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Association of Sympatric Small Mammal Species under Contrasting Environmental Conditions

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Abstract—The transformation of microenvironmental conditions in habitats of small mammals and related changes in their spatial structure, manifested in changing levels of interspecific contacts, have been studied in microhabitats of plots affected by anemogenic (windfall) and pyrogenic influence in a protected area of the Middle Urals. The association of the dominant species (the bank vole) and other species of the community (grey red-backed vole, northern red-backed vole, and common shrew) increases in environments disturbed by disastrous natural factors. Association of species is less pronounced in the pyrogenic area, compared to the anemogenic area. The type of association between species differs between stages of progressive succession depending on conditions in particular microhabitats and specific features of functional organization in populations of small mammal species.

Keywords: small mammals, association of sympatric species, windfall, fire, microhabitats

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The study of interactions between species is extremely important for revealing the mechanisms of evolutionary changes that take place in nature and are largely determined by two integration systems: the species system and the biocenotic system (Schwarz, 1980). The allocation pattern of individuals and groups in natural populations relative to each other and to particular elements of the landscape reflects the type of area utilization characteristic of the species. Spatial structure plays an important biological role, determining the most efficient use of environmental resources (related to food, defense, or microclimate), and thus affecting the level of competition between individuals in populations and between species in communities. For animals with a mobile mode of life, the levels of abundance and patterns of spatial allocation can give evidence of the degree of well-being in a particular environment (Shilov, 1997). The long-term presence of species in a certain area is possible due to adaptation of individuals to particular conditions under normal fluctuations of environmental factors, which allows the animals to survive under adverse environmental influences. Disastrous hurricanes resulting in windfalls or fires, which periodically affect forest biogeocenoses, lead to considerable transformations in the habitats of small mammals. The decreases in abundance that can be observed in the wake of such events and disturbances in the spatial structure of the small mammal community can cause, among other population responses, an increase in the migration activity of animals, which strongly depends on the degree of favorableness of the environment. Under unstable conditions, mobile migrating individuals prevail in the community, providing evidence for a reparative role of migrations (Lukyanov, 1997).

The increased activity of small mammals in transformed environments affects not only interpopulation contacts but also interactions at the interspecific level. If direct observation on interspecific interactions between small mammals under natural conditions is impossible, this problem can be studied indirectly, by quantitative estimation of spatial associability, which manifests itself in the composition of heterospecific individuals that can be recorded in the same areas of microhabitats.

The purpose of this study was to estimate the type and extent of changes in the microenvironment of small mammals and, on the basis of data on their associated trapping, evaluate the dynamics of their associability related to these changes in order to reveal and explain variations in the level of interspecific contacts between individuals of sympatric species under ecologically contrasting conditions: in stable environments and in environments destabilized by factors related to natural disasters.

MATERIAL AND METHODS

This study was performed in the Visim State Biosphere Reserve located in the southern taiga subzone

Table 1. Characteristics of the environment used for analysis of microhabitats for small mammals in test plots

Characteristic	Designation
Plot area, m^2:	
covered with moss	*MC*
covered with herbage	*HC*
covered with shrubs	*CS*
covered with fallen tree stems	*LC*
covered with branch litter	*BC*
Breadth of path not covered with vegetation, m	*BN*
Total number of living trees	*TN*
Total number of young trees in undergrowth	*AU*
Cross-section area of living tree stems, m^2	*TC*
Base cross-section area of stumps and dry tree stems, m^2	*SC*

of boreal conifer forests of the Middle Urals. The community of small mammals and characteristics of their habitats were studied from 1987 to 2010 in key areas of a tall fern fir–spruce forest and a linden fir–spruce forest with linden affected in June 1995 by a disastrous windfall. In June 1998, the windfall area was partially burned in a fire caused by a dry thunderstorm, which divided it into two parts more or less equal in size: an anemogenic area (affected by windfall but undisturbed by fire) of the linden fir–spruce forest and a pyrogenic area (affected by windfall and then by fire) of the tall fern and linden fir–spruce forests. In August 2010, both areas were again affected by fire: the anemogenic one for the first time, and the pyrogenic one for the second time. The period of this study was divided into the following stages: (1) before the disturbance (1987–1994); (2) early stages of anemogenic and anemogenic–pyrogenic successions after windfall and fire (1995–1999 and 1998–2002); (3) advanced stages of anemogenic and anemogenic–pyrogenic successions (2000–2009 and 2003–2009); and (4) early stage of pyrogenic succession after the second fire (2010).

