

Postcatastrophic Successions of a Rodent Population

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Abstract—Successions of a rodent population have been investigated in the forest biocenoses of the Visim Nature Biosphere Reserve (Sverdlovsk oblast, Middle Ural) after a catastrophic windfall and two fires. Differences in the values of the total abundance of rodents and their ratio in the community before natural catastrophes and at different postcatastrophic demutational succession stages are revealed. Structural alterations in a rodent population are associated with different responses of the species to the anemogenic and pyrogenic transformation of their microhabitat environment and can be considered compensatory mechanisms maintaining the sustainability of small mammal communities under the impact of natural catastrophic factors.

Keywords: anemogenic succession, pyrogenic succession, rodents, total abundance of species, microhabitat, reserve, windfall, fire

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INTRODUCTION

In nature, complex transformations of the structure of plant and animal communities (successions) occur under the influence of endogenic (biogeocenotic) and exogenous (weather climatic and anthropogenic) effects. According to the classification proposed by V.N. Sukachev (1926), successions are divided into endo- and exodynamic successions for plant communities. Continuous and postdisruptive (postcatastrophic) successions are distinguished with respect to the time scale. Postcatastrophic successions are secondary and have a restorative nature; they are observed after the cessation of the effect of the external factor that caused the disturbance. From the material and energy perspective, the application of the notion of succession to a separate component of ecosystems makes no sense, since the energy conversion proceeds in their food chains formed by the populations of species belonging to different trophic levels (Smirnova and Toropova, 2008). Consequently, studies of successions observed in the communities of first order consumer animals that are closely related to the plant components of ecosystems are particularly important. This is a group of widespread species of mouse-like rodents, which are of rather great interest for domestic and foreign ecologists. A number of works shows that successions of the population of small mammals that are caused by the natural climate variability of the conditions of biocenoses existence lead to regular alterations in the species structure of communities (Erdakov, 1981; Maksimov et al., 1981; Maksimov and Yerdakov, 1985; Erdakov et al., 1991; and Heroldova et al., 2005). Significant structural changes in the pop-

ulation of animals may also be recorded in the course of exodynamic successions observed after natural catastrophic phenomena, such as windfall and fire (Kerzina, 1952; Kuleshova, 1981; Zyus'ko et al., 2001; Istomin, 2009; Briani et al., 2004; Torre and Diaz, 2004; Zwolak and Foresman, 2007; Zwolak et al., 2012). Postcatastrophic cenotic alterations are associated with the adaptive population features of separate species and can be generally considered compensation mechanisms for maintaining the sustainability of small mammal communities under the impact of catastrophic factors. Consequently, studies of the effects of the natural environmental transformation for separate components of natural ecosystems are crucial in making long-range forecasts for biota conditions. The acquisition of new knowledge on the problem under consideration is particularly relevant due to the growth in the number and extent of natural disasters in recent decades both for the world in general and for Russia in particular. Currently, there are no studies of rodent population successions in the literature that are caused by the integrated effect of natural catastrophic factors. This has determined the objective of this work.

MATERIALS AND METHODS

Study Area. The works were performed from 1987 to 2012 in the Visim Nature Biosphere Reserve (57°20'–57°31' N and 59°30'–59°50' E). Over 26 years of observations, the reserve under investigation, with an area of 4 ha, was exposed to natural catastrophic disturbances three times. A strong windfall in June 1995 covered the entire territory under investi-

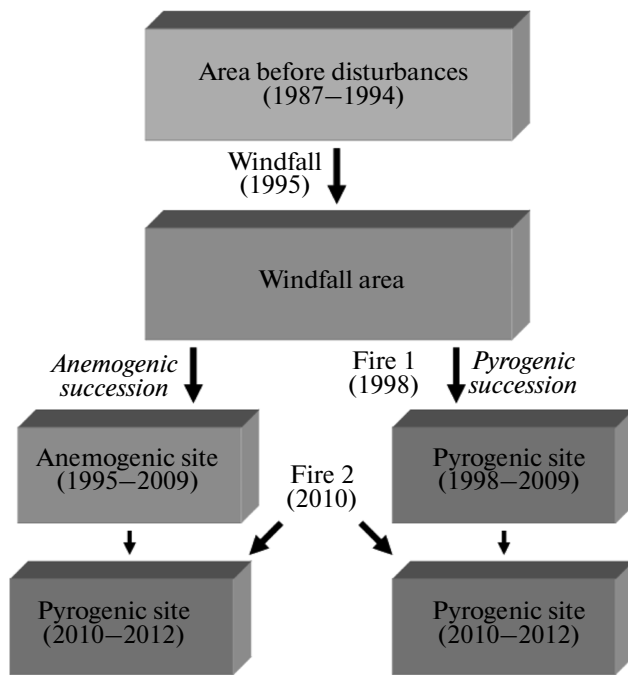


Fig. 1. Chart of sequence of the transformation of the study area in the Visim Reserve by natural catastrophic factors.

