye Zemli" Nature Reserve. In other years, the percentage of the burned area varied from 0.04 to 18%. From 1986 to 2020, the maximum number of fires was 10, and such territories accounted for 0.0001% of the total area of the "Chernye Zemli" Reserve.

According to remote sensing data, all the territory of "Chernye Zemli" Reserve has been burnt at least once in the last 15 years. Therefore, the vegetation cover of the reserve is a mosaic of areas belonging to initial or middle chronological stages. For this reason later stages of pyrogenic succession and communities that did not burn out during the period of availability of Landsat images (since 1984) were examined only outside the reserve, in the area of the Utta and Adyk villages (see Figure 1).

3.1. Comparative Analysis of Plant Communities in the "Chernye Zemli" Reserve and Beyond

Between the communities inside the reserve and outside of it with sagebrush projective cover <1%, the average number of species per 10 × 10 m plot did not significantly differ (p = 0.8; Table 2) in the reserve and in the pastures: 11 and 12 species, respectively. However, communities in the protected area and outside it differed significantly in projective cover of two species: the cover of *Stipa sareptana* was significantly higher in the reserve, and *Prangos odontalgica* (Pall.) Herrnst. And Heyn outside its border (Table 3). The average number of species per plot with sagebrush projective cover from 1 to 10% also did not differ in the reserve and in adjacent pastures (17 and 14 species respectively; p = 0.2) in the absence of species with significantly different projective cover in the reserve and outside it. The results obtained allow us to consider sites in the reserve and outside of it as a single data set.

Table 2. Comparison of species richness on plots in the "Chernye Zemli" Reserve and near it for two groups based on projective cover of *Artemisia* spp.

Projective Cover of *Artemisia* spp., %	Number of 10 × 10 Plots		Mean Number of Species on 10 × 10 m Plot		
	In Reserve	Outside Reserve	In Reserve	Outside Reserve	p-Value of Mann–Whitney Test
<1	24	9	11.4	11.9	0.8
[1–10)	6	7	17.3	14.0	0.2

Table 3. Occurrence of species in the "Chernye Zemli" Reserve and outside of it.

Species	Species Representation *		p Value of Significance of Differences **	Median Projective Cover, %	
	In the Reserve	Outside the Reserve		In the Reserve	Outside the Reserve
Communities with Sagebrush Cover <1%					
Alyssum desertorum Stapf	3.55	0.46	0.34	0.3	0.5
Bromus tectorum L.	2.05	0.11	0.29	0	0
Carduus uncinatus M.Bieb.	0.15	0.06	0.51	0	0
Carex stenophylla Wahlenb.	2.38	1.61	0.9	0.5	0.5
Ceratocarpus arenarius L.	0.13	0.17	0.78	0	0
Crepis sancta (L.) Bornm.	0.28	0.11	0.35	0	0
Descurainia sophia (L.) Webb ex Prantl	0.21	0.12	0.43	0	0
Erodium cicutarium (L.) L'Hér.	0.03	0.01	0.87	0	0
Filago arvensis L.	0.17	0.01	0.22	0	0
Gypsophila paniculata L.	0	0.11	0.11	0	0
Holosteum umbellatum L.	0.26	0.11	0.14	0.1	0
Medicago orthoceras (Kar. & Kir.) Trautv.	1.15	0.17	0.18	0.3	0
Myosotis stricta Link ex Roem. and Schult.	0.46	0.01	0.65	0	0
Poa bulbosa L.	10.9	18.67	0.031	4	10
Polygonum sp.	0.1	0.01	0.45	0	0
***Prangos odontalgica* (Pall.) Herrnst. and Heyn**	0.05	0.41	**<0.0001**	0	0.5
Ranunculus falcatus L.	0.32	0.39	0.47	0.5	0.5
Ranunculus oxyspermus Willd.	0.73	0.5	0.93	0.5	0.5
Ranunculus testiculatus Crantz	0.04	0.11	0.3	0	0
Salsola tragus L.	0.08	0.06	0.72	0	0
***Stipa sareptana* A.K.Becker**	3.65	0.12	**0.0009**	1	0
Veronica triphyllos L.	0.46	0.12	0.0052	0.5	0
Communities with sagebrush cover 1–10%					
Achillea leptophylla M.Bieb.	0.04	0.08	0.67	0	0
Agropyron fragile (Roth) P.Candargy	2.75	0.08	0.22	0	0
Alyssum desertorum Stapf	0.72	5.33	0.92	0.5	0.5
Anabasis aphylla L.	0.04	0.17	0.22	0	0
Artemisia arenaria DC	0.29	0.33	1	0	0

