

Assessment of Nonselective Elimination Effects in Rodent Communities by Methods of Geometric Morphometrics

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Received December 17, 2015

Abstract—Methods of geometric morphometrics and population phenogenetics have been used to evaluate morphogenetic rearrangements in two sympatric species of *Myodes* voles (*M. glareolus* Schreb. 1780 and *M. rutilus* Pall. 1779) from syntopic populations recovering after exposure to local “ecological vacuum” created as a result of rodent extermination in a natural focus of hemorrhagic fever in the southern taiga subzone of the Udmurt Republic. The model used in the study simulates the situation that arises upon nonselective elimination of rodent populations and communities in spring and their subsequent recovery. Analysis of variation in the size and shape of the mandible and in a complex of 30 nonmetric cranial characters has revealed similar (parallel) and species-specific morphogenetic and epigenetic changes occurring during the recovery of local rodent community. Species-specific differences in the pattern of change in the parameter characterizing within-group morphological disparity in the mandible shape (*MNND*) have been revealed between the dominant species (*M. glareolus*) and the subdominant species competing with it for territory (*M. rutilus*). Different reactions of close *Myodes* species in the course of filling the ecological vacuum are considered as a result of reduction in the level of competition for the subdominant species and a compensatory increase of morphological disparity in the dominant species under conditions of low density and incomplete composition of the community, in accordance with Chernov's (2005) ecological compensation principle.

Keywords: nonselective elimination, rodents, variation, Chernov's compensation principle, geometric morphometrics

DOI: 10.1134/S1067413616040159

The role of nonselective elimination as an evolutionary-ecological and population genetic factor potentially leading to rapid rearrangements in local population groups, based on the bottleneck mechanism or Mayr's (1968) founder principle, was widely discussed in terms of the synthetic theory of evolution in the 1970s (Shvarts, 1969; Timofeeff-Ressovsky et al., 1969; Nei et al., 1975; Bol'shakov and Vasil'ev, 1976). The corresponding concepts have regained relevance with the development of molecular genetic methods in phylogeography in the 21st century (Lee et al., 2015). However, the recent discovery of transgenerational epigenetic inheritance of DNA profiles altered under the effect of various stress factors and of related morphogenetic changes (Jablonka and Raz, 2009; Ledón-Rettig, 2013) suggests the possibility of reviewing these concepts in line with epigenetic views (Duncan et al., 2014).

Studies on the consequences of nonselective elimination and the mechanisms of recovery of populations and communities have become especially relevant in recent years, under conditions of rapid fragmentation of the earth's biotic cover under increasing anthropo-

genic impact (Salamin et al., 2010; Saul et al., 2013). There are grounds to consider that the factor of nonselective elimination also has a potential influence on the fate of newly formed local biotic communities (Saul and Jeschke, 2015). However, morphogenetic effects caused by nonselective elimination even at the level of taxocene—a fragment of the community comprising a taxonomically related set of sympatric species with similar biocenotic functions (Hutchinson, 1967; Nikolaev, 1977; Vasil'ev et al., 2013)—have not yet been properly studied. Methods of geometric morphometrics (Rohlf and Slice, 1990; Zelditch et al., 2004; Klingenberg, 2011) allow the manifestations of between-group variation to be interpreted morphogenetically (Klingenberg, 2011; Sheets and Zelditch, 2013) and thereby to approach the solution of the problem at issue. On the other hand, phenogenetic approaches based on evaluating the occurrence frequencies of nonmetric threshold skeletal characters provide the possibility of epigenetic and phenogenetic interpretation of morphological differences (Vasil'ev, 2005; Vasil'ev and Vasil'eva, 2009).

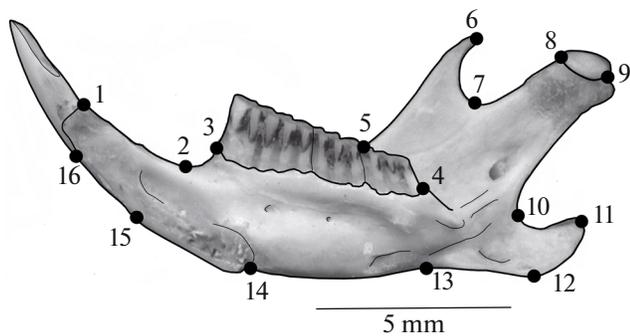


Fig. 1. Locations of landmarks (1–16) on the lingual side of the *M. glareolus* mandible.

