The Concept of Morphoniche in Evolutionary Ecology

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Abstract—The evolutionary-ecological concept of morphoniche is proposed where the morphoniche is regarded as part of the multidimensional ecological niche that characterizes the limits of phenotypic plasticity of individuals, cenopopulations, and taxocenes in the morphospace. The phenome—a morphofunctional "shell" of an individual—is the basic part of its ecological niche and a multifunctional "biological tool" allowing the individual to perform its generative, trophic, and environment-forming functions in the population and community. The phenome characterizes the morphophysiological habitus of an individual and serves as its personal morphoniche. Geometric morphometrics makes it possible to bring into correlation the locations of individual morphoniches in the common morphospace and evaluate coupled morphogenetic reactions of individuals to changes in aut- and synecological factors. The epigenetic system of a population parameterizes the potential morphospace, delimiting the fan of possible invariants of morphogenesis. The volume of population morphospace reflects morphogenetic reactions of a population to the range of local ecological factors and allows estimation of its realized morphoniche. An analysis of realized morphoniches over many years provides an estimate of the potential population morphoniche. Part of the community (taxocene) comprising cenopopulations of closely related sympatric species provides a model of the cenotic morphoniche. The ratios between the volumes of realized and potential morphoniches make it possible to evaluate the adaptive modification potential and optimality index of the realized morphoniches of individuals, cenopopulations, and taxocenes, the limits of their phenotypic plasticity, and the risk of an evolutionary-ecological crisis.

Keyword: evolutionary ecology, ecological niche, phenome, population, variation, morphospace, geometric morphometrics

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By the middle of the 21st century, evolutionary ecology may occupy a central position in biology due to the necessity of predicting rapid transformations of the biota under the impact of anthropogenic, climatogenic, and biotic changes in the environment [1, 2]. It is highly probable that regional and global biocenotic crises will develop by the end of the century against the background of general reduction of biodiversity [3–5]. Therefore, the need is discussed to revise the evolutionary-ecological views based on the concept of extended evolutionary synthesis (EES) that emerged at the beginning of the 21st century [6–8]. The EES concept is based on a new understanding of the role of epigenetic variation and heredity—the transgenerational inheritance of stress-induced epigenetic changes associated with the process of development—in rapid transformations of morphogenesis [9, 10]. This concept is complemented by the niche construction theory (NCT) [11], which claims that organisms can actively change the conditions of the individual and group environment (in particular, by building nests, trapping webs, burrows, and cocoons) and modify morphogenesis, individual behavior, and envi-

ronment-forming processes. This has influence on the living conditions and development of subsequent generations and on other species, changing the vector and degree of selection pressure, with "niche construction" turning into a special evolutionary-ecological factor [11].

A new epigenetic interpretation of the mechanisms of evolution in the EES context allows rapid evolutionary-ecological rearrangements within relatively short historical times [8–10, 12], which provides the possibility to reveal and predict microevolutionary and other rapid morphogenetic changes in the components of the biota. A key aspect in predicting the expected cenotic crisis phenomena is the development of new approaches to quantitative assessment of ecological niches and methodology for their monitoring. Such monitoring should be based on determining the limits of phenotypic plasticity [13, 14] and stability hierarchical biosystems under altered conditions.

Methods of geometric morphometrics [15–18] make it possible to separately analyze variation in the size and shape of objects and allow a morphogenetic interpretation of the observed differences [17, 19, 20].

These methods are suitable for studying coupled morphogenetic variation of differently sized species in a common morphospace and evaluating their coupled responses to changes in environmental factors [20]. In my opinion, a probable approach to such a study should involve the concept of morphological niche, or morphoniche (MN).

In this study, an attempt is made to use the methods of geometric morphometrics for developing an evolutionary-ecological concept of morphoniche as part of the multidimensional ecological niche that characterizes the limits of phenotypic plasticity of individuals, cenopopulations, and communities (taxocenes). Special attention is given to the development of general methodology and special methods for assessing the ratios of morphospaces occupied by the morphoniches of individuals, cenopopulations, and taxocenes and their changes under different conditions.