Table 3. *Cont.*

Species	Species Representation *		*p* Value of Significance of Differences **	Median Projective Cover, %	
	In the Reserve	Outside the Reserve		In the Reserve	Outside the Reserve
Artemisia lercheana Weber ex Stechm.	2.17	1.17	0.36	1.5	0
Artemisia santonicum L.	0.75	2	0.26	0	1
Astragalus dolichophyllus Pall.	0.13	0.02	0.65	0	0
Astragalus varius S.G.Gmel.	0.12	0.02	0.61	0	0
Bassia prostrata (L.) Beck	0.12	0.1	0.61	0	0
Bromus tectorum L.	0.04	0.27	0.016	0	0.3
Carduus uncinatus M.Bieb.	0.08	0.08	1	0	0
Carex stenophylla Wahlenb.	3.38	0.67	0.66	0.75	0.5
Ceratocarpus arenarius L.	0.01	0.02	0.67	0	0
Crepis sancta (L.) Bornm.	0.09	0.08	0.8	0	0
Descurainia sophia (L.) Webb ex Prantl	0.04	0.08	0.67	0	0
Elymus repens (L.) Gould	0.13	0.08	0.55	0	0
Eremopyrum orientale (L.) Jaub. and Spach	0.08	0.02	0.94	0	0
Gypsophila paniculata L.	0.04	0.08	0.67	0	0
Holosteum umbellatum L.	0.33	0.17	0.21	0.5	0
Lepidium perfoliatum L.	0.3	0.33	0.87	0.5	0.5
Medicago orthoceras (Kar. and Kir.) Trautv.	0.35	0.37	0.66	0.1	0.3
Meniocus linifolius (Stephan ex Willd.) DC.	0.08	0.1	0.56	0	0
Poa bulbosa L.	21	35	0.015	20	35
Polygonum sp.	0.09	0.12	0.43	0	0.05
Prangos odontalgica (Pall.) Herrnst. and Heyn	0.46	0.27	0.18	0.5	0.3
Ranunculus oxyspermus Willd.	0.34	0.42	0.52	0.05	0.5
Ranunculus testiculatus Crantz	0.13	0.17	0.95	0	0
Salsola tragus L.	0.04	0.02	0.73	0	0
Sisymbrium altissimum L.	0.04	0.08	0.67	0	0
Sisymbrium loeselii L.	0.12	0.08	0.75	0	0
Stipa sareptana A.K.Becker	0.13	0.5	0.086	0	0.5
Tanacetum achilleifolium (M.Bieb.) Sch.Bip.	0.25	0.17	0.87	0	0
Tulipa sylvestris subsp. *australis* (Link) Pamp.	0.04	0.08	0.67	0	0
Veronica triphyllos L.	0.21	0.18	1	0	0.05
Veronica verna L.	0.33	0.25	0.8	0.25	0.25

Note. * Mean projective cover in descriptions assigned to this group. ** Bold indicates differences that remain significant after Bonferroni correction for multiple testing.

3.2. Comparative Analysis of Plant Communities of the "Chernye Zemli" at Different Stages of Pyrogenic Succession

In the first few years of succession, (sub)shrubs are almost completely absent in pyrogenic communities, and sedges (*Carex stenophylla*) and cespitose grasses (large-turf *Stipa sareptana*, and less often, *S. lessingiana* and small-turf *Poa bulbosa*; Table 1) predominate. Annuals are numerous, among which the most common are *Ranunculus testiculatus, Alyssum desertorum, Veronica verna* or *V. triphyllos, Bromus tectorum,* and *Ceratocarpus arenarius*. Among the ephemeroids, the most typical are *Ranunculus oxyspermus*, and the less common are tulips (*Tulipa suaveolens* Roth, *Tulipa sylvestris* subsp. australis, *T. biflora*) and *Prangos odontalgica*. Species richness in the first few years after a fire can vary from 5 to 10 or more species per 100 m^2 and the total projective cover is usually below 10–15%. Species richness is the highest in areas that burned 5–10 years ago, where it varies from 7 to 20 or more species per 100 m^2.

With age, shrubby species begin to appear in some burnt areas, e.g., different sagebrushes (*Artemisia lercheana*, *A. santonicum*, *A. pauciflora* Weber ex Stechmann, etc.), *Bassia prostrata, Krascheninnikovia ceratoides*, and in saline areas—*Anabasis aphylla*. Most often, (sub)shrubs grow in communities starting from stage 3 (9–13 years after the fire). But in a number of cases, communities with considerable participation of sagebrush are also characteristic of the second stage. On heavily overgrazed pastures near the reserve and along its periphery at stages 3 and 4, on the contrary, (sub)shrubs do not play an important role in the communities to the point of disappearance, and *Poa bulbosa* prevails in the plant cover.