In this context, it appears especially expedient to analyze population–cenotic responses to nonselective elimination in model sympatric species, including the assessment of epigenetic and morphogenetic rearrangements and changes in morphological disparity upon subsequent recovery of their local communities (taxocenes). As an adequate model for such a study, we have chosen the craniological series of two background species of *Myodes* voles trapped at two consecutive seasonal stages of population recovery of the initial taxocene of these rodents after their nonselective elimination in spring.

The purpose of this study was to use the methods of geometric morphometrics and population phenogenetics to analyze the morphogenetic and epigenetic consequences of local nonselective elimination on the model of cenopopulations of two sympatric rodent species—the bank vole *Myodes glareolus* Schreb. and the northern red-backed vole *M. rutilus* Pall.—recovering after rodent extermination performed in spring in a natural focus of hemorrhagic fever in the Udmurt Republic.

MATERIAL AND METHODS

The study was performed with craniological collections from the Zoological Museum of the Institute of Plant and Animal Ecology (Ural Branch, Russian Academy of Sciences) that consisted of samples from syntopic cenopopulations of the two model sympatric species (*M. glareolus* and *M. rutilus*) collected in similar southern taiga biotopes in Kiznerskii raion of the Udmurt Republic (endemic for hemorrhagic fever) in September 1974. To reduce the risk of human infection during timber harvesting in the focus of hemorrhagic fever, measures to exterminate rodents by poisoning with zinc phosphide baits were taken in May to early June 1974. As a result, an ecological vacuum was created in this region (Evdokimov, 1979), which was then filled due to the in-migration and reproduction of rodents from the surrounding areas. Thereafter, samples of rodents were collected by the above author in summer and autumn from control and rodenticide-

treated (impact) plots located in similar southern taiga forest biotopes. The samples had a relatively even age structure, consisting of young of the year (juvenile and senile individuals were excluded). The animals in summer samples of *M. glareolus* and *M. rutilus* from the control plot (110 and 18 ind., respectively) were not exposed to rodenticide treatment in spring, whereas the animals from the impact plot (36 and 30 ind.) represented the population of a naturally recovered rodent taxocene. The autumn samples of *M. glareolus* and *M. rutilus* voles from the control (36 and 12 ind.) and impact plots (46 and 58 ind., respectively) were taken at sites displaced for 400–500 m from the summer sampling sites to exclude the possible effect of summer sampling on comparisons made in autumn. Judging from the numbers of animals in catches, *M. glareolus* dominated in the control plot both in summer and in autumn, with *M. rutilus* being a subdominant. In the impact plot, the two species were codominant in the course of community recovery in summer, but *M. rutilus* in fact gained dominance by autumn; i.e., the situation resembling the replacement of dominant species was observed.

Methods of geometric morphometrics were used to study variation in the shape and size of the mandible as a structure directly connected with the food-procuring function and the cenotic role of the species. Electronic images of the right mandibular rami from the lingual side were digitized at 1200 dpi with the TPS software (Rohlf, 2013a, 2013b), and the arrangement of 16 homologous landmarks was analyzed to characterize variation in the mandible shape in both species (Fig. 1). Variation in the overall mandible size was evaluated indirectly, from the centroid size (CS) in pixels calculated as the square root from the sum of squared distances from the center of the image to each of the landmarks (Rohlf and Slice, 1990). The imposition procedure was performed by the method of generalized orthogonal least-squares Procrustes analysis (GPA), and the resulting Procrustes coordinates (characterizing variation in the shape of test objects) were used for between-group comparisons by means of canonical analysis. Based on the results of canonical analysis, the hierarchy of differences between the samples was evaluated using cluster analysis of the matrix of generalized Mahalanobis distances (D) by the UPGMA method.

Epigenetic differences between the samples were revealed by analyzing 30 homologous nonmetric cranial characters (Vasil'ev and Vasil'eva, 2009). Based on the frequencies of corresponding phenes, multidimensional ordination of the samples was performed by the method of principal coordinates (PCO), and the results of comparisons were generalized by cluster analysis (UPGMA) of principal coordinate values.

Morphological disparity within the groups was evaluated by analyzing the pattern of mean nearest neighbor distances ($MNND$), with standard errors,

between ordinates within the variation polygon (Hammer, 2009). The significance of pairwise differences in *MNND* between the control and impact samples was estimated by several statistical tests, namely, Mann–Whitney median *U*-test with Monte-Carlo correction at $n = 10000$, *t*-test for unequal sample variances, and permutation *t*-test at $n = 10000$.

Statistical analysis was performed using programs PAST 2.17c (Hammer et al., 2001) and MorphoJ 1.6d (Klingenberg, 2011).