gation. The first intensive fire in 1998 did not affect the entire area transformed by the windfall; as a result, it was divided into two relatively equal adjacent sites: anemogenic (a windfall site that was not affected by fire) and pyrogenic (a windfall site that was affected by fire) (Fig. 1). In August 2010, the second violent fire occurred, which destroyed both sites of the area under investigation: the anemogenic site for the first time and the pyrogenic site for the second time (Fig. 1). Both fires were natural, since they were induced by lightning during dry storms. The first fire was distinguished by the presence of a large amount of combustible material accumulated in the vast windfall area of the reserve within three drought summer seasons. In the year when the second fire took place, the condition of plant communities was different from the situation established in the year of the previous pyrogenic effect. In 2010 there were a lot of dry grass and many partially burnt trunks and fallen dry tree trunks in the area of the old burnt area, and the share of dead wood was 14%. However, not all sites were affected by the fire, or, if so, they had a low combustion intensity in this case (Sibgatullin, 2012). Therefore, after the occurrence of natural catastrophic phenomena, the reserve area under consideration was found to be a unique natural test site for monitoring postcatastrophic (anemogenic and pyrogenic) demutational successions of the biological components of forest ecosystems.

Objects of Research

The long-term continuous study of the population of small mammals in the Visim Reserve included (1) the period before disturbances (1987–1994), (2) the early stages of postwindfall (anemogenic) (1995–1999) and postfire (pyrogenic) (1998–2002) successions, (3) the stages of the development of anemogenic and pyrogenic successions (2000–2009 and 2003–2009, respectively), and (4) the early stages (2010–2012) of pyrogenic succession after the secondary effect of fire. Before the effect of the first fire, the rodent population in the study area was considered in general terms, and then the population was studied individually on the anemogenic and pyrogenic sites.

The animals were caught by the trap-line method (Kucheruk, 1952). A total of 200 traps were used in the study area (10 traps per each site). They were arranged in line, being 10 m from each other, and were designated with constant sequence numbers, which made it possible to map rodent capture sites. The traps were exposed for five days, and, over the entire period of studies, they were placed in the center of the same test squares (microsites) with an area of 10 m, within which microhabitat quantitative descriptions were made before the disturbances (1993) and later at different stages of postcatastrophic restorative successions (1999, 2003, 2007, 2010, and 2011) based on the methods proposed by Lukyanov and Buyal'ska (Buyal'ska et al., 1995), with some amendments and additions. We analyzed the dynamics of five main characteristics determining the forage-protective conditions of rodent microhabitats: the area (m²) of the cover with moss (*MC*), herb vegetation (*HC*), shrub (*CS*), and fallen dead trunks (*LC*), and the abundance (samples) of arboreal wood undergrowth (*AU*) was also taken into account as well.

The relative abundance of small beasts was assessed by the number of their falls into traps over the first five capture days in terms of 100 trap days (samples/100 trap days). This work used the material collected within the same period of field seasons (late August to early September). A total of 3353 samples from six rodent species were caught, among which were wood mice (bank vole *Clethrionomys glareolus* Schreb.j, grey-sided vole *Cl. rufocanus* Sundev.j, and red-backed vole *Cl. Rutilus* Pall.), common voles (short-tailed vole *Microtus agrestis* L., and root vole (*M. oeconomus* Pall.), and wood mouse (*Sylvaemus uralensis* Pall.).

The statistical processing of the obtained data was made in the Statsoft STATISTICA v. 6.0 program for Windows.