A total of 15 species of insectivores and rodents were recorded during the study period. The species most abundant and constantly present in the study area were selected as models for analysis: the bank vole (*Clethrionomys glareolus* Schreber, 1780), gray red-backed vole (*Clethrionomys rufocanus* Sundevall, 1846), northern red-backed vole (*Clethrionomys rutilus* Pallas, 1779), and common shrew (*Sorex araneus* Linnaeus, 1817). The three *Clethrionomys* species and the common shrew are ubiquitous in the Middle Urals and dominate in taiga communities. The spectrum of habitats colonized by these species is extremely broad. Sometimes they live under similar biotopic conditions but nevertheless display different requirements for the environment (Bol'shakov et al., 2000). A total of over 3720 individuals of the four species have been used in this study.

Small mammals were collected by the trap-line method (Kucheruk, 1963). The trap line in each of the two test plots contained 100 traps (a total of 200 traps) set at 10-m intervals from each other; the censuses were taken simultaneously in both plots. The relative abundance of the animals was estimated from the number of trapped individuals per 100 trap-days during the first five days. Each trap was numbered, which made it possible to map the areas where the animals were collected, record the number of individuals collected in each trap, and, on this basis, evaluate the degree of association between sympatric species. The total surveyed area, estimated by Lukyanov's (1991) method, was 4 ha. During the entire period of the study, the traps were set in middle of the same 10-m^2 test squares in which ten quantitative characteristics of the microenvironment (Table 1) were assessed in 1993 and in 1999, and then once in every four years by the method proposed by Bujalska, Lukyanov, and Mieszkowska (1995), with some modifications.

The association of animal species was estimated by the index k, identical to the association index used for pairs of plant species (Kats, 1943; Voronov, 1973):

$$k = 100m/nq,$$

where m is the number of traps in which animals of both species were caught, n is the total number of traps in which animals of each of the two species were caught, and q is the index of the density of area occupation by the species: $q = (b/a) \times 100$, where a is the total number of traps, and b is the number of traps in which the animals were caught (Lukyanova and Lukyanov, 1992). Values of the association index smaller than 1 were considered to indicate rare co-occurrence of the two species in a given area (i.e., extremely weak interspecific contacts); values of the index greater than 1 were considered to indicate a high degree of co-occurrence. The spatial allocation of individuals was estimated by the aggregation index (Ag), a measure of the clustering of individuals calculated as the ratio between the specific abundance index (abundance of the species in microhabitats) and the occupation den-

Table 2. Changes in characteristics of microhabitats for small mammals in test plots before and after disturbances

Characteristic	Anemogenic area				Significance level	Pyrogenic area				Significance level
	before disturbance		after disturbance			before disturbance		after disturbance		
	$\overline{X} \pm m$	σ	$\overline{X} \pm m$	σ	*p*	$\overline{X} \pm m$	σ	$\overline{X} \pm m$	σ	*p*
MC	2.65 ± 0.23	2.31	0.03 ± 0.01	0.12	***	3.58 ± 0.24	2.41	0.95 ± 0.21	2.09	***
HC	1.75 ± 0.07	0.67	2.55 ± 0.17	1.67	***	1.96 ± 0.08	0.80	2.84 ± 0.19	1.87	***
CS	2.30 ± 0.18	1.75	2.17 ± 0.19	1.89	ns	1.10 ± 0.12	1.07	2.67 ± 0.18	1.85	***
LC	0.41 ± 0.04	0.45	0.75 ± 0.09	0.87	***	0.50 ± 0.06	0.62	1.87 ± 0.14	1.43	***
BC	0.08 ± 0.02	0.15	0.22 ± 0.02	0.22	***	0.08 ± 0.02	0.15	0.05 ± 0.01	0.09	*ns*
BN	0.28 ± 0.02	0.25	0.56 ± 0.02	0.18	***	1.33 ± 0.08	0.81	0.54 ± 0.03	0.26	***
TN	1.19 ± 0.08	0.81	0.15 ± 0.04	0.39	***	1.04 ± 0.08	0.78	0.02 ± 0.01	0.14	***
AU	1.70 ± 0.18	1.78	0.76 ± 0.09	0.89	***	1.37 ± 0.14	1.39	0.02 ± 0.01	0.14	***
TC	0.25 ± 0.04	0.41	0.02 ± 0.01	0.06	***	0.31 ±0.04	0.41	0.002 ± 0.001	0.02	***
SC	0.05 ± 0.02	0.16	0.26 ± 0.09	0.89	***	0.24 ± 0.06	0.55	0.46 ± 0.10	0.88	***