Communities of late chronological stages outside the boundaries of the "Chernye Zemli" Nature Reserve are characterized by varying participation of (sub)shrubs, which can have a projective cover of 1–5% and never act as dominants, giving way to small-turf species. In unburned areas outside the "Chernye Zemli" Nature Reserve, the cover of (sub)shrubs can range from 1 to 40% or more, which may be due to edaphic habitat conditions and varying intensity of grazing. At the same time, small-turf *P. bulbosa* and, less commonly, *C. stenophylla* also have high coverage, taking the position of a dominant or subdominant in the community.

To assess changes in plant communities over time after a fire, for each pair of chronological stages we compared the mean projective cover of species common to them, combining data on plots from the xerophytic-grass and (sub)shrub chronoseries to increase the sample size. The correlation of the average projective cover of common species was most pronounced between successive stages, especially in pairs of early stages 1–2 and 2–3. This indicates a gradual change in the community for at least 10 years after the fire (Table 4).

Table 4. Spearman's correlation of mean projective cover of the species common to a pair of chronological stages in the "Chernye Zemli" Reserve and near it for the merged dataset on xerophytic-grass and (sub)shrub chronoseries.

Stage		*p*	*r*	*N* Species at the Stage		
I	II			In Total	I	II
1	2	**0.0031**	0.7289	14	15	36
1	3	0.1403	0.4745	11	15	33
1	4	0.5905	0.1648	13	15	39
1	5	0.1365	0.4786	11	15	22
1	6	0.3724	0.2584	14	15	33
2	3	**0.0000**	0.7773	24	36	33
2	4	0.1621	0.2824	26	36	39
2	5	0.2700	0.2836	17	36	22
2	6	0.0738	0.3716	24	36	33
3	4	0.0522	0.4008	24	33	39
3	5	0.5561	0.1591	16	33	22
3	6	0.0656	0.3993	22	33	33
4	5	**0.0153**	0.5771	17	39	22
4	6	**0.0088**	0.5033	26	39	33
5	6	**0.0460**	0.4898	17	22	33

Note: *N*—number of species, *p*—*p*-value of Spearman correlation test, *r*—Spearman correlation coefficient. Significance levels $p < 0.05$ are marked in bold.

To determine whether the pre-fire cover of a species influences its likelihood to survive or regenerate after a fire, we compared the pre-fire projective cover of species that were detected and undetected in the early post-fire stage (stage 1). For each site from stage 1, the pre-fire stage was determined according to the age of the previous fire (see Section 2.4). Of the 30 species found in the pre-fire stage of the xerophytic-grass chronoserie, seven species (*Carex stenophylla, Ranunculus falcatus, Poa bulbosa, Prangos odontalgica, Ranunculus oxyspermus, Stipa sareptana, Veronica triphyllos*) were also found in the post-fire stage. In the (sub)shrub chronoserie, out of 33 species found in the pre-fire stage, 12 (*Alyssum desertorum, Artemisia lercheana, Carex stenophylla, Ranunculus testiculatus, Ranunculus falcatusr, Elymus repens, Lepidium perfoliatum, Poa bulbosa, Prangos odontalgica, Ranunculus oxyspermus, Tanacetum achilleifolium, Tulipa biflora*) were also present after the fire. It is interesting that in the pre-fire stages of both chronoseries, three species (five in total) from the order Caryophyllales were found: *Amaranthus* sp., *Anabasis aphylla, Bassia prostrata* (family Amaranthaceae), *Gypsophila paniculata, Holosteum umbellatum* (family Caryophyllaceae). But in the first year after the fire, not a single species of this order was discovered. In both chronoseries examined, species found in both pre-fire and post-fire stages had greater average projective cover in the pre-fire stage than species found only in the pre-fire stage (see Section 2.4, Table 5).

Table 5. A mean pre-fire projective cover of species found (+) and not found (−) in post-fire stage (two-tailed Mann–Whitney *U*-test), in the "Chernye Zemli" Reserve and outside of it.

Chronosequence	Number of Species		Species Projective Cover				*p*-Value
			Mean		Median		
	−	+	−	+	−	+	
(Sub)shrub	21	12	0.18	2.47	0.14	0.23	0.02
Xerophytic-grass	23	7	0.3	2.8	0.05	0.6	0.0003

3.3. Assessment of the Impact of Fire Frequency on Plant Communities of the "Chernye Zemli" Nature Reserve

The majority of species found in one group according to fire frequency were also found in the other (79% of species in the group with rare fires and 76% of species in the group with frequent fires). Along with a significant correlation of the average projective cover of these species in two groups (r = 0.64, p = 0.00002, Figure 3, right), this indicates the absence of significant differences in the species representation in areas with different frequencies of pyrogenic impact. When species that were found only in areas with rare or in areas with frequent fires were included in the analysis, correlation was similar (r = 0.54, p = 0.000004, Figure 3, left).

