

Effect of Ecotone at the Boundary of Windfall- and Fire-Damaged Forest Biocenoses on the Abundance of Rodents and Characteristics of Their Microhabitats

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Abstract—Environmental conditions developing at the boundary of windfall- and fire-damaged forest biocenoses at different stages of progressive succession have a positive effect on the total abundance of rodents, but the role of ecotone in forming the structure of their microhabitats is ambiguous. The complex of biotic and abiotic conditions in the ecotone has a positive influence on the size of shrub coverage area and the abundance of saplings, whereas the influence of the edge effect on other microhabitat parameters (namely, herbaceous and moss coverage) is negative or neutral.

Keywords: ecotone, edge effect, windfall, fire, biocenosis, rodents, microhabitat, nature reserve

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The notion of ecotone in ecology refers to the transitional zone at the boundary between two different habitats or communities, where the diversity and density of organisms show a tendency to increase. This phenomenon is termed edge effect. However, the increase in the abundance of biota at the edges of habitats is not a universal process, since organisms differ in ecological response to habitat conditions in ecotones [1, 2]. In particular, the effect of ecotone may be positive, negative, or neutral [3], with the density (abundance) of organisms in the edge habitats increasing, decreasing, or remaining unchanged, respectively.

It has been shown that there is a dynamic balance between plant and animal communities at the edges of forest habitats and that heterogeneity of the borderline landscape can have a stabilizing effect on populations of different species [4–6]. Small mammals are an important biological component of natural ecosystems, playing a major role in the flow of energy in biocenoses and their renewal. Hence, they are widely used as model objects in ecological research. Most of relevant studies deal with the structure of small rodent and insectivore communities at the edges of forest biocenoses fragmented under anthropogenic impact. Because of differences in ecological preferences, some species positively respond to the conditions of such habitats [6–8], while the edge effect on other species is opposite [6, 9–13]. The latter may also be due to the increased risk of predation at habitat edges [14, 15].

The impact of natural factors such as forest fire leads to the formation of distinct boundaries between

communities [1]. The patchiness of habitats at the edges of corresponding areas—the tree, shrub, and herbaceous layers and open areas formed after fire—has an effect not only on physical parameters of biotopic conditions (wind, temperature, snow cover, illumination level) but also on the structure of animal communities. Studies on the pattern of animal abundance in habitats at the boundary of habitats formed under the impact of natural disastrous factors (e.g., windfall and fire) have major ecological significance for solving problems in forest management and for the conservation of ecosystem biodiversity in general [2, 3, 16].

The purpose of this study was to analyze the effect of ecotone on the abundance of rodents and basic characteristics of their microhabitats at the boundary of forest biocenoses damaged by windfall and fire.

MATERIAL AND METHODS

This study was performed in the Visim State Biosphere Reserve (57°20′–57°31′ N, 59°30′–59°50′ E) in 1998 to 2012. The natural environment of the reserve is characteristic of the southern taiga subzone of the Urals, where fir–spruce (boreal) forests are the main zonal vegetation type. In June 1995, all forests of the reserve were damaged to different extents by a disastrous windfall; in the subsequent period, the disturbed forest biocenoses were affected by two powerful forest fires (in 1998 and 2010), both caused by dry thunderstorms. Three summer seasons after the wind-

throw were droughty, and a large amount of combustible material accumulated in a large part of the reserve territory by the time of the first fire. Our study area (4 ha) included fir–spruce forest sites of tall-fern and linden types growing on the mild slope of Mt. Lipovyi Sutuk, where up to 90% of the tree layer was damaged as a result of windfall [17]. The first fire affected half of this territory (2 ha), dividing it into two parts: a windfall area undisturbed by fire and a burned-out area (below, referred to as anemogenic and pyrogenic plots). The boundary between them was marked by birch (*Betula pendula*) undergrowth preserved in the anemogenic plot. Thus, a kind of ecotone was formed. The second fire (2010) spread throughout the study territory, so that the anemogenic plot was burned for the first time and the pyrogenic plot, for the second time.

Small mammals in both plots were collected by the standard trap line method [18]. A total of 200 traps were arranged in a line at 10-m intervals so that the boundary between the anemogenic and pyrogenic plots (formed after the first fire) passed through the center of this line (2 km long), with 100 traps being on each side of the boundary. It was conditionally assumed that the ecotone was 400 m wide, extending for 200 m to the anemogenic plot (zone I) and to the pyrogenic plot (zone II).