RESULTS AND DISCUSSION

Initially, digitization of mandible images and landmark placement were repeated twice, and comparison of the results did not reveal any bias in estimates of mandible shape depending on operator errors or animal sex: the differences in both cases were statistically nonsignificant. Therefore, the male and female samples were pooled for subsequent analysis, and the images were digitized only once.

With respect to the centroid size (CS) indirectly characterizing the size of the mandible in pixels, the differences between the control and impact samples of both vole species proved to be nonsignificant in most cases. Statistical significance was observed only for the seasonal increase in the mandible size in *M. glareolus* voles from the impact plot (574.59 ± 1.85 in autumn vs. 564.66 ± 2.14 in summer; $t = 3.50$, $df = 68$, $p < 0.01$), unlike in those from the control plot (569.63 ± 2.17 vs. 564.21 ± 1.73 ; $t = 1.95$, $df = 78$, $p > 0.05$).

Comparisons of the shape of mandibular rami in all summer and autumn samples from syntopic *M. glareolus* and *M. rutilus* populations of the control and impact plots were made using canonical analysis of Procrustes coordinates (Figs. 2, 3). Differences in the mandible shape along the axes of the first five canonical variables proved to be statistically significant, with the first variable accounting for 61.2%, and the first three variables, for 90.1% of between-group variance (Table 1). Figure 2 shows between-group differences along the axes of the first and third canonical variables. Judging from the positions of centroids (with regard to standard errors), interspecific differences characterizing trophic specialization of the two vole species manifested themselves along the first axis; in this case, the differences were expected and commonplace. Along the third axis (13.4% of between-group variance), distinct differences were revealed between the control and impact samples, which proved to be of similar direction in both species. The latter also follows from similar changes in the signs of sample centroids, which are positive or close to zero in control samples but negative in all impact samples (see Table 1). In Fig. 2, the centroids of control and impact samples (without discrimination by species) are combined into two polygons of between-group variation located in the upper and lower parts of the plot, respectively. The

shaded contours of the mandible at the periphery of the plot characterize the extreme states of its shape along the corresponding canonical axes. In both species, the mandible shape in both summer and autumn samples from the impact plot characteristically differs from that in samples from the control plot: the diastema is shorter, the coronoid and condylar processes are displaced aborally, and the relative tooth row length is greater.

In Fig. 3, the results of canonical analysis of between-group variation in the mandible shape are presented in the plane of the second and third canonical variable axes (CV2 and CV3). It can be seen that seasonal variation manifested itself along the second axis (15.5% of the total variance): the centroids of summer samples of both species are located on the left, and the centroids of autumn samples, on the right, with differences between the control and impact samples in either species being manifested more strongly in summer than in autumn. It is noteworthy that almost parallel changes in the mandible shape are observed in summer samples of both species and that the differences in the mandible shape between the impact and control samples are greater in *M. glareolus* than in *M. rutilus*.

An interesting fact is that the interaction of factors “season” and “nonselective elimination” is observed along the CV2 and CV3 axes: the directions of between-group differences in the mandible shape between the centroids of control and impact samples (indicated by arrows) are not the same in summer and in autumn. In both species, these arrows in summer point down and left, whereas in autumn they point down and right. The differences in the mandible shape along the second and third axes between the control and impact samples decrease by autumn in both species. Changes in the shape of shaded mandible contours along the second axes indicate that, in general, the mandible in *M. glareolus* and *M. rutilus* voles from autumn samples was generally more slender, with the diastema and tooth row being longer than in animals trapped in summer. Thus, both species demonstrate interrelated changes in the mandible shape depending on the season and on the effect of nonselective elimination.

To evaluate the hierarchy of between-group differences in the mandible shape, we performed cluster analysis (UPGMA) of the matrix of generalized Mahalanobis distances (*D*) between the samples of *M. glareolus* and *M. rutilus* voles using the chord distance metric (Fig. 4a). This metric was chosen because it allowed us to obtain the highest cophenetic correlation in cluster analysis (Coph $R = 0.989$), compared to 18 other best-known metrics, including the Euclidean metric.

The resulting dendrogram shows distinct segregation by the mandible shape between the samples of *M. glareolus* and *M. rutilus* voles, which form two