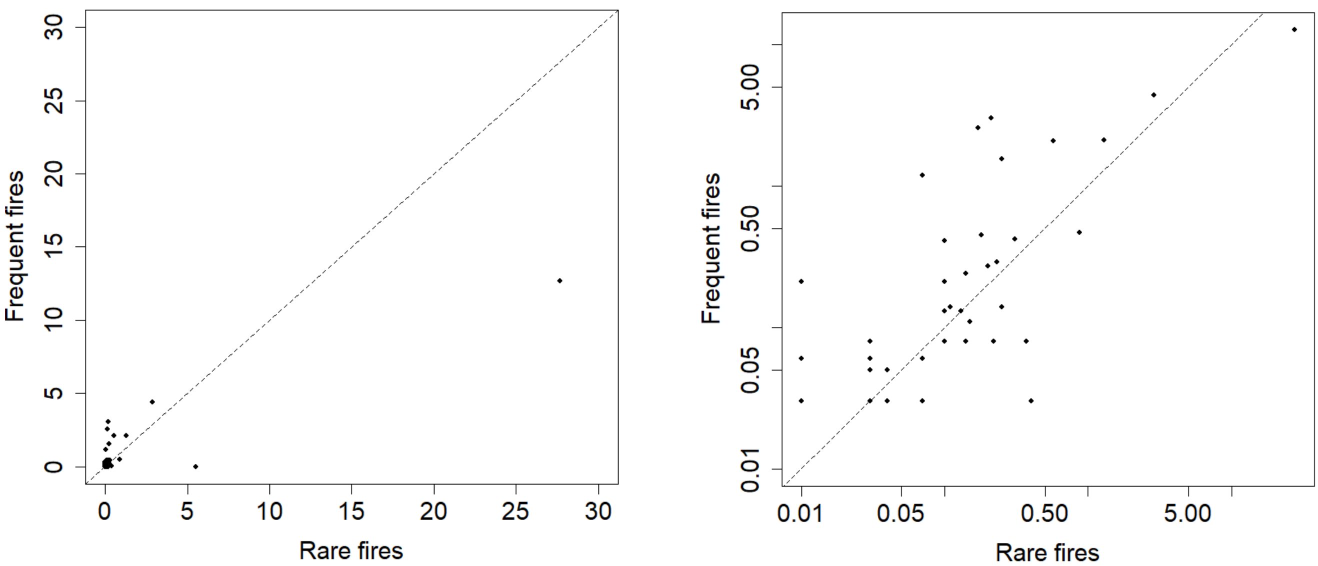

Figure 3. Average projective cover of all species found in (**left**) or common species between (**right**) areas with rare and frequent fires in the "Chernye Zemli" Reserve and near it. The dotted line is the bisector. On the right, scales are logarithmic with base of 10.

In each of the two groups, four indicator species were identified. In rarely burned areas, these were *Lepidium perfoliatum* (p = 0.021), *Artemisia lercheana* (p = 0.008), *Chorispora tenella* (Pall.) DC (p = 0.030), *Tanacetum achilleifolium* (p = 0.025). In frequently burned ones, these were *Stipa sareptana* (p = 0.002), *Medicago orthoceras* (p = 0.013), *Crepis sancta* (p = 0.019), and *Filago arvensis* L. (p = 0.010). In the two groups, projective covers differed most noticeably in *Artemisia lercheana* and two cespitose grasses—*Poa bulbosa* and *Stipa sareptana* (Table 6).

3.4. Non-Metrical Multidimensional Scaling

The results of NMDS (Figure 4A) show a fairly uniform transition of communities from one chronoserie to another among the collected data array. At the same time, communities assigned to the (sub)shrub chronoserie are mainly presented on the right side of the diagram, and communities of the xerophytic-grass chronoserie are presented on the left.

The centroids of groups of geobotanical descriptions (Figure 4B), corresponding to the stages of different chronoseries, are also grouped in the same way. At the same time, the centroids of groups 4 and 8, corresponding to the fourth stages of the xerophytic-grass and (sub)shrub chronoseries, respectively, are located close together. This reflects the smooth transition of communities from the xerophytic-grass to subshrub chronoserie under the influence of grazing at this stage.

Table 6. The results of the Mann–Whitney U-test for the projective cover of plants on plots with rare (I) and frequent (II) fires in the "Chernye Zemli".