Note: Three asterisks (***) indicate that differences from zero are statistically significant at $p < 0.001$ (*t*-test); *ns*, nonsignificant ($p > 0.1$).

sity, or occurrence frequency of the species (Lukyanova and Lukyanov, 1992).

The data were processed by methods of multivariate statistics: ANOVA and discriminant analysis, and by the nonparametric Spearman's correlation (*r*). The differences between data sets were estimated by the *t*-test, *F* test, and χ^2 test (Sokal and Rohlf, 1981).

RESULTS AND DISCUSSION

Analysis of the environment of microhabitats in different areas before and after anemogenic and pyrogenic disturbance revealed considerable changes in its characteristics, except for parameters of shrub coverage (*CS*) in the anemogenic area and branch litter coverage (*BC*) in the pyrogenic area (Table 2). Classification of microenvironmental characteristics based on discriminant analysis has shown that the greatest contribution to discrimination between microhabitat environments in the compared plots is that of variables of the first two functions, which account for 79 to 86% of the total variance (Table 3). Judging from the values of standardized coefficients, which indicate the contribution of the variables to the first discriminant function, the characteristics especially weighty in the anemogenic environment are those that describe moss coverage (*MC*) of the plot and tree stem cross-section area (*TC*). The variables especially weighty in pyrogenic habitats are those that describe the breadth of the path not covered with vegetation (*BN*) and tree stem cross-section (*TC*). In both plots, a considerable contribution to the second discriminant function is that of variables *HC* and *CS*.

In nature, competition between species of the genus *Clethrionomys* is believed to be common and ubiquitous (Koshkina, 1967). Sympatric species have a wealth of adaptations that help them to reduce competition, including utilization of different habitats and differences in diet, mobility, and diurnal activity. However, natural disasters can stimulate manifestations of potential species-specific abilities that normally cannot be observed (Shilova, 1993). Therefore, it can be assumed that species-specific responses of small mammals to such disturbances can be especially distinct. In our case, they are traceable in the structure of the small mammal community. Figure 1 shows changes in the abundance of test species before and after disturbance in forest biogeocenoses of the Visim Nature Reserve. Before the disturbance, the bank vole was dominant in the study territory (Fig. 1a), with its abundance being considerably higher than that of any of the three other species. The dominance of the bank vole in small mammal communities over the whole area of the nature reserve before the disturbance was also reported by other authors (Marin, 1992; Berdyugin, Kuznetsova, and Sharova, 1996).

Changes in the small mammal community of the anemogenically disturbed area were revealed one year after the windfall (Fig. 1b). The abundance of the bank vole considerably decreased, and the grey red-backed vole became dominant in the group of *Clethrionomys* voles. Changes in the composition of dominant species in windfall-affected areas at early stages of progressive succession have also been reported by other authors (Istomin, 1992; Zyus'ko et al., 2001; Kuznetsova et al., 2001; Dobrinskii, 2005). According to Istomin (1992), who studied small mammal communities in southern taiga ecosystems disturbed by windfall, their territories are characterized by a complex, diverse, and fairly even mosaic pattern of preserved areas and new microhabitats formed in places of disturbance.