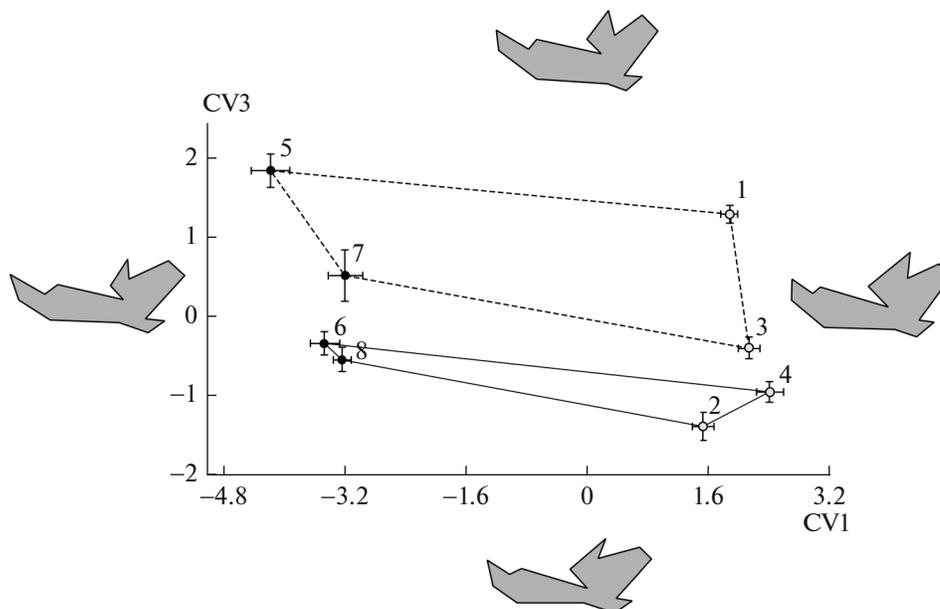


Fig. 2. Results of canonical analysis of Procrustes coordinates characterizing variation in the shape of the mandible in control (odd numbers) and impact (even numbers) samples of (1–4) *M. glareolus* and (5–8) *M. rutilus* voles (1, 2, 5, 6) in summer and (3, 4, 7, 8) in autumn along the first and third canonical variables (CV1 and CV3). Shaded contours of the mandibles correspond to the maximum and minimum values on the canonical axes. Dashed and solid lines delimit the polygons of between-group variation for the centroids of control and impact samples, respectively (with standard errors, SE).

independent clusters. However, the cluster of *M. rutilus* is divided into two seasonal subclusters of summer (5, 6) and autumn samples (7, 8), whereas in *M. glareolus* only the autumn subcluster is segregated in such a way. The hierarchy of summer samples in the structure of the *M. glareolus* cluster is different: the impact sample (2) proved to be basal relative to the control sample (1), with the latter, in turn, being hierarchically connected with the subcluster of autumn samples (3, 4). The level of between-group differences conditioned by nonselective elimination in the impact *M. glareolus* sample is slightly higher than the level of seasonal morphological differences in *M. rutilus*. Therefore, the overall morphogenetic effect of nonselective elimination is stronger in the former than in the latter species.

Figure 4b shows the results of UPGMA cluster analysis of principal coordinates (PCO) matrix calculated from the frequencies of 30 nonmetric cranial characters in the samples of *M. glareolus* and *M. rutilus* voles. The dendrogram was also plotted using the chord distance metric, which was chosen because it allowed us to obtain the highest cophenetic correlation (Coph $R = 0.94$), compared to 18 other metrics. Its structure is more ordered than that of the dendrogram based on the mandible shape (see Fig. 4a). As in the previous case, there are two species clusters, but each of them is divided into two seasonal subclusters that, in turn, comprise the corresponding control and impact samples. Thus, only the lowest hierarchical level of clustering reflects the effects of nonselective elimination.

Judging from the structure of this dendrogram, the level of morphological differences between summer samples from the control and impact populations of *M. glareolus* corresponds to the level of seasonal differences in *M. rutilus* and is also markedly higher than the level of differences between summer samples from the control and impact populations of the latter species. Thus, the amplitude of differences arising under the effect of nonselective elimination either in the mandible shape or in the complex of nonmetric cranial characters is greater in *M. glareolus* than in *M. rutilus*. Since the frequency of nonmetric threshold characters reflects epigenetic and phenogenetic differences between population groups (Berry and Searle, 1963; Vasil'ev, 2005; Vasil'ev and Vasil'eva, 2009), it may be concluded that the epigenetic system of *M. glareolus* has proved to be more responsive to the effect of nonselective elimination and abrupt rearrangement of the community structure.