ECOLOGICAL NICHE
AND ITS MORPHOFUNCTIONAL
CHARACTERISTICS

Well known are the classical studies by Joseph Grinnell [21], who proposed the concept of ecological niche (EN) as a habitat, and Charles Elton, who regarded EN as the functional potential of a species [22]. George Hutchinson [3] formulated the concept of multidimensional niche of a species that characterizes the limits of its tolerance for factors (conditions and resources) of the environment. From this standpoint, the set of environmental requirements of the species applies to the combination of all conditions and resources necessary for its survival and existence, and the results of multidimensional ordination of the states of an individual or a population in the space of all necessary resources and conditions may be represented as a hypervolume in a hyperspace. Hutchinson also developed the concepts of fundamental and realized niches [24]. In his understanding, the fundamental niche is the maximum possible hypervolume characterizing the entire complex of the states of factors limiting the survival of individuals of a given species, and the realized niche is a smaller (or, theoretically, equal) hypervolume occupied within the fundamental niche under given conditions of the biotic environment. On this basis, the maximum possible realization of EN is sometimes referred to as the potential niche [25]. Apparently, the study of a community should involve analysis of the ENs of all its constituent species in the common "niche space" [25, 26].

Traditionally, EN is a category conditioned by the species itself rather than by characteristics of its habitat conditions [27, 28]. Vacant niches do not exist; there are only vacant resources that the species can utilize upon developing corresponding adaptations, i.e., realized niches. When a species disappears (goes extinct), its niche in the community disappears as well. More-over, cenopopulations of syntopic species in a biocenosis are "offered" ecological licenses (ELs), i.e., potentially available habitats with required conditions and resources that may be vacant or partially utilized by other species. The term "ecological license" was introduced by Günther [29], but its more meaningful interpretation was given by Levchenko and Starobogatov [27, 30]. This helped to resolve the collision of terms upon substitution "potentially vacant niche" by "vacant license." Levchenko interpretes EL as a vacant position for a species [27], while Odum compares the fundamental niche of a species to its "profession" in the ecosystem [26]. The EL is a potentially available (vacant) part of the environment that may be occupied by the EN of a species. The concept of EL is principally important for the theory of EN but unfortunately receive scant attention from ecologists and evolutionists [31].

One of the dogmas in community ecology is the competitive exclusion principle by Gause [32] and Park [33], according to which two ecologically close competitor species cannot coexist for a long time in the same place (biotope or locality). This principle accounts for the main mechanism of niche differentiation that alleviates intra- and interspecific competition. Studies on insular communities provided a basis for formulating the principles of competitive release (niche widening when a species is released from interspecific competition) [34, 35], limiting similarity, species sorting, and species packing [36, 37]. The concept of EN is central in community ecology, being closely related to the problem of competition and its role in organization of communities and the mechanisms (rules) of their assemblage, including the influence of ecological filtering [14, 37, 38]. This concept is still a subject of discussion, in particular, between representatives of two opposing schools of thought: determinists [39, 40] and stochasticists [41−43]. The discussion has led to revision of methodological approaches, the use of null models in a biologically correct form [42, 43], correction of certain rules of community assemblage [42−44], and introduction of multivariate statistical methods [31, 45, 46] in testing the hypotheses about the processes of community assemblage, evaluation of competitive relationships [47], and niche differentiation and overlap [48, 49]. The diversity of late 20th century views on EN, the role of competition in community organization and structuring, and the possibilities of using morphological methods for characterizing EN are considered in reviews [50−52].

Analysis of the processes of community assemblage and formation of species ENs is usually performed taking into account the ratio between competition and ecological or habitat filtering of the species [38, 53]. The problems of intra- and interspecific competition and its role in community assemblage and EN formation are considered in a number of studies [e.g., 35, 51, 52, 54−56].

In this study, it is important to discuss views on the possibility of using morphological and morphofunctional approaches for characterizing and comparing ENs. Such an idea was long ago conceived by Grinnell [57], who regarded morphological traits as certain morphofunctional indicators allowing indirect characterization of similarity between the ENs of the compared species.

MacArthur [58] concludes that the terms "niche" and "phenotype" are largely analogous to each other: they contain an indefinitely large number of variables (including those common to both of them) and are useful for comparisons between individuals and species. Consistent with this idea is a specific approach to comparison between niches based on morphological traits. Van Valen [34] was among the first to implement this approach by using bill length and width as functional parameters for estimating trophic niche width (NW) in six bird species. Comparing variation in these parameters on the islands and on the mainland, he revealed a direct correlation between NW and the range of morphological variation. This finding proved to be promising and useful, although some conclusions of the author have been questioned on a statistical basis [see 50–52].