Table 3. Standardized coefficients of discriminant canonical functions (DCF 1, DCF 2, and DCF 3) for microenvironmental variables in different plots

Variable	Anemogenic area			Pyrogenic area		
	Discriminant canonical function					
	DCF 1	DCF 2	DCF 3	DCF 1	DCF 2	DCF 3
MC	0.605	–0.148	–0.316	–0.475	0.281	–0.250
HC	–0.221	0.780	–0.587	0.310	0.932	–0.212
CS	0.268	0.738	–0.072	0.020	0.670	0.379
LC	–0.137	0.281	0.050	0.209	–0.083	0.491
BC	–0.170	0.490	0.135	–0.258	0.151	0.177
BN	–0.159	0.256	0.420	–0.632	0.102	0.176
AU	0.027	0.059	–0.339	0.125	0.221	–0.370
TC	0.696	0.297	0.375	–0.559	0.083	–0.221
SC	0.139	0.195	0.302	–0.217	0.004	0.299
Eigenvalue	1.226	0.678	0.511	3.120	1.590	0.757
Canonical correlation	0.742	0.636	0.582	0.870	0.784	0.656
Wilks' Λ	0.177	0.394	0.662	0.053	0.220	0.569
χ^2	679.2	365.2	162.0	1150.4	594.7	221.2
Variance, %	50.76	28.08	21.16	57.07	29.09	13.84
Number of degrees of freedom	27	16	7	27	16	7
Significance level, *p*	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

The microenvironmental conditions established at early stages of anemogenic succession in the studied protected area (loss of the tree stand and changes in the composition of herbaceous plants) probably had an adverse effect on the bank vole, the species that was dominant before the disturbance, changing some aspects of its ecology and, possibly, thereby reducing its competitive potential. The formation of a large number of hollows (shaded shelters with a favorable microclimate) apparently better satisfied the ecological requirements of the gray red-backed vole, since microclimatic factors play an important role in the choice of habitats by this species (Berdyugin, 1984). In the following years, the gray red-backed vole remained dominant in the anemogenic plot, except in 1999, 2000, 2009, and 2010 (Fig. 1b). In the pyrogenic plot, the bank vole remained dominant and prevailed in abundance in all years except 2006 and 2007 (Fig. 1c). The abundance of the common shrew increased in both areas. In the community of the anemogenic plot, this species was dominant in 2005, and in 2006 it was as abundant as the northern red-backed vole (Fig. 1b). In the pyrogenic area, the common shrew dominated by abundance in 2002 (Fig. 1c) and in the period from 2004 to 2010, except in 2007, when it was somewhat less abundant than the gray red-backed vole, which was dominant in the area during this period (3 and 4 ind./trap-days, respectively).

The levels of species association under different microenvironmental conditions were compared by two parameters: the association index (*k*) and Spearman's correlation coefficient (*r*). This coefficient characterizes the relationship between the population dynamics of two species and changes in the pattern of these dynamics. The relationships between the abundance of the bank vole and each of the two other *Clethrionomys* species were found to be similar, and the association index and Spearman's correlation coefficient had opposite values: low for *k* and high for *r* (Table 4). High values of the correlation coefficient provided evidence for synchronism in population dynamics of the species compared, and low values of the association index indicated that interspecific contacts in undisturbed habitats were extremely weak. The correlation in population dynamics between the bank vole and common shrew was less distinct before the disturbance.

The type of changes in population dynamics of the species compared became very different after the disturbances (Table 4). Changes in the abundance of the bank vole and gray red-backed vole were asynchronous at early and at advanced stages of the anemogenic and pyrogenic succession (Fig. 1b), which is confirmed by low values of the correlation coefficient, and the increased values of the association index for these two species, especially in the anemogenic area, reflected a