Plant Species	Projective Cover in the Group, %				*p*-Value	
	Mean		Median		Without Bonferroni Correction	With Bonferroni Correction
	I	II	I	II		
Achillea leptophylla M.Bieb.	0.07	0.03	0	0	0.44	1
Agropyron fragile (Roth) P.Candargy	1.3	2.1	0	0	0.8	1
Alyssum desertorum Stapf	2.9	4.4	0.5	0.5	0.61	1
Amaranthus sp.	0	0.03	0	0	0.41	1
Anabasis aphylla L.	0.4	0.03	0	0	0.19	1
Androsace maxima L.	0.01	0	0	0	0.29	1
Artemisia arenaria DC.	0.4	0.1	0	0	0.66	1
Artemisia austriaca Jacq.	0	0.05	0	0	0.41	1
Artemisia lercheana Weber ex Stechm.	5.5	0	0	0	0	0.2
Artemisia santonica Lam.	0.9	0.5	0	0	0.45	1
Astragalus dolichophyllus Pall.	0.04	0.03	0	0	0.46	1
Astragalus longipetalus Chater	0.03	0.06	0	0	0.46	1
Astragalus varius S.G.Gmel.	0.01	0.03	0	0	0.48	1
Bassia prostrata (L.) Beck	0.11	0	0	0	0.05	1
Bromus tectorum L.	0.2	2.6	0	0	0.46	1
Buglossoides arvensis (L.) I.M.Johnst.	0	0.05	0	0	0.22	1
Carduus uncinatus M.Bieb.	0.1	0.2	0	0	0.39	1
Carex stenophylla Wahlenb.	0.6	2.1	0	0.5	0.36	1
Centaurea diffusa Lam.	0.03	0	0	0	0.29	1
Ceratocarpus arenarius L.	0.11	0.14	0	0	0.96	1
Chorispora tenella (Pall.) DC	0.08	0	0	0	0.02	1
Convolvulus arvensis L.	0.03	0.05	0	0	0.72	1
Crepis sancta (L.) Bornm.	0.1	0.4	0	0.5	0.02	1
Delphinium consolida subsp. *divaricatum* (Ledeb.) A.Nyár.	0	0.03	0	0	0.41	1
Descurainia sophia L.	0.14	0.24	0	0.1	0.24	1
Elymus repens (L.) Gould	0.13	0.13	0	0	0.8	1
Eremopyrum orientale (L.) Jaub. and Spach	0.03	0	0	0	0.29	1
Eremopyrum triticeum (Gaertn.) Nevski	0.07	0	0	0	0.12	1
Erodium cicutarium (L.) L'Hér.	0	0.03	0	0	0.22	1
Erodium hoefftianum C.A.Mey.	0.03	0	0	0	0.29	1
Filago arvensis L.	0.01	0.21	0	0	0.03	1
Gypsophila paniculata L.	0.07	0.06	0	0	0.91	1
Holosteum umbellatum L.	0.2	0.27	0	0.5	0.3	1
Lappula patula (Lehm.) Menyh.	0.03	0.03	0	0	0.9	1
Lepidium perfoliatum L.	0.22	0.1	0.1	0	0.02	1
Leymus racemosus (Lam.) Tzvelev	0	0.05	0	0	0.22	1
Linaria sp.	0.03	0	0	0	0.29	1
Medicago orthoceras (Kar. and Kir.) Trautv.	0.3	1.6	0	0.5	0.02	1
Meniocus linifolius (Stephan ex Willd.) DC.	0.1	0.1	0	0	1	1
Myosotis stricta Link ex Roem. and Schult.	0.01	0.06	0	0	0.4	1
Nonea caspica (Willd.) G.Don	0	0.08	0	0	0.12	1
Phlomis herba-venti L.	0	0.01	0	0	0.41	1
Poa bulbosa L.	28	13	30	5	0	0.13
Polygonum sp.	0.15	0.11	0	0	0.21	1
Prangos odontalgica (Pall.) Herrnst. and Heyn	0.25	0.14	0.1	0	0.18	1
Ranunculus falcatus L.	0.23	0.29	0	0.5	0.44	1
Ranunculus oxyspermus Willd.	0.31	0.42	0.5	0.5	0.63	1
Ranunculus testiculatus Crantz	0	0.08	0	0	0.12	1
Salsola tragus L.	0.04	0.05	0	0	0.88	1
Senecio sp.	0	0.1	0	0	0.07	1
Sisymbrium altissimum L.	0.1	0.13	0	0	0.69	1
Sisymbrium loeselii L.	0.1	1.2	0	0	0.32	1
Stipa lessingiana Trin. and Rupr.	0	0.32	0	0	0.12	1
Stipa sareptana A.K.Becker	0.2	3	0	0.5	0	0.23
Tanacetum achilleifolium med	0.2	0	0	0	0.02	1
Tulipa biflora Pall.	0	0.03	0	0	0.41	1
Tulipa sylvestris subsp. *australis* (Link) Pamp.	0.03	0.08	0	0	0.44	1
Veronica triphyllos L.	0.2	0.5	0	0.5	0.03	1
Veronica verna L.	0.14	0.08	0	0	0.43	1

Note. For all species, differences were no longer significant after Bonferroni correction.