RESULTS AND DISCUSSION

Total abundances of rodents and their ratio in the community. The rodent community in the study area of the Visim Reserve was monodominant before the natural catastrophic phenomena, with the predomi-

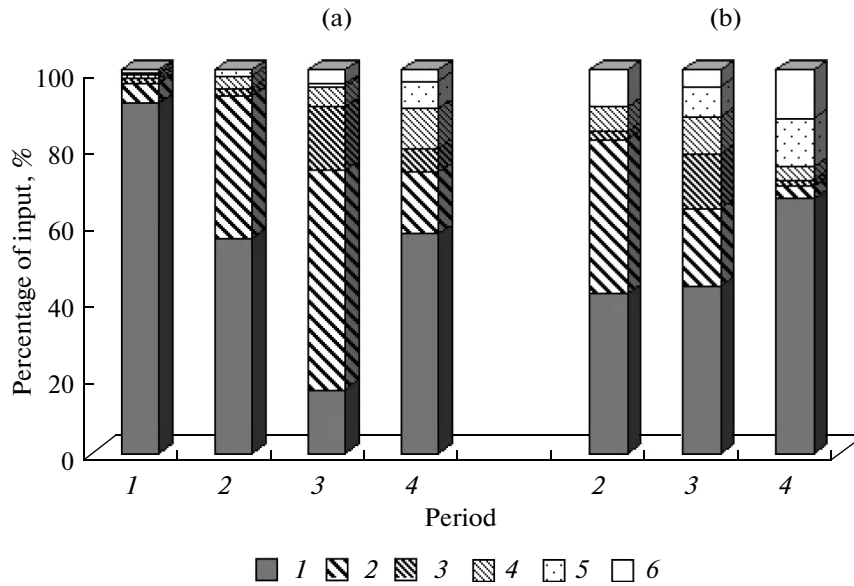


Fig. 2. Contribution of bank (1), grey-sided (2), red-backed (3), root (4), and short-tailed (5) voles and wood mouse (6) to the population of rodents on the anemogenic (a) and pyrogenic (b) sites in the Visim Reserve before disturbances (1) and at different stages (2–4) of postcatastrophic successions.

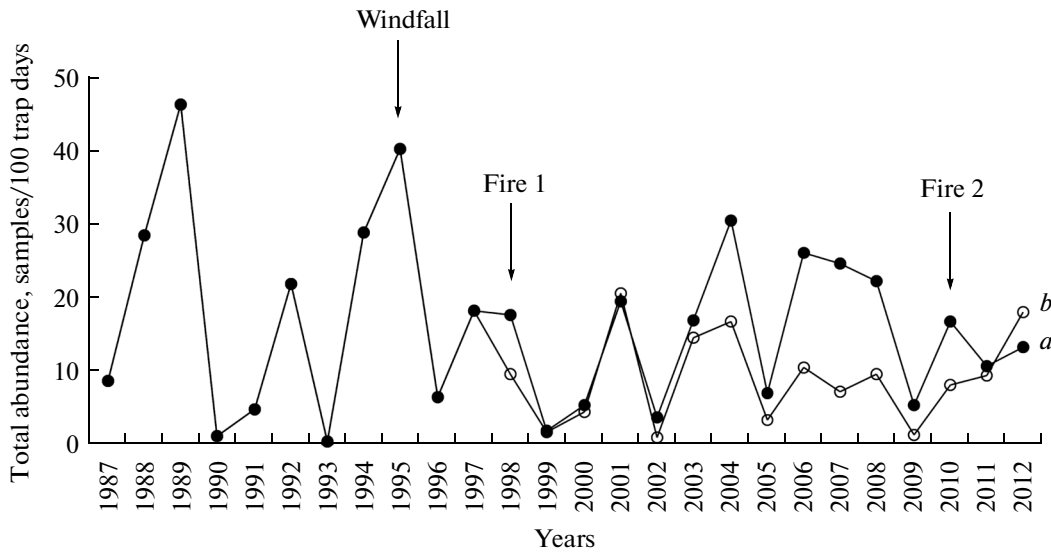


Fig. 3. Dynamic of the total abundance of rodents before natural catastrophic phenomena and under disturbed environmental conditions on the anemogenic (a) and pyrogenic (b) sites in the Visim Reserve area.

nance of the bank vole. Its ratio in the population was 91.2%; therefore, the nature of the dynamic of the total abundance of rodents in this period was determined by this species. Grey-sided and red-backed voles were only 5.2 and 1.1%, respectively, and the total share of grey-sided voles and wood mice in the community did not reach even 1% (Fig. 2a, period 1). The highest level of the values of the total abundance of rodents was recorded at the peak phase in 1989. It was 46.2 samples/100 trap days and became the maximum one over the entire period of observations (Fig. 3).