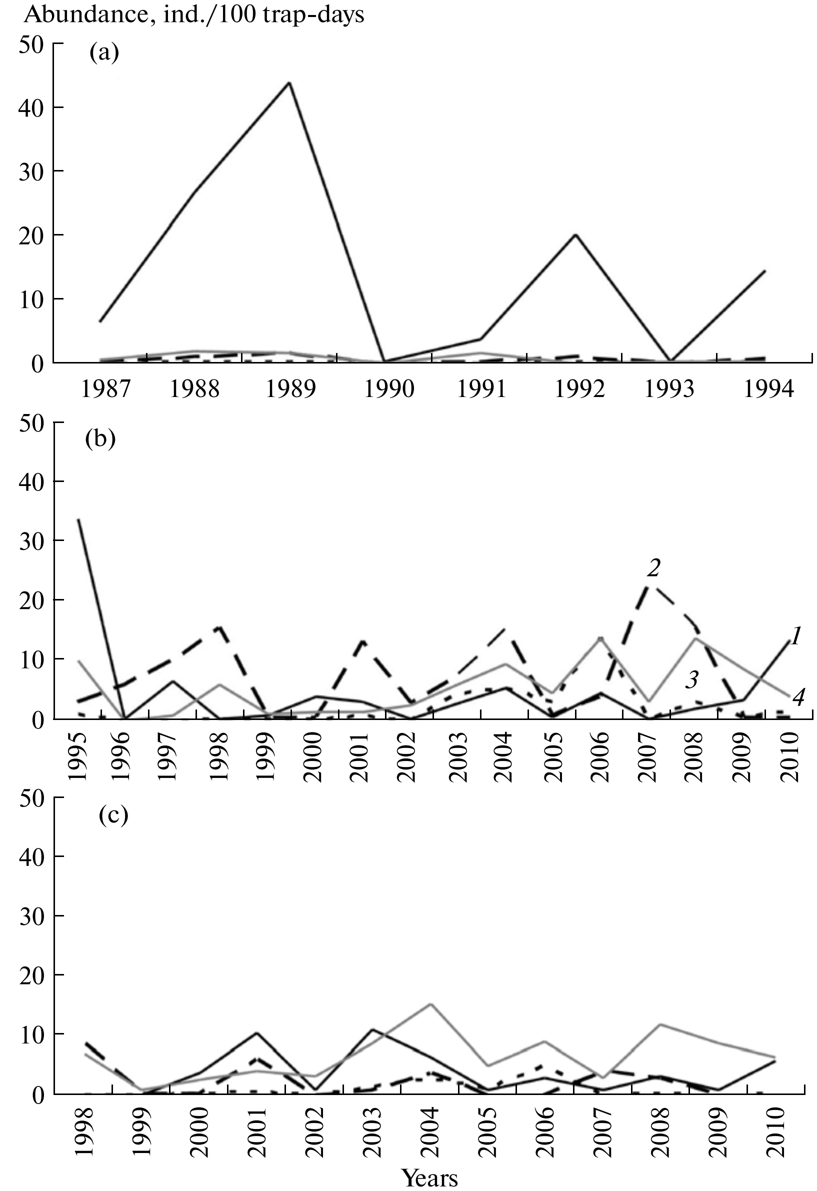

Fig. 1. Dynamics of abundance of sympatric small mammal species in the Visim State Biosphere Reserve (a) before disturbance and after (b) windfall or (c) fire: (*1*) bank vole; (*2*) gray red-backed vole; (*3*) northern red-backed vole; (*4*) common shrew.

considerable increase in the levels of interspecific contacts.

Judging from the values of *r* and *k*, the types of changes in the abundance of the bank vole and northern red-backed vole in the area before the disturbances and at early stages of progressive successions following the windfall and following the fire were similar. At advanced stages of progressive succession, changes in the abundance of the two species became asynchronous in both plots, and the levels of interspecific contacts between them became considerably higher, especially in the anemogenic area, where the abundance of the northern red-backed vole in this period increased considerably (Table 4; Fig 1b).