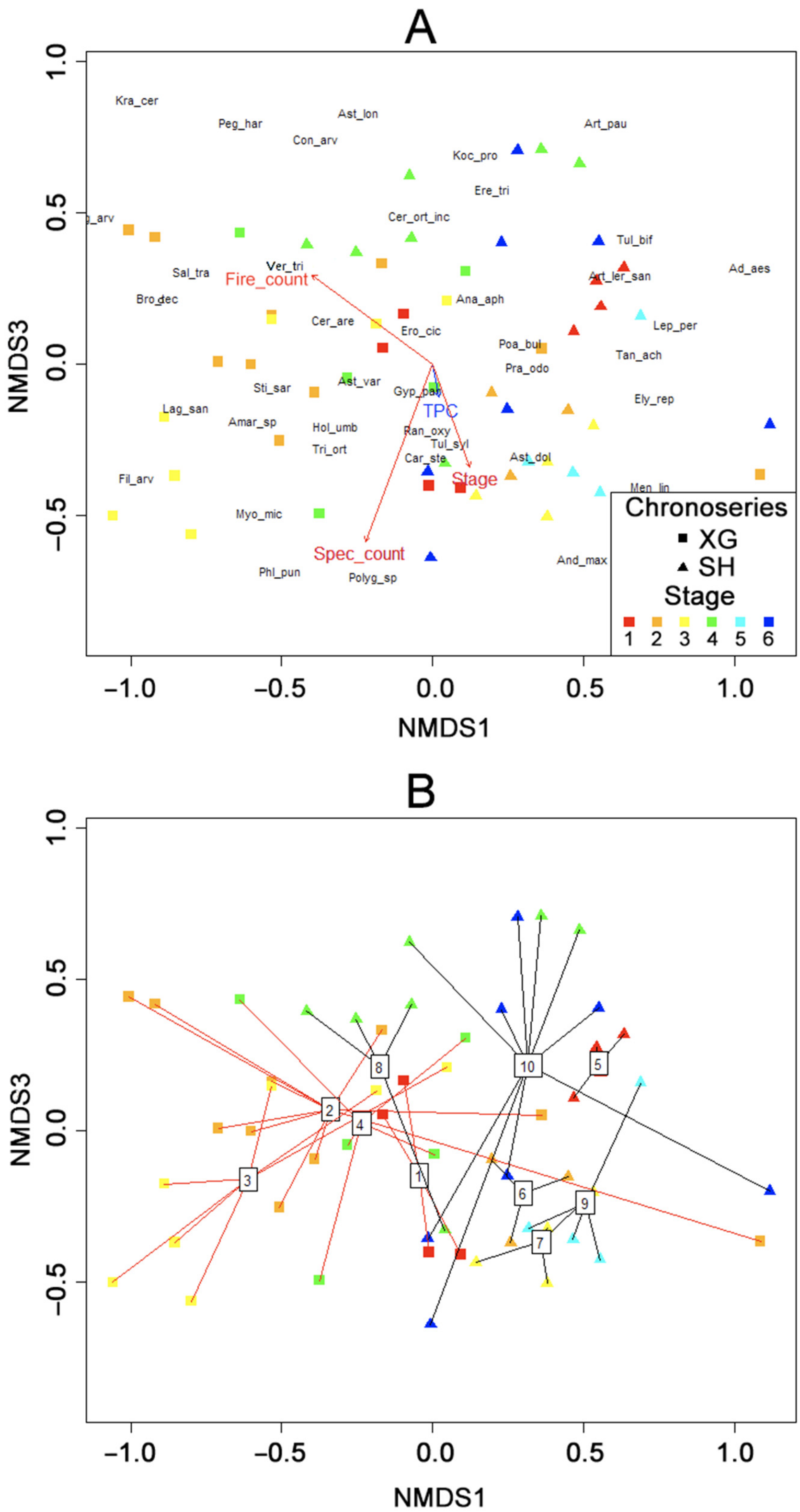

Figure 4. NMDS ordination diagrams. (**A**)—ordination diagram with species abbreviations and vectors. Designations: stage—chronological stage from 1 to 6; fire_count—frequency of fires; TPC—total projective cover of vegetation, spec_count—species richness of community; vectors with $p < 0.05$ are colored in red. (**B**)—ordination diagram with centroids of groups. Numbers 1–4 correspond to stages 1–4 of XG chronoserie and lines are colored in red. Numbers 5–10 correspond to stages 1–6 of SH chronoserie and lines are colored in black.