The traps were exposed for 5 days. They were assigned ordinal numbers, which made it possible to map the points of capture and quantitatively describe environmental characteristics in microhabitats of rodents. Parameters of the microenvironment were evaluated by the method proposed by Bujalska et al. [19], with some modifications.

A comparative analysis of the dynamics of rodent abundance was based on the material collected at early stages of postpyrogenic recovery of forest biocenoses (after fires in 1998, 2010, and 2011) at the early stage of succession (2001) and in the course of its development (2004 and 2007). The effect of habitat edge on the pattern of rodent abundance was studied in several stages. At the first stage, analysis was performed of the data on the numbers of animals trapped during the first 5 days in the ecotone (by 20 traps in zones I and II) and away from it (20 traps in each plot at 1000 m from the boundary between them). Since the abundance of different rodent species in catches showed a wide scattering of values, they were expressed as logarithms ($\log X + 1$). At the second stage, the values of total rodent abundance were compared within the ecotone (between zones I and II) and between the distant (control) zones of the two plots. Finally, the data on animal abundance were pooled over the years when this parameter did not differ between the zones in order to analyze its average values based on the results of catches in 40 traps set in the ecotone and in the control areas.

On the whole, data on the catches of rodents in 80 traps were used in the study. Each trap was in the center of 10-m² test square where quantitative description

was made of four basic microenvironmental parameters determining foraging and shelter conditions in animal habitats: the size of areas (m²) covered by herbaceous plants, shrubs, and mosses, and the abundance (numbers) of saplings. These parameters were assessed for the first time on the next year after fire (1999) and then once in every four years (2003, 2007, and 2011). Thus, a total of 320 descriptions of 80 squares were obtained. The traps remained in the same places throughout the study period, which provided the possibility to study the dynamics of small mammal abundance and characteristics of the microenvironment in the same habitats at different stages of postcatastrophic recovery.

The total catch used in the study amounted to 363 rodents of 6 species: the bank vole *Clethrionomys glareolus* Schreb., gray-sided vole *Cl. rufocanus* Sund., northern red-backed vole *Cl. rutilus* Pall., field vole *Microtus agrestis* L., root vole *M. oeconomus* Pall., and pygmy wood mouse *Sylvaemus uralensis* Pall.

The results were processed statistically with STATISTICA for Windows 6.0 software using multiple regression analysis and the nonparametric Mann–Whitney *U* test for pairwise comparisons of variables in independent samples.

RESULTS AND DISCUSSION

Obviously, the role of edge effect in forming the structure of the environment in rodent habitats can be characterized by the values of particular parameters. The results of quantitative description of the microhabitats in the edge zones and 1000 m away from the boundary between the two plots at different stages of postcatastrophic recovery proved to be ambiguous. Comparisons of herbaceous coverage areas in test squares at early stages of postpyrogenic succession (1999 and 2011) revealed differences between the edge and control biotopes in both anemogenic and pyrogenic plots (zones I and II, respectively).

According to the Mann–Whitney test, the herbaceous coverage area in both plots in 1999 was significantly lower at a distance of 200 m from the boundary between them than in the control zones distant from the boundary ($U = 85$; $Z = 3.11$; $p = 0.001$ and $U = 65$; $Z = 3.65$; $p < 0.001$, respectively), indicating a negative influence of the ecotone on this microhabitat parameter (table, Fig. 1). The edge effect on the moss coverage area in the pyrogenic plot at the early stage of recovery after the first fire also proved to be negative, but this effect on the same parameter was not observed in the anemogenic plot (table, Fig. 1). The complex of abiotic and biotic conditions formed in the edge habitats of the anemogenic plot prior to the 2010 fire had a positive influence on the shrub coverage area, while the values of this parameter in the pyrogenic plot remained unchanged at the early stages of recovery

Influence of ecotone on characteristics of rodent microhabitats at the boundary of anemogenic and pyrogenic plots in the Visim reserve: (+) positive, (–) negative, (0) neutral

Year	Anemogenic plot				Pyrogenic plot			
	herbs	shrubs	saplings	mosses	herb	shrubs	saplings	mosses
1999	–	+	–	0	–	0	0	–
2003	0	+	+	0	–	+	+	–
2007	–	+	0	–	0	+	+	–
2011	–	0	+	–	0	0	+	0

(1999 and 2011); i.e., the effect of the ecotone was neutral (table).