Some approaches to estimating NW are described in the book by Giller [59]. A common practice is to use mean square deviation or the distribution range of values of a certain resource parameter, i.e., a measure of its variation in a given species [60]. To estimate niche overlap between two species, it was initially suggested to use the ratio of the difference between the mean values of the corresponding distributions to the generalized average value of within-group mean square deviations [see 59]. Other methods for estimating NW and niche overlap based on a set of resources have also been proposed [61–64]. They are applicable to pairwise comparisons of species by certain resource parameters, but methods for multivariate comparisons should be different [65].

Hutchinson [66] proposed an empirical rule for the guilds of taxonomically close species (in our terms, taxocenes) according to which the ratio of average sizes of the body or feeding organs (e.g., the bill in birds) between similarly sized sympatric species is about 1.28–1.30 (Hutchinson's rule, or Hutchinson's ratio). This ratio was interpreted as a result of species sorting and selection out of the regional species pool, with the observed size shift (variation) in sympatric species contributing to alleviation of interspecific competition. However, the regularity of the 1.3 ratio was not confirmed when Hutchinson's data were recalculated using a null model [43]. Nevertheless, the shift in dimensional parameters between the species is a real fact that has been confirmed in a number of studies [see 50, 67].

Variation in morphological and morphofunctional characteristics is used to assess the structuring of communities and analyze the relationship between the factors of competition and habitat filtering of species within the framework of a new direction of ecological research referred to as trait-based ecology (= ecomorphology) [68–70] as well as functional ecology [71, 72]. It has been proposed to use the ratio of variances in morphological traits at four hierarchical levels—individual, population, cenotic, and regional—to evaluate the relative contributions of external and internal filters to the organization and functioning of populations and communities [14].

Another approach deals with estimation of the hypervolume of species' spaces modeling ENs and their arrangement in a multidimensional space [38, 73]. There also are many methods and indices for assessing functional diversity [74, 75]. For this purpose, it is promising to use measures of within- and between-group morphological disparity compared by variance- and distance-based methods [76–78].

One more approach is based on analyzing the ratio between phylogenetic diversity and morphological disparity [79, 80], which makes to possible to relate the functional properties of communities to their evolutionary establishment. The revision of some evolutionary ideas in the context of epigenetic theory of evolution (ETE) and the concept of extended evolutionary synthesis (EES) makes it necessary to reconsider previous interpretations in trait-based ecology (ecomorphology) and give new interpretation to rapid evolutionary ecological transformations in the light of recent discoveries in epigenetic soft heredity [9, 10, 12].

Hunchinson [81] distinguishes two variants of EN segregation based on species adaptation: to regional abiotic conditions—scenopoetic variables, which are not related to each other and not responsible for interspecific competition, and to local biotic conditions—bionomic variables, which may stimulate competitive relationships. In the field of geographic modeling and mapping of niches [31, 82], conditions of the first group may be used for modeling the "Grinnellian niche," characterizing the habitat environment. The second group of local functional resources (trophic and other biotic variables) should be taken into account when modeling the local "Eltonian niche." The data obtained by using GIS techniques and methods of geographic EN modeling provide an idea that the models of these niches have different spatial scales [31]. Methods developed for modeling the potential spatial distribution of species ENs, such as ENFA [83] and Maxent [84]), make it possible to perform species distribution modeling (SDM) [83] and ecological niche modeling (ENM) [31]. Similar approaches, referred to as ecometrics [85] and functional biogeography [80], have been developed for geographic modeling of changes in the morphospace for certain taxonomic species groups and metacommunities.

Even this brief review shows how complex and contradictory is the range of problems related to the gen-

eral theory of EN, evaluation of the relationship between competition and species filtering from the regional pool, and the rules and mechanisms of community assemblage. The data presented above give grounds for using the morphological disparity of populations, species, and taxocenes for indirect characterization of ENs [86].

THE PHENOME AS A PRIMARY ECOLOGICAL NICHE AND AN INDIVIDUAL MORPHONICHE

As shown above, characterization of EN and analysis of community organization are often performed using functional morphological and morphophysiological traits [34, 46, 52, 80]. They include total body size and mass, dimensions of feeding morphostructures and locomotor organs, the size and shape of leaves and other plant organs, and also the absolute and relative masses of certain internal organs as morphophysiological indicators [87]. The use of such traits facilitates interpretation of differences in EN between the compared groups. Hence, it is necessary to define the morphofunctional component of EN, or the morphoniche.