Communities of the xerophytic-grass chronoserie are mostly located at the end of the vector of fire frequency, whereas communities of the subshrub chronoserie are mostly located in the opposite direction. It reflects the generally low resistance of subshrubs to fire. At the same time, resistance to frequent fires apparently varies also among annuals. An increase in the frequency of pyrogenic impact is associated with an increase in the contribution of such annual species as *Buglossoides arvensis* (Bug_arv), *Bromus tectorum* (Bro_tec), *Salsola tragus* (Sal_tra), *Veronica triphyllos* (Ver_tri). Communities with a low frequency of fires are characterized by an increase in the contribution of *Meniocus linifolius* (Men_lin), *Veronica verna* (Ver_ver, in the diagram under the legend), and *Androsace maxima* (And_max).

4. Discussion

Pyrogenic dynamics of treeless communities are studied worldwide, e.g., sagebrush communities of Great Basin in North America [30–32], Mediterranean heathlands [33], meadows in Scandinavia [34–36], etc. However, such studies are far fewer than studies of pyrogenic succession in forests [37,38]. Central Asia is especially understudied in this aspect due to social-economic problems after the USSR breakup in the early 1990s [6].

An unambiguous interpretation of the results of assessing the impact of fires on the vegetation of the "Chernye Zemli" Nature Reserve and its vicinity is impossible due to the mosaic nature of the vegetation cover and the influence of grazing. Nevertheless, in this work a number of patterns have been discovered that make it possible to improve the understanding of pyrogenic successions in desert plant communities of the region.

The projective cover of most plant species did not differ between the protected area and beyond. Based on the data presented, we can conclude that the protective status of the "Chernye Zemli" Reserve does not affect the species richness of plant communities and has virtually no effect on the plant species representation. The lack of influence of territory conservation on species richness does not correspond to the known data on the consequences of excluding grazing in arid communities, where long-term absence of cattle reduces the species richness of phytocenoses (e.g., [39–41]). We can assume that this is probably due to the absence of fences along the perimeter of the reserve, which allows the livestock grazing near the borders to invade its territory, increasing the grazing load. In addition, one can assume a considerable impact from wild ungulates (*Saiga tatarica* L., 1766) on the territory of the reserve, especially in large calving aggregations in the spring, numbering a total of 4000–6000 individuals [42]. Thus, even within the "Chernye Zemli" Reserve, a noticeable influence of large herbivores on the course of pyrogenic succession cannot be ruled out. Meanwhile, some studies provide information about the low impact of cattle on species richness for vegetation of some biomes, e.g., sagebrush communities in Wyoming, USA [43,44].

The correlation of the mean projective cover of species at different age stages of succession was calculated for a combined sample of xerophytic-grass and (sub)shrub chronoseries, since communities with a predominance of (sub)shrubs can be considered as the indigenous vegetation of the region under the conditions of previous land use [15,19,45]. The smooth transition of communities from the xerophytic-grass to subshrub is confirmed by our NMDS analysis (Figure 4B). The degree of participation of (sub)shrubs in pyrogenic communities depends on the parameters of fires and the intensity of grazing. At the same time, communities of the (sub)shrub chronoserie, despite the presence of sagebrush, at the early stages of pyrogenic succession have obvious features of xerophytic-grass communities. The most pronounced correlation of the average projective cover of species was observed between the early chronological stages of pyrogenic succession. Projective cover of individual species at chronological stages 1–2 and 2–3 significantly correlates with a coefficient of $r > 0.7$. At the same time, for the pair of stages 1–3 the correlation is insignificant, $r < 0.5$. Based on this, it can be assumed that during the first ten years after a fire, the role of species in the community changes gradually. For the three subsequent stages, the correlation is significant for all pairs of stages (4–5, 5–6 and 4–6), but modest with r = 0.5–0.6. Based on this, we hypothesize that 10 years after a fire, the role of fire age in community formation declines and other factors become more important. Meanwhile, this change in priority factor may not mean the end of pyrogenic succession, and at this stage, communities are not equal to climax vegetation observed at non-burnt territories in Kalmykia. Though 10–15 years of pyrogen cyclic is typical for sagebrush communities in Western Kazakhstan, not far from the studied "Chernye Zemli" Reserve, for other sagebrush communities worldwide, the time of self-restoration after fires can last for decades [46,47], and so pyrogenic succession longer than 10–15 years can take place in Kalmykia in modern conditions.