At the early stage of pyrogenic succession after the first fire (1999), the numbers of saplings in the anemogenic plot (not affected by fire) were lower near the boundary (zone I) than in the distant (control) biotopes, which was indicative of a negative effect of ecotone on this parameter (table; Fig. 1, zone I). However, their effect on the same parameter in both plots proved to be positive in the early period of recovery after the second fire (2011) (table, Fig. 1). In the course of progressive succession, the edge effect was not reflected in the size of herbaceous coverage area in the anemogenic plot in 2003, and the same was true of the pyrogenic plot in 2007 (table). On the other hand, the herbaceous coverage area at the same stage of succession (2003) in the pyrogenic plot proved to be significantly smaller in biotopes near the boundary than in distant biotopes ($U = 118$; $Z = 2.22$; $p < 0.05$), which

was evidence for a negative influence of the ecotone (table; Fig. 1, zone II).

This influence also manifested itself in the formation of moss cover in the course of progressive succession in 2007: the moss coverage area in ecotonal zones I and II was smaller than in distant control zones ($U = 60.5$; $Z = 3.77$; $p < 0.001$ and $U = 40.5$; $Z = 4.31$; $p < 0.001$, respectively). In the same period, a positive role of the edge effect was revealed for the shrub coverage area and the numbers of saplings (table, Fig. 1). The Mann–Whitney test confirmed that the sizes of shrub coverage area in both plots in 2003 were significantly greater in edge biotopes than in distant biotopes ($U = 93$; $Z = 2.89$; $p = 0.003$ and $U = 108.5$; $Z = 2.48$; $p = 0.01$). The numbers of samplings in the pyrogenic plots in 2007 were significantly greater in biotopes near the boundary than at 1000 m from it ($U = 88$; $Z = 3.03$; $p = 0.001$). Thus, it can be concluded that ecotonal conditions have an ambiguous effect on the formation of micro-