Neither the term "morphoniche" nor the use of morphological traits for comparing ecological niches is a novelty. The idea of using morphological volume as part of the morphospace occupied by the ordinates of individuals or centroids of species has long been known [45, 46, 78]. The possibility to compare the morphological volumes of samples (morphological analogs of ENs) in the morphospace based on different methods for estimating morphological disparity has been demonstrated in studies by Foote [76], Erwin [77], and Pavlinov [78]. Both morphoniches and "functioniches" of species are considered by Chaikovskii [88]. Ozerskii [89] associates morphoniche with the ecological subniche of a certain morph in populations. The term "morphological niche" is mentioned in the study by Puzachenko and Abramov [90].

Barnosky [91] and subsequently Fontaneto et al. [92] have used the term "morphoscape" to designate the variation polygon/ellipsoid of ordinates (2D, 3D convex hull) of a local community in the morphospace in characterizing the generalized morphological component of biodiversity. New approaches to multidimensional characterization of ENs as hypervolumes [38, 93, 94] are in line with the studies by Ricklefs and his colleagues [45, 46, 86] and develop principally novel methods for estimating the volumes of ENs within the convex hull and measures of their overlap in the hyperspace with regard to empty spaces between ordinates [73]. This is evidence for the necessity to terminologically define the morphological aspect of EN in the morphospace, from individual to community, using a taxon-free approach [14, 95].

Thus, the term "morphoniche" is not exclusively our invention. However, the most important to us is the conceptual aspect of this notion, which is based on epigenetic and morphogenetic ideas about the formation of morphological disparity during individual development and the "Ricklefsian niche" model (see below). It should also be emphasized that, since the niche construction theory (NCT) implies an active role of individuals in the formation of EN and habitat environment [11], special attention should be given to morphogenetic "design" of morphofunctional features necessary for the survival of individuals, which is based on realization of certain adaptive modifications in the course of development. The pool of potentially available modifications is historically accumulated in the epigenetic system of the population due to transgenerational epigenetic inheritance and replication of altered DNA profiles that specify certain morphogenetic trajectories as adaptive responses to environmental transformations [9, 12],

I regard the morphoniche as part of the multidimensional ecological niche that characterizes the acceptable limits of phenotypic plasticity of syntopic biological objects realized in the course of individual development. On the one hand, this is a multidimensional characteristic of the morphological habitus (structure, shape, and size) of individuals, cenopopulations, or communities (taxocenes); on the other hand, this is the region of morphospace occupied by their ordinates (the morphological hypervolume). In the latter case, this region is directly associated with niche [see 45, 46, 78]. Since niche is a certain space (receptacle), the morphoniche is part of multidimensional morphospace delimited by the limits of acceptable phenotypic plasticity of morphostructures for a given individual or a group of individuals. In many respects, I agree with Shenbrot, who considers that "... Using morphological indicators, it is apparently possible to adequately reflect the mutual arrangement of the centers of ecological niches in the resource space, since the relationship between ecological features of animals and morphological structures accounting for these features is a general rule (although the multifunctionality of morphological structures allows for exceptions to this rule)" [51, p. 14]. The niche variation hypothesis (NVH) proposed by Van Valen [34] implies that an increase in the width of population niche is related to a higher degree of individual specialization.

Apparently, it is on the basis of this hypothesis that Shenbrot has arrived to the conclusion that "... The use of morphological indicators for estimating the width and overlap of niches appears questionable, since the hypothesis of relationship between the amplitude of morphological variation and niche width implies that populations consist of the sets of narrowly specialized phenotypes, and the wider the niche, the greater the ranges of these sets" [51, p. 14]. However, Ricklefs [46] performed a multivariate morphometric