Notwithstanding their limitations, space-for-time studies [16,26] provided valuable insights into the average state of plant communities with the time since fire. In fact, the actual state of communities in specific areas in different periods may vary due to the characteristics of weather conditions, micro topography, grazing and other factors. However, we consider this approximation sufficient for the analysis presented in this research, since we compare two groups of species: those found and not found after the fire, and do not draw conclusions based on each target species. The mean pre-fire projective cover was significantly higher for fire-tolerant species, i.e., those found after the fire, than for fire-intolerant species—not detected after the fire. There are several possible but not mutually exclusive reasons for this:

(a) For some species, conditions are not optimal both before and after the fire, so their projective cover is low both in the pre-fire and post-fire stages;
(b) During a fire, individuals of species with higher prevalence are more likely to be found in loci less affected by open fire and high temperatures, and thus survive;
(c) After a fire, seeds invade from adjacent territories, and the supply of diaspores is higher for species with a higher number of individuals (vicinism according to [48]);
(d) For the introduction of some minor species, an important role can be played by the primary plant cover, which can provide partial protection of seedlings from negative environmental factors due to shading or moisture retention in the accumulated dead litter in the spring [16]; therefore, such plants cannot appear in the early stages of pyrogenic succession.

Although it is often believed that frequent fires reduce the vascular plant species diversity in arid ecosystems and form special pyrogenic communities [14,49], the effects of fire on the characteristics of arid phytocenoses are ambiguous. Various publications note both positive and negative effects of the pyrogenic factor on communities [50]. Some recent studies have investigated methods of excluding fire from some grasslands in order to maintain high biodiversity [51].

According to our data, frequently and rarely burned areas at the territory of the "Chernye Zemli" Nature Reserve and its surroundings do not differ in the total number of species found (49 and 47, respectively) and are similar in species composition (>75% of common species). However, there are some species that are typical for areas with different fire frequencies. According to NMDS, subshrub communities are more likely to be found on rarely burned areas, whereas xerophytic-grass communities are more likely to be found on frequently burned areas. In addition to the time since fire, an important factor in the structure of pyrogenic communities is the history of pyrogenic impact, as has been shown for grass communities in South Africa [52]. There, maximum species richness was achieved with a combination of different fire regimes. This idea corresponds with the basic strategy of using prescribed burning for maintaining biodiversity in managed territories, both for woods [51] and treeless vegetation [37]. It is also possible that communities in our study were transformed by frequent fire over millennia, as with some other treeless ecosystems [53,54]. This is consistent with the concept of the historical genesis of arid communities under the influence of the pyrogenic factor [55]. It is known that periodic fires played a major role in the evolution of arid grasslands (including steppes) over millions of years [53,54], so the species in these communities are well adapted to persist with a range of fire regimes.

Despite the similar species richness, four indicator species were identified for frequently burned areas (*Stipa sareptan*, *Medicago orthoceras*, *Crepis sancta*, and *Filago arvensis* L.) and four for rarely burned areas (*Lepidium perfoliatum*, *Artemisia lercheana*, *Chorispora tenella* (Pall.) DC, and *Tanacetum achilleifolium*). Projective cover on frequently and rarely burned plots differed most markedly for *Artemisia lercheana* and two cespitose grasses, *Poa bulbosa* and *Stipa sareptana*. *P. bulbosa* was more common in areas with rare fires, and *S. sareptana* was more common in areas with frequent fires. Since a lot of mortmass accumulates in *S. sareptana* communities, and *P. bulbosa*, on the contrary, forms very little mortmass due to its small size, it can be assumed that the probability of fire increases with the increasing role of *S. sareptana* and decreases with the increasing role of *P. bulbosa*. The high projective cover of *S. sareptana* on frequently burned areas may be maintained due to fast recovery or high tolerance, as there is evidence that large-turf species tolerate fire better than small-turf species [9,56]. *Artemisia lercheana* is more common in rarely burned areas, which is consistent with previous studies showing a decreasing role of sagebrush under the influence of fires [14,57,58].

5. Conclusions

It was shown for the first time that inside the "Chernye Zemli" Nature Reserve and nearby, pyrogenic succession is characterized by a gradual long-term change in plant communities, and the relative representation of species at the initial stage of pyrogenic succession is largely determined by the composition of the pre-fire community. Species composition and projective cover of individual species were similar in areas with different frequencies of pyrogenic impact. Our results suggest that plant communities in the study area are adapted to periodic fires, which can be considered as a natural environmental factor for this area.

On the one hand, the data obtained are consistent with other studies on the pyrogenic dynamics of vegetation in steppes and deserts in general and in the "Chernye Zemli" Nature Reserve in particular. On the other hand, the absence of considerable influence of fire frequency on species richness is a rather unusual situation which requires further research.

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