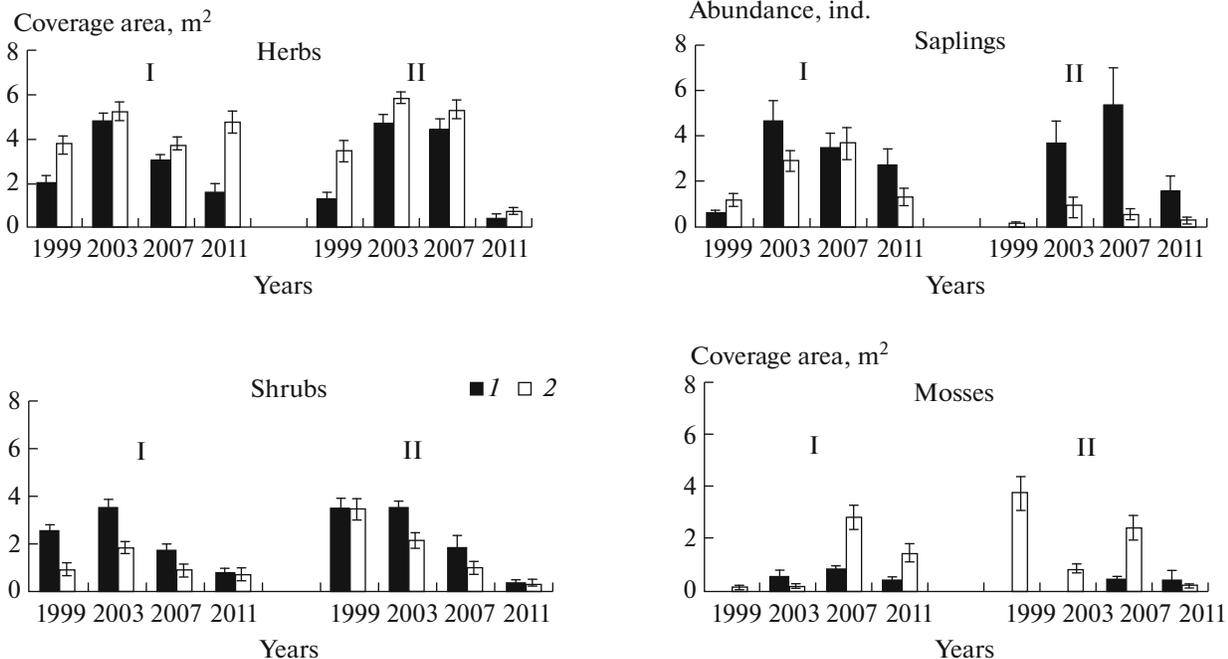


Fig. 1. Changes in characteristics of rodent microhabitats in (I) anemogenic and (II) pyrogenic plots at distances of (1) 200 m and (2) 1000 m from the boundary between them (mean values with standard errors).

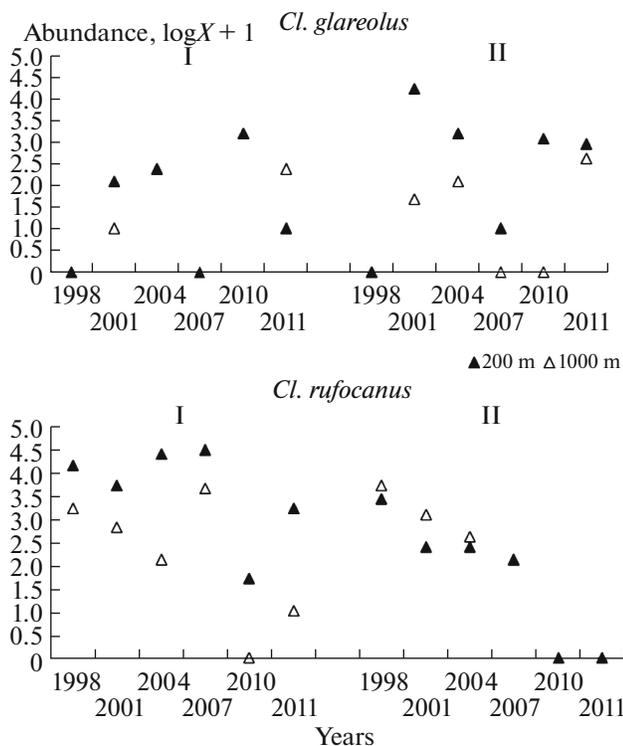


Fig. 2. Abundance of dominant rodent species in (I) anemogenic and (II) pyrogenic plots at different distances from the boundary between them.

environment in small mammal habitats in different periods of recovery of forest biocenoses after natural disasters.

An analysis of abundance of individual rodent species at different distances from the boundary between the disturbed biogeocenoses showed that they ambiguously responded to changes in habitat conditions. The data presented below concern only two species, the bank vole *Cl. glareolus* and grey-sided vole *Cl. rufocanus*, which were the most abundant in the study region and exchanged dominant roles at different stages of postcatastrophic succession [20]. In the year of the first fire (1998), *Cl. glareolus* was completely absent in both plots, either near the boundary (200 m) or away from it (1000 m) (Fig. 2). The same was observed in the anemogenic plot in 2007, while in the pyrogenic plot this species in 2007 and 2010 was absent in catches from near the boundary. The edge effect was not reflected in the abundance of the species in anemogenic habitats at early stages of postpyrogenic recovery in 1998 and proved to be negative in 2011 (Fig. 2, I). In contrast, conditions at habitat edge in the pyrogenic plot (damaged for the second time) had a positive effect on the abundance of *Cl. glareolus* (Fig. 2, II). On the whole, the edge effect in the anemogenic plot proved to be positive for this species only at the early stage of postcatastrophic succession (2001)

(Fig. 1, I), and in the pyrogenic plot, at all successional stages (Fig. 2, II).

The response of codominant *Cl. rufocanus* to environmental conditions at habitat edges was different from that of *Cl. glareolus*. In the anemogenic plot, these conditions had a positive effect on the abundance of this species, which was higher than in distant biotopes at all stages of succession. In the pyrogenic plot, in contrast, the edge effect was negative for *Cl. rufocanus* at the early stage of succession and did not manifest itself at subsequent stages (a neutral effect) (Fig. 2, II).