The following peak of the total abundance of rodents before natural catastrophes was observed in 1992; however, its level was significantly lower, being equal to 21.8 samples/100 trap days. Sharp declines (in 1990 and 1993) inducing the state of deep depressions in the rodent population (1.1 and 0.3 samples/100 trap days, respectively) were observed after the phases of the high abundance of mouse-like rodents in the period before natural disturbances. In the scientific literature, such a phenomenon is considered to be a consequence of the activation of endogenic (intrapopulation) mecha-

nisms of regulation whose role usually increases under optimal habitat conditions (Koshkina, 1966; Okulova and Myskin, 1973; Ivanter, 1975; and Zhigal'skii, 2002).

In the year of catastrophic windfall impact (1995), the level of the values of the indicator of the total rodent abundance corresponded to the peak phase, being equal to 40.1 samples/100 trap days; however, at the early stage of anemogenic succession (1996), the increase in the total abundance of animals did not lead to a deep depression (the indicator value was 6.5 samples/100 trap days), which had taken place in the community before the windfall disturbance in 1990 and 1993 (Fig. 3). This fact can be explained by structural alterations in the rodent population that were induced by the windfall effect. It is known that windfall phenomena generally have a positive effect for many species of small mammals by significantly increasing the protective conditions of their microhabitats. The non-uniformity (mosaic structure) of the habitat, the range of available resources, and the total accumulation of debris on sites increase (leading to a growth in the number of suitable refuges and an increase in their quality), and the multilayer covering of the soil surface with fallen tree trunks creates a positive environment for the existence of many rodent species. As a result of the prevailing conditions, the species diversity may increase at different restorative stages of postwindfall successions, with a quick dominance change being observed (Zyus'ko et al., 2001; Dobrinskii, 2005; and Istomin, 2009).

As was shown above, the windfall transformation of the environment of small mammal habitats led to the formation of favorable conditions for the habitat of the grey-sided vole, whose abundance significantly increased at the early stages of anemogenic succession, and the dominance changed in the rodent community (Lukyanova and Lukyanov, 2004). The share of the grey-sided vole grew to 37.2% in this period, while the participation of the bank vole, in contrast, decreased to 55.9%. The red-backed vole in the rodent population was only 2%; the contribution of common voles increased insignificantly, and the wood mouse on the anemogenic site was absent in captures in this period (Fig. 2a, period 2). In the course of the development of anemogenic restorative succession (period 3), changes took place in the structure of the rodent population again. A further decrease (up to 16.8%) in the ratio of the bank vole was observed, while the ratio of the grey-sided vole increased to 56.7% and the contribution to the red-backed vole community increased significantly, being 16.6% of the total abundance of rodents (Fig. 2a, period 3).

After the effect of the first fire in 1998, the population of rodents on the two adjacent sites within the reserve area under study had structural alterations, which were reflected in the nature of the dynamic of the total abundance of species. At the early stages of pyrogenic restorative succession (period 2), the bank

and grey-sided voles were codominant species in the fire-disturbed habitats in the burnt area; their ratio in the population was 41.4 and 40.3%, respectively. Common voles were represented only by one species, namely, the root vole (6%), and the share of the wood mouse was 9% of the total abundance of rodents on the pyrogenic site (Fig. 2b, period 2). The nature of the dynamic of the values of the total abundance of species in the period of early stages of postfire restoration was different from the analogical stages of anemogenic succession. Higher values of this indicator than those recorded in pyrogenic habitats were observed at the phase of the high abundance of rodents in 1998 on the windfall site (Fig. 3). In the course of the development of the pyrogenic restorative process (Fig. 2b, period 3), the bank vole occupied the status of the dominant species in the burnt area (43.7%), while the share of the grey-sided vole decreased twice (20.1%). Like on the anemogenic site, the share of the red-backed vole in the rodent community increased, being 14.2%, which may be due to conditions established in this period that were favorable for the habitat of the species whose abundance was previously low in the study area of the Visim Reserve (Lukyanova, 2011). As a result, in 2006 the red-backed vole occupied the dominant position in the population of rodents on both sites for the first time over the period of observations. Common voles in pyrogenic habitats were 16% on the whole (the short-tailed vole was 7% and the share of the root vole increased to 9%), while the contribution to the wood mouse population decreased twice (4.5%) (Fig. 2b, period 3). Therefore, unlike anemogenic habitats, the growth in the total contribution to the wood mouse and common vole community was observed in the pyrogenically disturbed habitat at the early succession stages, with the increase in the ratio of the latter being observed in pyrogenic habitats during the development of the postcatastrophic restorative process. This is due to the formation of conditions in open burnt spaces (increase in illumination, increase in day time temperatures, and quick regeneration of grain associations) that meet the environmental preferences of phytophagous rodents (Kerzina, 1952; Kuleshova, 1981; Kuleshova and Averina, 2002; and Zwolak and Foresman, 2007). According to a number of works, whereas the abundance of separate species of small mammals may have no differences in the course of pyrogenic vegetation successions, their total abundance and species diversity increases at the early postfire restoration stages. Among factors that caused the increase in the rodent abundance on burnt sites, the high forage efficiency of habitats in open spaces is the most important (Briani et al., 2004; Torre and Diaz, 2004; Zwolak et al., 2012).