comparison of passerine birds from the avifaunas of temperate and tropical latitudes and found that the ordinates of species clustered toward the center of the common morphospace (the 3D sphere plotted along the first three principal components), contrary to the rule that, to minimize competition, centroids of species should tend toward even spacing and uniform density in the morphospace. He concluded that this phenomenon, indicating the possibility of considerable overlap between trophic niches, (especially in the tropics), should be associated with multifunctionality of morphostructures and overabundance of food objects. The latter does not disprove the NVH but partly contradicts it and indicates that the range of morphological differences should not be directly extrapolated to differences between other components of ecological niche. On the other hand, a direct relationship between morphology and the pattern of spatial and trophic resource use at both inter- and intraspecific levels was revealed in studies on closely related cichlid fish species [70]. Contrary to the above finding, this indicates the possibility to evaluate community structure and specific features of spatial and trophic niches based on variation in morphofunctional traits, with the accuracy of indirect EN estimates increasing when intraspecific morphological variation is taken into account [14, 70]. Thus, the simplified interpretation that morphological variation and resource-factor components of EN are directly related to each other should apparently not be supported, but there is obviously an indirect relationship between them [see 70, 86]. Therefore, I consider that the morphological aspect of niche (morphoniche) comparison characterizes a separate morphofunctional component occupying an intermediate position between the Grinnellian and Eltonian niches [31, 82].

What is the specificity of my morphoniche concept? I emphasize that the morphoniche is a separate, special component of EN that can be formally counterposed to other components characterizing the aggregate resource niche (spatial, temporal, trophic, biotic, and functional). Many authors regard all these components as relatively independent [31, 51, 96]. The development of novel ecometric approaches [85], construction of taxon-free community weighted means (CWM) models [72], and new methods of functional biogeography based on geometric morphometrics at the level of regional metacommunities in a similar taxon-free model [80] have provided evidence that the patterns of morphofunctional reflection of the properties of Grinnellian and Eltonian niches are specific in many respects.

Therefore, I propose to complement these two niche types with the third type, the Ricklefsian niche, which characterizes in a multivariate way—by a complex of morphological and morphofunctional traits—the specific part of EN corresponding to my concept of morphoniche and reflects the adaptive plasticity of phenomes in the course of individual development.

Note that Ricklefs was one of the first to characterize EN with regard to the morphological volume occupied in the morphospace by ordinates of objects (individuals or species averages) [45, 46, 86], and in one study [46] he designated this volume as niche, although with a question mark (= niche?).

The Ricklefsian niche (= morphoniche) occupies an intermediate position between the Grinnellian and Eltonian niches but has its own specific properties. Its formation markedly depends on regional conditions and local resources, but it can adaptively change its functional capacities for utilizing spatial, temporal, trophic, and other biotic resources and, in part, regulate the influence of regional conditions. In this sense, the morphoniche can actively respond to climatic, geographic, and trophic changes, with consequent modifications resulting in the construction of a distinct niche. This is in line with the ideas of NCT [11] concerning the features of behavior that change the living environment of individuals, populations, and communities. The alteration of morphoniche due to morphofunctional changes inevitably leads to change in its functional properties (widening of the ecological license and niche shift) and to modification of behavior aimed at optimization of conditions. Therefore, the idea of morphoniche substantially complements the argumentation of NCT. This is particularly important in the context of the concept of extended evolutionary synthesis (EES) [8], which includes the factor of NCT. Since the EES concept envisages the possibility of rapid stress-induced epigenetic rearrangements that can be transgenerationally inherited and change ontogenetic trajectories [7–9, 12], analysis of epigenetic and morphogenetic changes of morphoniche theoretically makes it possible to directly relate real-time EN reconstruction to long-term evolutionary-ecological processes on different time intervals.

It should also be noted that the morphoniche is actually the primary, basic part of EN. All other components should be attributed to the category of secondary EN (the evolutionary-ecological attribute of primary EN). I consider that a specific resource of individuals of a certain species in the multidimensional model of Ricklefsian niche is represented by the species phenome itself, which dynamically changes at different stages of ontogeny, and also by its modification potential. The combination of properties of the primary (Ricklefsian) and secondary niches (Grinnellian and Eltonian) forms the generalized EN. The morphoniche (MN) is not equal to the generalized EN but comprises only part of its hypervolume. Another aspect of MN is that its phenotypic plasticity is potentially limited by the features of epigenetic and morphogenetic systems historically and phylogenetically formed in a natural population (cenopopulation) identical by descent. In our understanding, which is based on the results of long-term phenogenetic research [97], each individual (phenome) can realize a certain range (fan) of ontogenetic [98] and morphoge-

netic trajectories [98], which is invariant for representatives of a given local population.