These specific features in the response of the two rodent species to environmental conditions at habitat edges are related to differences in their ecological preferences [20]. For *Cl. glareolus*, the environment of burned-out areas is far more favorable than that of windfall areas. Conversely, *Cl. rufocanus* avoids burned-out areas, while windfall creates favorable living conditions for this species. Consequently, the abundance of *Cl. rufocanus* at the habitat edge proved to be higher in the anemogenic than in the pyrogenic plot.

Analyzing the effect of ecotonal conditions on the total abundance of rodents, evidence was obtained for its positive influence on this parameter at habitat edges. As follows from Fig. 3a, the highest abundance of rodents in the anemogenic plot was recorded in 2004 at 200 m from the boundary. In the pyrogenic plot, a peak of their abundance was also recorded in the same zone in 2001, at the early stage of recovery after the first fire (Fig. 3b).

In the anemogenic plot, the numbers of animals in catches were greater in the edge zone I (200 m from the boundary) than in the distant zone in all years except 2010. The edge effect in the pyrogenic plot (zone II) was distinct only in 2001, with the difference between the values of animal abundance at distances of 200 and 1000 m being statistically significant ($U = 97$; $Z = 2.79$; $p = 0.005$). In the anemogenic plot, this difference was significant in 2004 ($U = 107$; $Z = 2.52$; $p = 0.01$) (Fig. 3).

A comparative analysis of animal abundance at different distances from the boundary revealed significant differences between its values recorded in 2007 at 200 m ($U = 96.5$; $Z = 2.80$; $p = 0.005$) and in 2010 at 1000 m ($U = 135.5$; $Z = 1.74$; $p = 0.03$). On this basis, the data on zones I and II were summed up over all years except 2007 and 2010 in order to estimate the general effect of the ecotone on the distribution of rodents. As follows from Fig. 4, a tendency toward a positive edge effect was observed at all stages of recovery after fire. Highly significant differences in animal abundance between the ecotone and distant (control) biotopes were revealed at the early successional stage in 2001 ($U = 76$; $Z = 3.35$; $p < 0.001$), in the course of pyrogenic succession in 2004 ($U = 106.5$; $Z = 2.53$; $p = 0.005$), and at the initial stage of recovery after the second fire in 2011 ($U = 123.5$; $Z = 2.07$; $p < 0.05$).

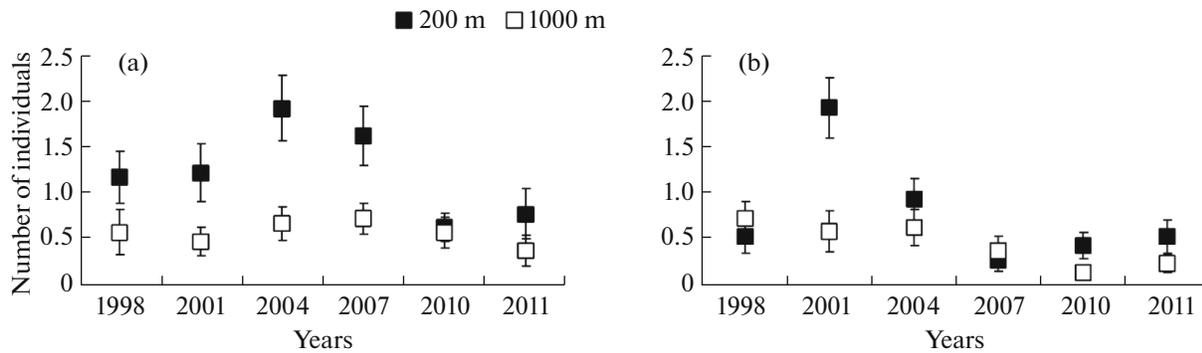


Fig. 3. Total abundance of rodents in (I) anemogenic and (II) pyrogenic plots at different distances from the boundary between them (mean values with standard errors).

These results confirm the positive effect of ecotonal conditions on the abundance of rodents at habitat edges at different stages of progressive succession in the study area of the Visim reserve. The only exception is the initial stage of pyrogenic succession after the first fire, at which the effect of the ecotone was neutral.