A comparative analysis of the values of the total abundance of rodents in the year of the occurrence of the first (1998) and second (2010) fires, as well as of rodents at the initial stages of pyrogenic successions (1999 and 2011) on the two sites under comparison

within the reserve area being considered, has identified similar and distinctive features. The level of the values of the total abundance of rodents was similar on the anemogenic site in 1998 and 2010, being 17.6 and 16.7 samples/100 trap days, respectively, and on the pyrogenic site it was 9.6 and 8.0 samples/100 trap days, respectively (Fig. 3). A year after the first fire (1999) at the initial stage of postcatastrophic restoration in anemogenic and pyrogenic habitats, the values of the total abundance of rodents decreased synchronously to 1.8 and 1.6 samples/100 trap days, respectively. At the initial stage of pyrogenic succession after the second fire (2011), asynchronous change in the total abundance of rodents was observed (2011): on the anemogenic site disturbed by the fire for the first time, the values decreased to 10.6 samples/100 trap days, and on the pyrogenic site burnt for the second time, they increased to 9.4 samples/100 trap days. Therefore, the nature of changes in the total abundance of rodents after the first and repeated fires was different, which may be due to different responses of species to the existing conditions of the habitat environments in the period under comparison. At the early stage of postcatastrophic restoration after the fire of 2010, the ratio of the bank vole in the population of rodents on the anemogenic site disturbed by the fire for the first time and the pyrogenic site burnt for the second time was 57.1 and 66.4%, respectively. Unlike the bank vole, the effect of the second fire for the grey-sided vole was more substantial than that of the first pyrogenic phenomenon. At the initial regenerative stages after the secondary effect by the fire, its share in the rodent population on the anemogenic site decreased to 16.0%, while on the pyrogenic site it decreased to 3.5% (Figs. 2a and 2b). The response of other species of the community to the two fires distinguished by the time of occurrence was also diverse. After the first fire, the ratio of the short-tailed vole and wood mouse on the pyrogenic site was 12.6%, which was higher than that on the anemogenic site. The growth in the abundance of the root vole was observed in the year preceding the first fire, and, on the contrary, its decrease was observed in the year of the effect of fire, and the abundance of the root vole on the pyrogenic site reached the highest values at the time of the development of restorative successions. The effects of the second fire caused the opposite response of this species. In the second year after its effect, a sharp increase in the abundance of root vole was observed on the anemogenic site, while on the pyrogenic site, this indicator was significantly lower. A number of features were identified in the response to changes in the conditions of the habitat environment for the short-tailed vole, which is a species that is ecologically similar to the root vole. Over the entire multiyear period of observations, the abundance of this species was low, except for 1995 and 2007, as well as 2011, which is included in period 4, i.e., the early stage of pyrogenic succession after the effect of the second fire. In this

period, the increase in the share of the short-tailed vole was observed in the rodent population on both sites (Figs. 2a and 2b). An analysis of the dynamic of the ratio of wood mouse in the community has shown its increase on the pyrogenic site at the early stages of restorative successions after both fires (Fig. 2b, period 2 and period 4). This shows favorable conditions of the habitat environment in recently burnt areas for the existence of this species.