Another aspect of this study concerns the assessment of within-group morphological disparity in the mandible shape based on calculating *MNND*. Calculations were made using the values of the second and third canonical variables (CV2 and CV3), which most closely reflect the effects of factors “season and “nonselective elimination.” Thus, Spearman's coefficient of rank correlation between CV3 and factor “nonselective elimination” was $R_{Sp} = 0.68$ ($p < 0.0001$) in *M. glareolus* and $R_{Sp} = 0.57$ ($p < 0.0001$) in *M. rutilus*, and that between CV2 and factor season was $R_{Sp} = 0.67$ ($p < 0.0001$) and $R_{Sp} = 0.80$ ($p < 0.0001$), respec-

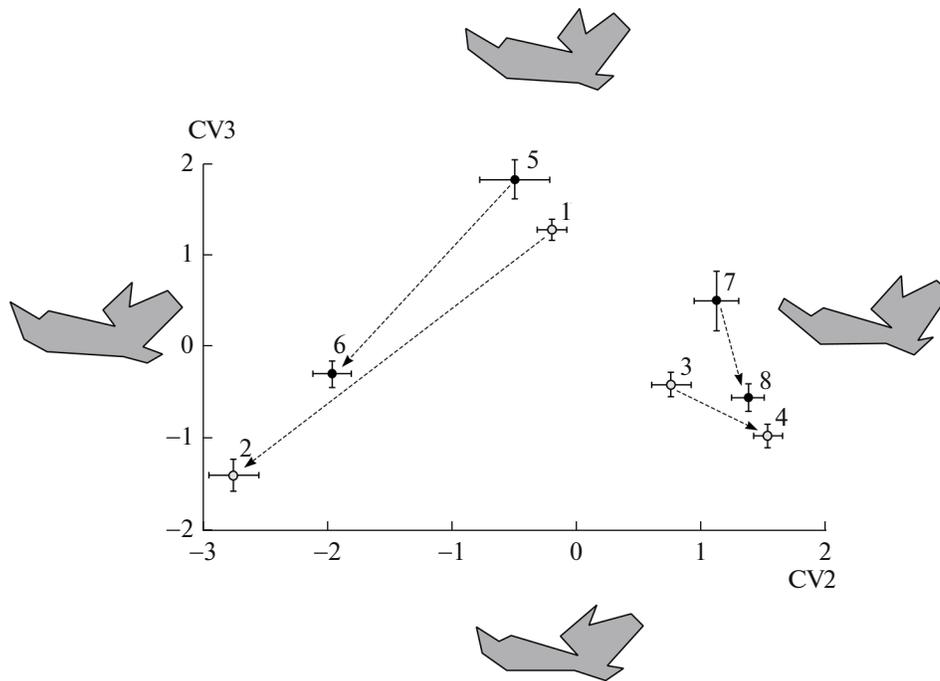


Fig. 3. Results of canonical analysis of Procrustes coordinates characterizing variation in the shape of the mandible in control and impact samples of *M. glareolus* and *M. rutilus* voles in summer and in autumn along the second and third canonical variables (CV2 and CV3). The samples are numbered as in Fig. 2. Arrows show the directions of change in the shape of the mandible in impact compared to control samples.

tively. A significant correlation was also revealed between CV3 and factor “season”: $R_{Sp} = 0.46$ ($p < 0.0001$) in *M. glareolus* and $R_{Sp} = 0.23$ ($p < 0.0141$) in *M. rutilus*.

Calculations of *MNND* for each sample were made in two ways: based on canonical coordinates CV2 and CV3 for all individuals (the number of observations in this case could differ between the samples) or on the standardized (minimum) sample sizes obtained after scaling down by the rarefaction procedure. The results were largely similar but not identical ($R_{Sp} = 0.88$, $p = 0.007$). Therefore, we present data on between-group comparisons of *MNND* as calculated in either way (Fig. 5). It can be seen that the index of morphological disparity in *M. glareolus* from the impact plot significantly increases in midsummer, at the first stage of rodent community recovery after nonselective elimination, compared to the control (see Table 2). Conversely, the index of morphological disparity in *M. rutilus* significantly decreases at this stage (Fig. 5). The significance of pairwise between-group differences in *MNND* was verified by different statistical tests, which yielded concordant results (Table 2).

In autumn, *MNND* values in *M. glareolus* from the impact plot decrease and approach the control level, while these values in *M. rutilus* remain significantly higher in the control than in the impact sample (Fig. 5, Table 2).

Since *MNND* is a measure characterizing the scattering of ordinates of the objects within the variation

polygon, it indirectly reflects the degree of disparity in the morphogenetic trajectories of individuals in the sample (Hammer, 2009; Sheets and Zelditch, 2013; Vasil’ev et al., 2013). An increase in *MNND* value indicates that the ordinates increasingly deviate from each other in the morphospace. Therefore, the results presented above may be interpreted as follows. At the first stage of rodent community recovery and reproduction in the vacant territory (in midsummer), the *M. glareolus* cenopopulation is in the situation where the dominant species is no longer exposed to the pressure of rodent population density, unlike in the control plot. Conditions for the newly formed impact cenopopulation at this stage correspond to the typical population-ecological state of the species at its extremely low abundance and almost complete absence of other species (mono- or oligospecific community).