Multiple regression analysis was used to reveal specific biotopic preferences of rodents at habitat edges and in distant zones. As shown in our previous studies, different rodent species ambiguously respond to microhabitat parameters under different biotopic conditions [21, 22]. Here, the influence of microhabitat conditions at habitat edges on the total abundance of rodents was evaluated by analyzing the value of standardized regression coefficients. In the anemogenic plot, evidence was obtained for a statistically significant direct relationship between the abundance of rodents and the shrub coverage area at 1000 m from the boundary between biocenoses at the early stage of postfire recovery in 2011 ($\beta = 0.86$; $p < 0.001$) and an inverse dependence of their abundance distribution of the herbaceous coverage area at habitat edges unaf-

ected by fire in 1998 ($\beta = -0.92$; $p < 0.05$). In the pyrogenic plot, the growth of tree saplings was found to have a positive effect on the total abundance of rodents in distant biotopes in the course of progressive succession (2004) ($\beta = 0.45$; $p < 0.05$).

CONCLUSIONS

One of a very few studies on the role of edge effect in forming the structure of small mammal communities in forest habitats fragmented by fire provides evidence that the spatial pattern of abundance distribution of individual species positively depends on biotopic conditions in edge zones [23]. The authors consider that small mammal species more tolerant of environmental changes at the edges of pyrogenic habitats have higher chance to survive under given conditions. Our data also show that the edge effect plays a positive role, providing for an increase in the abundance of individual species and rodent community as a whole at different stages of postpyrogenic recovery of bordering forest habitats in the Visim reserve. However, its manifestations in the formation of microhabitat structure at the edges of rodent habitats at different stages of progressive succession proved to be ambiguous. Thus, the complex of abiotic and biotic conditions developing at habitat edges has a positive effect on the shrub coverage area and the growth of tree saplings, whereas its influence on other microenvironmental parameters (herbaceous and moss coverage areas) is negative or neutral. The abundance distribution of rodents shows a relationship with some microhabitat parameters at certain stages of progressive succession at different distances from the boundary between disturbed biocenoses, but this does not allow the conclusion that the microenvironment is the main factor providing for the increase of animal abundance at habitat edges.

Thus, the effect of ecotone on the abundance distribution of rodents and the structure of their microhabitats is ambiguous, which is evidence that particular characteristics of the microenvironment alone can-

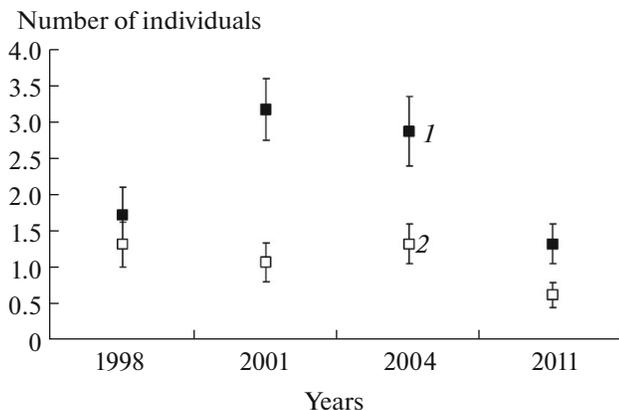


Fig. 4. The abundance of rodents (1) in the ecotone and (2) in distant (control) biotopes of the study area (mean values with standard errors).

not account for the increase in the abundance of these animals at habitat edges. This increase is apparently due to the complex effect of abiotic and biotic conditions developing at the boundary between windfall- and fire-damaged forest biocenoses.