Therefore, the notion of morphoniche should be characterized using the notion of phenome as the aggregate of properties of an individual that are dynamically transformed throughout ontogeny (from zygote to senile stage), including all subcellular, cellular, tissue, organ, morphophysiological, and ethological feature that serve as indispensable resources for its survival and involvement in reproduction. The phenome may be regarded as a specific "developmental resource" forming a primary morphofunctional shell in the course of ontogeny, which plays the role of basic EN of an individual. This shell allows the maintenance of autonomicity, integrity, and metabolic exchange both within it and with the environment, thereby maintaining it in a steady unbalanced thermodynamic state characteristic of living matter. At the same time, the phenome of an individual is a multifunctional "biological tool" that has been formed over a long evolutionary history and performs necessary ecological functions (mainly trophic, reproductive, and environment-forming/transforming) in the population and community [99]. The species phenome is a compromise system solution both for its carrier (an individual of a given species) and for the community to which it belongs. In this sense, the phenome indeed functions as primary EN and provides for the functioning of secondary EN, i.e., for the availability of ambient physical, chemical, and biological resources necessary for an individual.

My notion of MN is based on the model of population ontogeny [97] and invariability of potential morphogenetic trajectories of individuals in a population (cenopopulation) [20]. All these individuals are characterized by an invariant set of basic modifications of development conditioned by the integrated epigenetic system (epigenetic landscape) of the population. The volume of MN increases under unfavorable conditions due to stress-induced expansion of the variation fan and decreases to a minimum under favorable conditions [20, 100], provided the majority of individuals are capable for regulating developmental norm (in Schmalhausen's understanding).

Since the phenome is perceived primarily as the morphological or morphophysiological habitus of an individual at all stages of its development, it may be regarded at a macro level as an individual morphological or morphophysiological niche (IM). In general, IM is the aggregate of all morphophysiological, ethological, and environment-forming properties of the phenome that provide for its autonomicity, integrity, and metabolic exchange both within it and with the environment.

A good example of IM is diversity in size, shape, and structure of leaves taken from different parts of the crown of a tree as a modular organism. The leaves of the same tree are a priori variable because of differences in their functions and conditions of development (e.g., shade and light leaves), and their morphology reflect specific features of the ecological niche of a given tree. In multivariate analysis for a complex of morphological traits (e.g. PCA), ordinates of individual leaves cluster into a certain hypervolume (3D volume) in the common morphospace. The model of IM and its relationship with hierarchically higher population and taxocene MNs (PM and CM) can be presented as a general scheme (Fig. 1a).

The pattern of ordinates in the space of the first three principal components represents a dispersion ellipsoid. If all marginal ordinates are connected by lines using the Delaunay triangulation, the ellipsoid will be contoured as a polyhedron with the surface formed by triangular facets (Fig. 1a), with its boundaries characterizing the realized individual morphoniche (r-IM) for leaves from the crown of a model tree. In some years, the dispersion pattern of ordinates and the volume they occupy may be displaced relative to the long-term average. If the observed configuration of ordinates is obtained for pooled samples taken in different years, they will approach the hypervolume/volume corresponding to the potential individual morphoniche (p-IM). The latter situation will characterize the fan of allowable morphogenetic trajectories of an individual in the morphospace, and the hypervolume will approach the limits of its norm of reaction (NoR). Moreover, the morphospace will reflect realization of the maximum possible range of morphogenetic modifications (subprograms of development) of the leaves from a given tree in the adult state; i.e., its individual phenotypic plasticity with respect to the structure, shape, and size of morphostructures included in analysis.