According to Chernov’s (2005) ecological compensation principle, when the abundance of a taxocene/community is low and its composition is impoverished, some of its constituent species (the fittest ones) should show a compensatory increase in abundance and variability; this allows the taxocene to maintain its cenotic function and stability on account of a few species. Indeed, *M. glareolus* voles from the impact plot were characterized not only by marked changes in the mandible shape but also by a sharp increase in its morphological disparity.

Table 1. Results of canonical analysis of Procrustes coordinates characterizing variation in the shape of the mandible in *M. glareolus* and *M. rutilus* voles from control and impact cenopopulations at the summer and autumn stages of community recovery

Samples and parameters	Canonical variables		
	CV1	CV2	CV3
Centroids of <i>M. glareolus</i> samples			
Control, summer	1.87 ± 0.09	-0.22 ± 0.11	1.28 ± 0.10
Impact, summer	1.53 ± 0.14	-2.75 ± 0.19	-1.40 ± 0.17
Control, autumn	2.13 ± 0.13	0.73 ± 0.16	-0.42 ± 0.13
Impact, autumn	2.40 ± 0.18	1.50 ± 0.125	-0.97 ± 0.13
Centroids of <i>M. rutilus</i> samples			
Control, summer	-4.17 ± 0.26	-0.53 ± 0.27	1.83 ± 0.21
Impact, summer	-3.46 ± 0.21	-1.94 ± 0.16	-0.34 ± 0.14
Control, autumn	-3.19 ± 0.23	1.09 ± 0.17	0.51 ± 0.34
Impact, autumn	-3.23 ± 0.13	1.34 ± 0.12	-0.55 ± 0.15
Eigenvalue	5.535	1.402	1.212
Proportion of variance, %	61.2	15.5	13.4
Wilks' lambda	0.0077	0.0595	0.1729
χ^2 test	1599.9	926.5	576.6
Number of degrees of freedom	175	144	115
Significance level	$p < 0.0001$	$p < 0.0001$	$p < 0.0001$

Table 2. Results of statistical evaluation of differences in *MNND* between the pairs of control and impact samples of *M. glareolus* and *M. rutilus* voles (1) in summer and (2) in autumn (sample sizes were standardized by a random rarefaction procedure)

Samples compared	Mann–Whitney <i>U</i> test	<i>z</i>	<i>p</i>	Monte-Carlo test (<i>p</i>)	<i>t</i> -test	<i>p</i>	Permutation <i>t</i> -test (<i>p</i>)
<i>M. glareolus</i> :							
Control (1) – Impact (1)	85	-2.421	0.016	0.0151	2.04	0.049	0.0486
Control (2) – Impact (2)	152	-0.301	0.764	0.7648	0.05	0.960	0.9606
<i>M. rutilus</i> :							
Control (1) – Impact (1)	88	-2.326	0.020	0.0186	2.23	0.033	0.0323
Control (2) – Impact (2)	45	-2.606	0.009	0.0075	3.01	0.008	0.0028

Such a morphogenetic response of the dominant species can be regarded as a compensatory phenomenon related to the necessity for modifying trophic functions in the disturbed community with an impoverished species composition and to increasing variation in the shape of the mandible as a food-procuring organ allowing the species to perform its biocenotic role. In other words, a directional compensatory change in morphogenesis takes place under new conditions, which is a modification of development that the species has acquired in response to a given natural situation that has repeatedly occurred during the period of species' existence. The increasing disparity of morphogenetic trajectories in *M. glareolus* at the

first stage of cenopopulation recovery (indicated by high *MNND* values) is evidence for a kind of morphogenetic stress in migrant animals upon transition from the population state in the control plot (a low morphological disparity of the dominant species in the community with complete species composition) to a different state characteristic of impact (vacant) plot. In autumn, the morphological disparity of the species in both plots decreases and becomes almost equal, which indirectly indicates the alleviation of morphogenetic stress due to normalization of developmental conditions. Nevertheless, the autumn *MNND* values in the control plot are significantly higher than the summer values ($t = 3.76$, $df = 144$, $p < 0.01$) and approach