The association between the bank vole and common shrew in both anemogenic and pyrogenic plots changed after the disturbances. The values of *r* were similar at the early stage of succession in the anemogenic plot and at the advanced stage in the pyrogenic plot, as well as at the early stage in the pyrogenic plot and at the advanced state in the anemogenic plot (Table 4). This is indicative of opposite changes in the abundance of the two species at different stages of progressive succession, probably reflecting specific features of population dynamics in representatives of two different ecological groups, voles of the genus *Clethrionomys* and shrews. The high *k* value at the advanced stage of pyrogenic succession provides evi-

Table 4. Values of Spearman's correlation coefficient (*r*) and asssociation index (*k*) between the bank vole (*Clethrionomys glareolus*) and the sympatric small mammal species at different stages of progressive succession in forest biogeocenoses

Succession stage	*Clethrionomys glareolus* + *Cl. rufocanus*		*Clethrionomys glareolus* + *Cl. rutilus*		*Clethrionomys glareolus* + *Sorex araneus*	
	r	*k*	*r*	*k*	*r*	*k*
Before disturbance	0.98***	0.05	0.88**	0.01	0.59	0.13
Anemogenic succession						
Early stage	–0.30	1.63*	0.89**	0.06	0.70	0.56
Advanced stage	–0.13	1.11	0.56	1.21	0.32	0.79
Pyrogenic succession						
Early stage	0.05	0.40	0.89**	0.09	0.30	0.40
Advanced stage	0.27	0.53	0.41	0.53	0.65	1.81*

Note: Asterisks indicate significance levels of statistical difference from zero by *t*-test and χ^2 test: (*) $p \leq 0.05$; (**) $p \leq 0.01$; (***) $p \leq 0.001$.

dence for a high frequency of encounters between individuals of the two species in this plot, where the common shrew dominated by abundance in the community during this period (Fig. 1).

Since dominance at different stages of environment transformation was mainly distributed between the bank vole and gray red-backed vole, a detailed analysis of the association index was performed for these two species (Fig. 2). Before the anemogenic and pyrogenic disturbances in the habitats, the values of *k* in the plots were low (Fig. 2, curve *1*). The stronger association of the bank vole and gray red-backed vole in the year of the windfall indirectly confirms the increase in interspecific contacts under altered ecological conditions, followed by a decrease in the next year after the disturbance. Higher values of the association index were recorded in the anemogenic plot in years of high abundance of the two species (Fig. 2, curve *1*), while this parameter in the pyrogenic plot was low in the same years (Fig. 2, curve *2*). After the second fire in 2010, the values of the association index in the anemogenic plot became lower again.

Low values of the association index recorded in the area before the disturbances indicate extremely weak interspecific contacts and can be explained by the combined action of two important factors: specific structural features of the environment in microhabitats and levels of abundance of the dominant species. First, the structure of the phytocenoses before the windfall was being formed by dynamic processes natural for forest biocenoses and was distinctly stratified (with the tree, shrub, and herb–dwarf-shrub layers), and only indigenous plant species participated in the redistribution of ecological niches in the undisturbed soil and ground vegetation (Belyaeva, 2007). In the naturally heterogeneous environment of the study area, undisturbed microhabitats provided small mammals with sufficient food and shelter resources (Table 2); this probably accounted for the relatively even distribution of individuals of different species over the area and almost ruled out interspecific contacts. Second, the high abundance of the bank vole prior to the disturbance suggests that the population of the dominant species was represented mainly by animals associated with their individual territories. It is known that populations of many small mammal species under optimal environmental conditions include mostly settled individuals, the proportion of which considerably decreases if the quality of the environment deteriorates under the effect of various factors (Berdyugin, 1983; Shchipanov, 1990, 2002; Lukyanov, 1997).

The functional heterogeneity of the populations in the transformed environment proved to have an effect on the type of association between the bank vole and gray red-backed vole after disturbance in the structure of microhabitats. Under unstable environmental conditions, the proportion of mobile individuals in the two vole species appears to increase, and this leads to a higher level of interspecific contacts, which is confirmed by the values of *k*; individuals of the two species more frequently meet each other in the same areas, and the association between the species strengthens. This also follows from the results of our analysis for the aggregation of individuals. We have found that the value of the aggregation index for the bank vole and gray red-backed vole in both anemogenic and pyrogenic plots was significantly lower before the disturbances than after the action of disastrous factors ($\chi^2 = 48.9$; $df = 1$, $p < 0.001$ and $\chi^2 = 35.2$; $df = 1$, $p < 0.001$, respectively).