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REFERENCES

1. Odum, E., *Basic Ecology*, Philadelphia: Saunders, 1983. Translated under the title *Ekologiya*, Moscow: Mir, 1986, vol. 2.
2. Lidicker, W.Z., Jr., Responses of mammals to habitat edges: An overview, *Landsc. Ecol.*, 1999, vol. 14, pp. 333–343.
3. Ries, L., Fletcher, R.J., Battin, J., and Sisk, T.D., Ecological responses to habitat edges: Mechanisms, models, and variability explained, *Annu. Rev. Ecol. Evol. Syst.*, 2004, vol. 35, pp. 491–522.
4. Hansson, L., Landscape ecology and stability of population, *Landsc. Plan.*, 1977, no. 4, pp. 85–93.
5. Stenseth, N.C., Spatial heterogeneity and population stability: Some evolutionary consequences, *Oikos*, 1980, vol. 35, pp. 165–184.
6. Manson, R.H., Ostfeld, R.S., and Canham, C.D., Responses of a small mammal community to heterogeneity along forest–old field edges, *Landsc. Ecol.*, 1999, vol. 14, no. 4, pp. 355–367.
7. Pardini, R., Effects of forest fragmentation on small mammals in an Atlantic forest landscape, *Biodiv. Conserv.*, 2004, vol. 13, pp. 2567–2586.
8. Starčević, M., Mrakovčić, M., and Brigić, A., Effects of edges on small mammal communities in Dinaric beech–fir forest, *Abstr. VI Eur. Congr. of Mammalogy*, Paris, 2011, p. 57.
9. Kingston, S.R. and Morris, D.W., Voles looking for an edge: Habitat selection across forest ecotones, *Can. J. Zool.*, 2000, vol. 78, pp. 2174–2183.
10. Silva, M., Abundance, diversity and community structure of small mammals in forest fragments in Prince Edward Island National Park, Canada, *Can. J. Zool.*, 2001, vol. 79, pp. 2063–2071.
11. Anderson, C.S., Cady, A.B., and Meikle, D.B., Effects of vegetation structure and edge habitat on the density and distribution of white-footed mice (*Peromyscus leucopus*) in small and large forest patches, *Can. J. Zool.*, 2003, vol. 81, pp. 897–904.
12. Tallmon, D.A. and Mills, L.S., Edge effects and isolation: Red-backed voles revisited, *Conserv. Biol.*, 2004, vol. 18, no. 6, pp. 1658–1664.
13. Delattre, P., Morellet, N., Codreanu, P., et al., Influence of edge effects on common vole population abundance in an agricultural landscape of eastern France, *Acta Theriol.*, 2009, vol. 54, no. 1, pp. 51–60.
14. Wolf, M. and Batzli, G., Forest edge: High- or low-quality habitat for white-footed mice (*Peromyscus leucopus*)?, *Ecology*, 2004, vol. 85, no. 3, pp. 756–769.
15. Wilson, J.W., Stirnemann, R.L., Shaikh, Z.S., and Scantlebury, M., The response of small mammals to natural and human-altered edges associated with Afro-montane forests of South Africa, *For. Ecol. Manag.*, 2010, vol. 259, pp. 926–931.
16. Harris, L.D., Edge effects and conservation of biotic diversity, *Conserv. Biol.*, 1988, vol. 2, pp. 330–332.
17. Sibgatullin, R.Z., The 1995 catastrophic windfall and its consequences for forests of the Visim Biosphere Reserve, *Problemy zapovednogo dela: Mat-ly nauch. konf. (Problems of Nature Reserve Management: Abstr. Sci. Conf.)*, Yekaterinburg, 1996, pp. 99–101.
18. Kucheruk, V.V., Quantitative census of the main species of pest rodents and shrews, in *Metody ucheta chislennosti i geograficheskogo raspredeleniya nazemnykh pozvonochnykh (Methods for Evaluating the Abundance and Geographic Distribution of Terrestrial Vertebrates)*, Moscow, 1952, pp. 9–45.
19. Bujalska, G., Lukyanov, O.A., and Mieszkowska D., Determinants of local spatial distribution of numbers of red-backed vole island population, *Russ. J. Ecol.*, 1995, vol. 26, no. 1, pp. 35–45.
20. Lukyanova, L.E., Postcatastrophic successions of a rodent population, *Sib. Ekol. Zh.*, 2015, no. 6, pp. 832–841.
21. Lukyanova, L.E. and Bobretsov, A.V., Local abundance distribution of sympatric forest vole species under microhabitat conditions of destabilized and stable habitats, *Usp. Sovrem. Biol.*, 2008, vol. 128, no. 5, pp. 541–552.
22. Lukyanova, L.E. and Bobretsov, A.V., Microhabitat selection by the bank vole (*Clethrionomys glareolus* Schreber, 1780) under destabilized and stable habitat conditions, *Vestn. Tomsk. Gos. Univ., Ser. Biol.*, 2014, no. 4 (28), pp. 88–107.
23. Pires, A.S., Fernandez, F.A.S., Freitas, D.D., and Feliciano, B.R., Influence of edge and fire-induced changes on spatial distribution of small mammals in Brazilian Atlantic forest fragments, *Stud. Neotrop. Fauna Environ.*, 2005, vol. 40, no. 1, pp. 7–14.

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