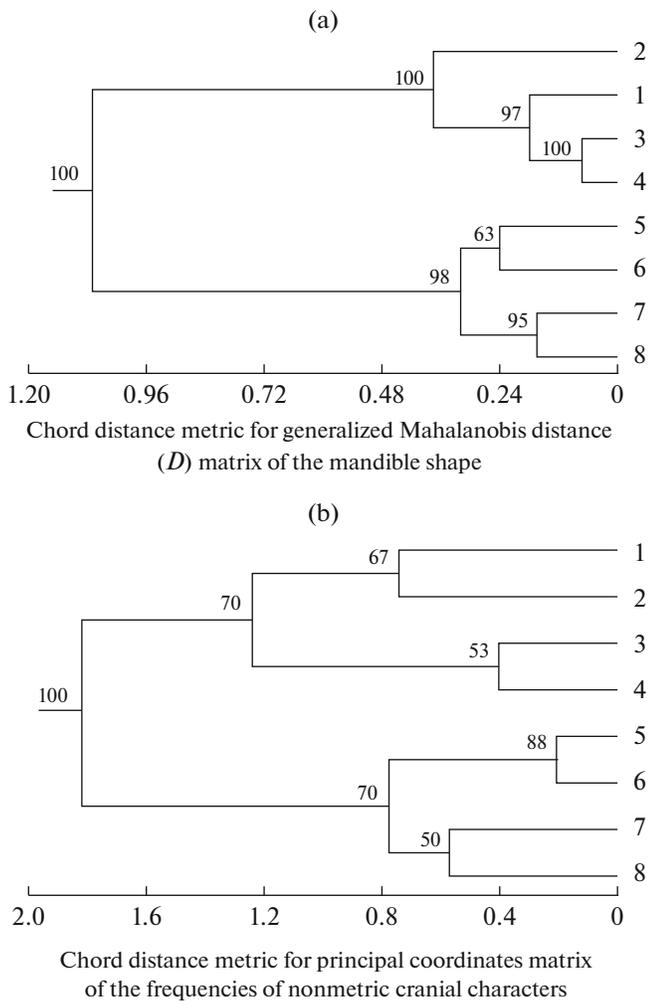


Fig. 4. Results of UPGMA cluster analysis of a generalized Mahalanobis distance matrix based on canonical analysis of (a) Procrustes coordinates of the mandible shape and (b) principal coordinates (PCO) matrix calculated from the frequencies of 30 nonmetric cranial characters in *M. glareolus* and *M. rutilus* voles sampled from the control and impact cenopopulations in different seasons. The samples (1–8) are numbered as in Fig. 2.

those in the impact plot ($t = 0.41$; $df = 80$; $p > 0.05$). This can be explained by directional seasonal rearrangements of morphogenesis and reproductive system in *M. glareolus* young of the year and consequent increase of developmental stress.

Myodes rutilus in the complete, undisturbed community of the control plot is a typical subdominant species that is much less abundant than *M. glareolus*, being obviously suppressed by the dominant species. A similar situation of competitive territorial relationships between these vole species at high abundance of one of them was previously described by Koshkina et al. (1972) in a different region. Therefore, the markedly higher morphological disparity manifested in the summer control sample of *M. rutilus* voles (Fig. 5)

should be attributed to morphogenetic stress resulting from competition with dominant *M. glareolus*. In contrast, morphological disparity in *M. rutilus* at the same stage of community recovery but in the impact (vacant) plot decreases abruptly (Fig. 5), which appears to be due to a lower level of competition, compared to the control plot.

The effect of significant decrease in *MNND* values calculated in both variants for *M. rutilus* from the impact plot is also observed at the second (autumn) stage of community recovery (Fig. 5). Therefore, it is highly probable that this decrease in the impact cenopopulation of *M. rutilus* is explained by alleviation of morphogenetic stress under conditions of relatively vacant area and low territorial competition with *M. glareolus*. The response to this situation is manifested as an increase in the abundance of *M. rutilus* in the impact plot, where, as noted above, this species formally becomes dominant in autumn.

CONCLUSIONS

The results of this study show that the two sympatric vole species, *M. glareolus* and *M. rutilus*, in the southern taiga subzone of the Udmurt Republic show similar morphogenetic and epigenetic changes in the course of recovery of their cenopopulations in the impact area after nonselective elimination. Changes in the mandible shape in the impact samples of both species at the first stage of community recovery have approximately the same direction and are almost parallel. Morphological differences associated with the factor of nonselective elimination are comparable in amplitude to those depending on the seasonal factor but have a different direction. At the second (autumn) stage of recovery, both species also show an almost unidirectional seasonal change in the mandible shape, and morphological differences between animals from the control and impact cenopopulations become smaller. Changes in the epigenetic system marked by the frequencies of 30 nonmetric cranial characters have a similar pattern, leading to similarity in the hierarchy of interspecific, seasonal, and post-elimination effects. Thus, changes in the mandible shape and frequencies of nonmetric cranial characters in both sympatric species under the effect of nonselective elimination and seasonal factor have largely similar pattern and direction, which in our opinion reflect the high coevolutionary potential of these species (Vasil'ev et al., 2013; Bol'shakov et al., 2015).