On the whole, the results of our studies have shown that, after natural disturbances, the level of values of the total abundance of rodents was higher on the anemogenic site, except for the early stages of postcatastrophic restoration after the effect of the first fire (1999–2001 and 2011), when the values on the sites under comparison were similar. Only in 2012, at the early stage of pyrogenic succession after the repeated occurrence of fire was the total abundance of rodents higher on the pyrogenic site for the first time over the entire postcatastrophic period of observations (Fig. 3). To explain the identified peculiarities of the dynamic of the numerical ratio of rodents at different stages of postcatastrophic restorative successions, we carried out a quantitative analysis of the characteristics of the environment of animal microhabitats.

Rodent microhabitat environment. It is known that the negative effects of external factors, especially natural fires, have an indirect impact on the population of small mammals by changing forage and protective characteristics of habitats (Oreshkov and Shishikin, 2003; Shilova et al., 2007; Hengriques et al., 2000; Torre and Diaz, 2004; Litt and Steidl, 2011). As was noted above, after the windfall effect, the mosaic structure of rodent habitat sites increases due to the emergence of vegetation “spots” and their uneven distribution in the disturbed area. In our view, this results in an increase in the ecological capacity of the environment and, as a consequence, in an increase in the total abundance and species diversity of small mammals in windfall biocenoses. At the initial stages of restorative successions induced by the effect of fire, depending on its intensity and the evenness of its propagation on burnt sites, a decrease in the environmental unevenness (mosaic structure) is observed.

Results of the quantitative description of microhabitat characteristics of rodent habitats in the study area have shown that, before the occurrence of natural catastrophes, the values of variables such as the area of cover with moss and herb vegetation, as well as the abundance of underwood, were distinguished by low variability, which characterizes the undisturbed environment of animal microhabitats as relatively homogeneous according to these indicators (Table 1). The high values of the coefficient of the variation of the characteristic assessing the accumulation of debris in microsites indicates an uneven cover of sites with fallen dead trunks, which is characteristic of undisturbed habitats. The most variable microhabitat characteristic at the early stage of anemogenic succession

Table 1. Characteristic of the microenvironment of rodent habitats on the sites of the study area in the Visim Reserve before disturbances (1) and at different stages (2–4) of postcatastrophic successions

Notation of the indicator	Anemogenic site				Pyrogenic site		
	1	2	3	4	2	3	4
	\bar{X} s C_v	\bar{X} s C_v	\bar{X} s C_v	\bar{X} s C_v	\bar{X} s C_v	\bar{X} s C_v	\bar{X} s C_v
MC	3.11 2.40 77	0.03 0.12 400	0.26 0.66 254	1.46 1.95 134	0.95 2.09 220	1.03 1.69 164	1.04 1.97 189
HC	1.85 0.74 40	2.55 1.67 65	4.12 2.13 52	3.59 2.92 81	2.84 1.87 66	4.84 1.98 41	3.34 3.15 94
CS	1.70 1.57 92	2.19 1.89 86	3.49 2.30 66	0.73 1.08 148	2.67 1.85 69	1.13 1.45 128	0.17 0.58 341
AU	1.54 1.60 104	0.76 0.89 117	4.67 7.14 153	1.50 3.57 238	0 0 0	3.44 5.78 168	1.49 3.05 205
LC	0.63 0.76 121	0.89 0.70 79	1.09 0.81 74	0.70 0.63 90	1.87 1.43 77	0.72 0.55 77	0.88 0.66 75

\bar{X} , mean; s , standard deviation; and C_v , coefficient of variation.

(period 2) on the windfall site was the area of the cover of sites with moss (Table 1). After the windfall effect, the value of the coefficient of variation of this variable was maximal when compared with other succession stages, which shows a high variability of this characteristic in anemogenic microhabitats. On the pyrogenic site, the variability of this indicator was lower in the period of early succession stages; this confirms the statement that the evenness of the microenvironment of animal habitats after the effect of fire is spatially more pronounced. The degree of the variability of the characteristic assessing the cover of sites with herb vegetation at the early succession stages after the first fire (period 2) had no differences on the sites under comparison (Table 1). The comparative analysis of the values of characteristics of rodent microhabitats at the early restorative stages after the first and repeated pyrogenic effect has identified a number of distinctive features. As was noted above, the fire of 1998 almost completely destroyed forest phytocenoses in the study area of the Visim Reserve; as a result, the environment of all the analyzed rodent microhabitats on the pyrogenic site was transformed. After the repeated fire effect, the habitats of small mammals on the sites under comparison differed in regards to the level of disturbance. On the windfall site, which was exposed to fire in 2010 for the first time, only 19% of the total area of microhabitats was completely burnt. The same portion of microsites (19%) was partially affected by fire; the fully preserved microhabitats after the effect