The type of association between the bank vole and northern red-backed vole at early stages of anemogenic and pyrogenic succession differs from that between the bank vole and gray red-backed vole, which can be explained by specific features of the functional organization of gray red-backed vole populations. This species belongs to the regenerative type, to the subgroup of species capable of changing the

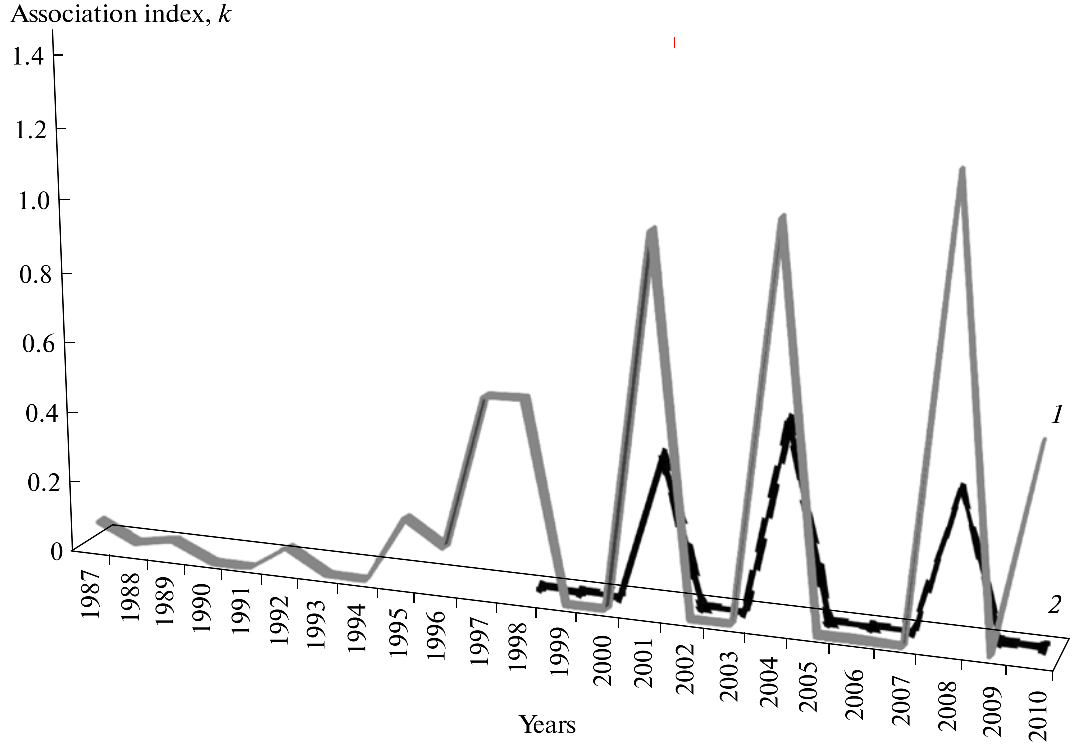

Fig. 2. Dynamics of association index between bank vole and gray red-backed vole in different areas of the Visim State Biosphere Reserve: (*1*) undisturbed and anemogenic areas, (*2*) pyrogenic area.

functional structure of their populations (the ratio of mobile and. settled individuals) as a result of general rearrangements accompanying the population dynamics, rather than under particular unfavorable conditions (Shchipanov, 2002). The red-backed vole in the study area had consistently low abundance before the disturbances and at early stages of anemogenic and pyrogenic successions. Therefore, destabilization of the environment in microhabitats probably did not affect the functional structure of this species, and the type of association between the bank vole and northern red-backed vole did not change during this period, as indicated by the same values of *r* and very close values of *k*. At advanced stages of succession, when the abundance of the northern red-backed vole increased, the proportion of mobile individuals in the population probably also increased (Figs. 1b, 1c), resulting in a higher frequency of encounters between individuals of the two species, especially in the anemogenic plot; this is confirmed by high values of *k* (Table 4).

Therefore, the method used in this study has made it possible to reveal specific features of contacts between small mammals of different species under contrasting environmental conditions. On the whole, it can be concluded that the frequency of contacts between sympatric species in the same areas with microhabitat conditions that have been dramatically altered by a natural disaster is determined by changes in the spatial and functional organization of populations resulting from transformations of the environment caused by this disaster.

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