However, the dynamics of change in mandible morphological disparity differs between the species both at the first and second stages of rodent taxocene recovery in the impact plot. The dominant species (*M. glareolus*) in this plot (cleared of other rodent species) is exposed to stress caused by the necessity of transition from the morphogenetic state corresponding to the epigenetic tuning of the developmental process under conditions of high population density and

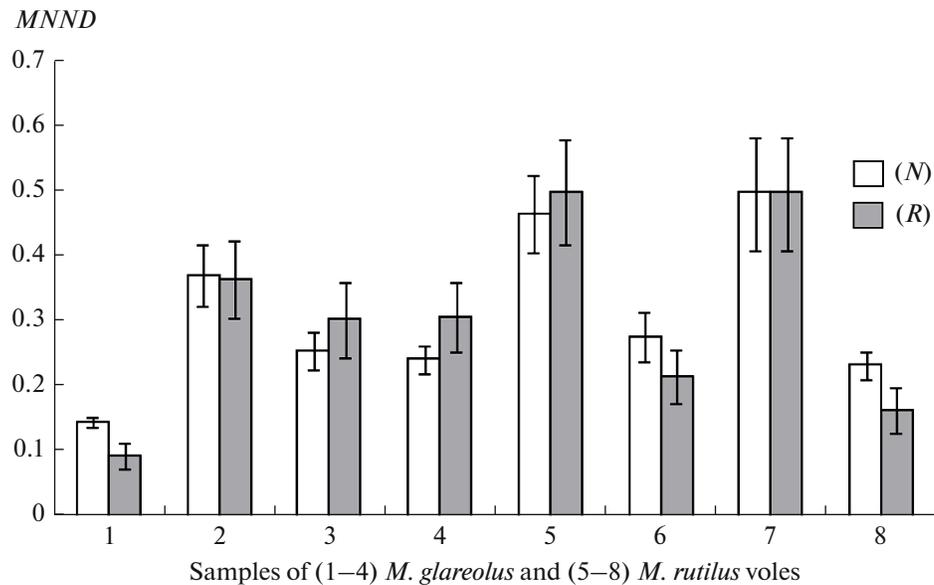


Fig. 5. Comparison of mean nearest-neighbor distances ($MNND \pm SE$) in samples of *M. glareolus* and *M. rutilus* voles taken from the control and impact cenopopulations in different seasons as calculated based on the total sample sizes (N) and on the standardized (minimum) sample sizes (R) obtained after scaling down by the rarefaction procedure. The samples are numbered as in Fig. 2.

complete composition of the rodent taxocene to the state characteristic of disturbed community with extremely low density and mono- or oligospecific composition. We consider that, in accordance with the Chernov's (2005) ecological compensation principle, the dominant species increases its abundance and morphological disparity in the impact area to provide for population and cenotic stability, performing the functions of other species and counterbalancing their absence in the biotic community. On the other hand, developmental conditions for the impact cenopopulation of *M. rutilus*, the subdominant species, become more favorable as it colonizes the vacant area, since it is no longer suppressed by *M. glareolus*. As a consequence, the abundance of the species sharply increases, and decrease in general stress level in the new favorable environment leads to reduced manifestation of morphological disparity. Thus, the impact cenopopulation of *M. rutilus* recovers at a higher rate, and this species starts to behave as dominant by autumn. The level of morphological disparity in the control cenopopulation of this species, which is still exposed to stress from dominant *M. glareolus*, remains high in both seasons. Therefore, the consequences of nonselective elimination in the given rodent community include not only the local replacement of dominant species in autumn but also normalization of its morphogenesis.

Different reactions of close *Myodes* species in the course of filling the ecological vacuum are considered as a result of reduction in the level of competition for the subdominant species (*M. rutilus*) and a compensatory

increase of morphological disparity under conditions of low density in the dominant species (*M. glareolus*).

The proposed population-cenotic approach to the study of coupled morphological variation and disparity in cenopopulations of sympatric species is based on the combination of methods of geometric morphometrics and population phenogenetics. It provides new possibilities for interpreting population phenomena in the context of analysis of morphogenetic and epigenetic changes in the course of research in the field of population and evolutionary ecology.

ACKNOWLEDGMENTS

The authors are grateful to the Zoological Museum of Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, for the collections provided for analysis.

This study was supported by the program "Living Nature" no. 12 of the Ural Branch, Russian Academy of Sciences (project no. 15-12-4-25) and the Russian Foundation for Basic Research (project no. 16-04-01831a).

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Translated by N. Gorgolyuk