of fire were 9%, while 53% of all the investigated microstations of rodents were burnt; however, a path with unburnt vegetation was preserved within their area, which possibly served as a “corridor” for small beasts saving themselves from the fire. There were statistically very significant distinctions of the rodent microhabitat environment at the early stages of succession after the first and second pyrogenic effect on the anemogenic site, according to four of the five characteristics, and on the pyrogenic site, according to all the analyzed indicators (Table 2). Therefore, it can be stated that differences in the response of cohabitant rodent species to the transformation of the habitat at early stages of pyrogenic restoration after the two fires differing by the time of occurrence may be due to the prevailing conditions of microhabitats with different levels of ecological favorability for the existence of different species.

CONCLUSIONS

As a result of the study, the features of post-catastrophic successions in the population of rodents and the features of their microhabitats in the forest communities of the Visim Reserve have been identified. It has been shown that cohabitant species of small mammals play a diverse role in maintaining the structure of the community in the course of anemogenic and pyrogenic successions. The level of ecological favorability of the prevailing environmental condi-

Table 2. Characteristic of the environment of the rodent microhabitat on two sites in the Visim Reserve at the early stages of pyrogenic succession

Notation of the indicator	1999		2011		Level of significance
	\bar{X}	<i>s</i>	\bar{X}	<i>s</i>	<i>p</i>
Anemogenic site					
MC	0.03 ± 0.01	0.12	2.40 ± 0.22	2.24	***
HC	2.55 ± 0.17	1.67	5.96 ± 0.19	1.93	***
CS	2.19 ± 0.19	1.89	0.77 ± 0.12	1.22	***
AU	0.76 ± 0.09	0.89	1.39 ± 0.26	2.62	***
LC	0.89 ± 0.07	0.70	0.70 ± 0.06	0.63	ns
Pyrogenic site					
MC	0.95 ± 0.21	2.09	1.92 ± 0.24	2.41	***
HC	2.84 ± 0.19	1.87	6.09 ± 0.20	2.01	***
CS	2.67 ± 0.18	1.85	0.18 ± 0.06	0.57	***
AU	0	0	0.61 ± 0.18	1.79	***
LC	1.87 ± 0.14	1.43	0.89 ± 0.06	0.64	***

\bar{X} , mean ± error of mean; *s*, standard deviation. Level of the significance of difference of statistics from zero according to the *t*-criterion: ns, statistically insignificant (*p* > 0.05) and *** *p* < 0.001.

tions of transformed habitats for different rodent species depends on their adaptive physiological features, which determines different responses of animals on the effect of natural catastrophic factors. It has been found that, for the bank vole, a pyrogenic habitat is more favorable than anemogenic habitats. In contrast, the habitat in burnt areas is the least favorable for the grey-sided vole, while the windfall effect has positive influence by improving the existence conditions for this species. As a result, the abundance of the grey-sided vole in anemogenic habitats increases sharply, which leads to a significant increase in its contribution to the community. The abundance of the red-backed vole depends on the impact of disturbing factors of natural genesis to a lesser extent than the two other ecologically similar wood mice species; however, conditions established in the course of development of postcatastrophic restorative successions are the most favorable habitat conditions for the red-backed vole in terms of ecology. The intermediate position with respect to the response to the transformation of the structure of habitats due to natural catastrophic factors is occupied by the root vole, the short-tailed vole, and the wood mouse. The conditions of pyrogenic habitats at early stages of restorative successions are most favorable for these species. Therefore, the variability of the response of cohabitant rodent species both to separate natural disturbing factors and their integrated impact has an effect on the structure of the community. Significant alterations are observed in it: species are redistributed by their contribution and there is a quick shift of dominance, as a result of which species that were small in number before disturbances occupy

the status of dominant species. Structural alterations observed in the rodent population can be considered compensatory mechanisms allowing communities to maintain sustainability under disturbed conditions of the environment of forest biocenoses after the occurrence of natural catastrophic conditions.

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