Consider a specific example of variation in leaf size and shape in silver birch trees (*Betula pendula* Roth.) growing in plots with different levels of heavy metal pollution at different distances from the Middle Ural Copper Smelter (MUCS), Sverdlovsk oblast. Leaf samples were taken in July from model trees in the impact, buffer, and background (control) plots located at 0.5−1, 3−5, and 30 km from the MUCS, respectively. Estimates of toxic pressure from industrial pollutants in the plots were based on the data from [101]. Only the leaves growing on shortened shoots (brachyblasts) were included in analysis. Samples in each cenopopulation were taken from five trees, five shoots per tree. In each shoot, all leaves (two to four) were collected from the second basal elementary shoot. These leaves were scanned with a flatbed scanner at constant resolution. Leaf images were processed with tpsDig2 [102] to supplement them with 18 landmarks (Fig. 2a) whose pattern characterized variation in leaf shape and, in part, the arrangement of veins. Leaf size was indirectly estimated from the area of polygon contoured along external landmarks. This parameter was the highest in samples from the control plot, the lowest in samples from the impact plot, and intermediate
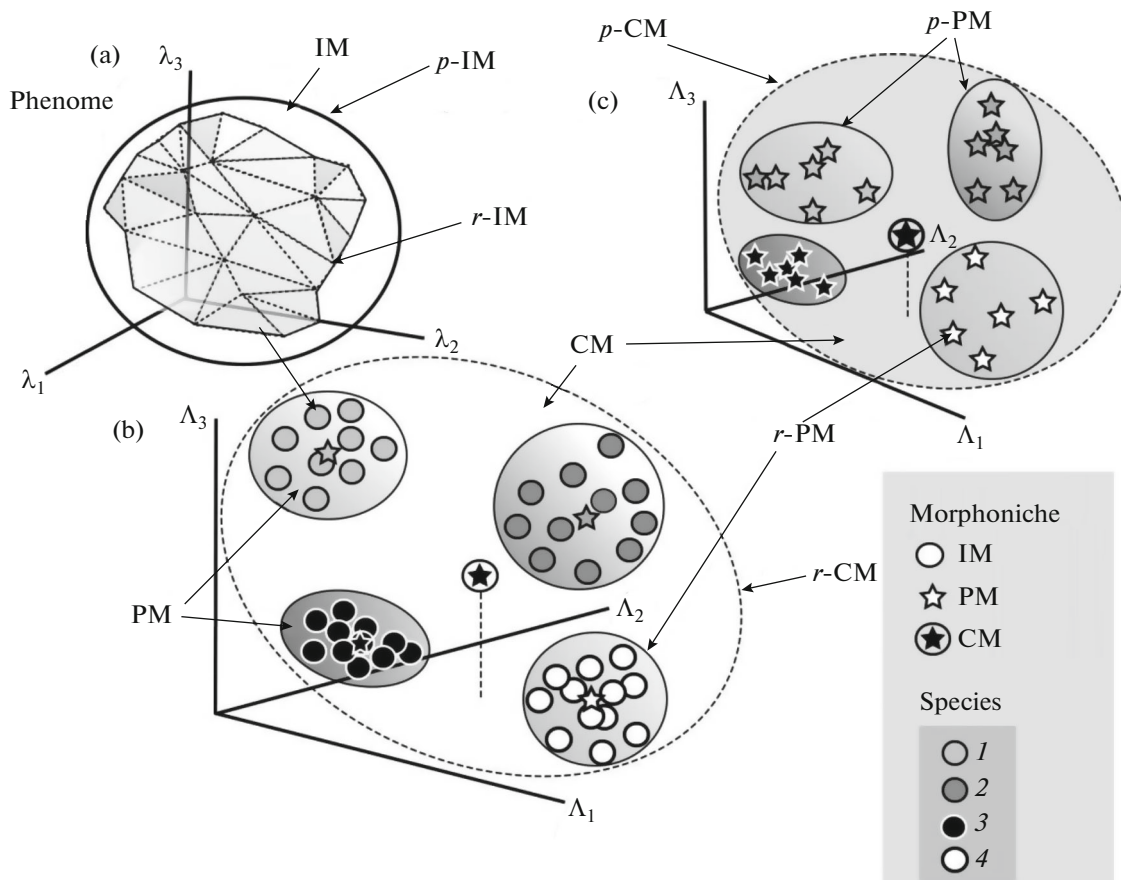
Fig. 1. A conceptual scheme of the hierarchy of morphoniches at the levels of (a) individual (phenome), (b) cenopopulation/population, and (c) taxocene/community and interrelations between them. Designations of morphoniches: (IM) individual, (PM) cenopopulation/population, (CM) taxocenotic/cenotic; (*r*) realized, (*p*) potential; $\Lambda 1 - \Lambda 3$, axes of the 3D morphospace enclosing the ordinates and centroids of cenopopulations comprising a taxocene (cenosis); dashed lines show the contours of morphoniches. Symbols: circles, ordinates of individuals; stars, centroids of realized PMs; stars in circles, centroids of realized and potential cenotic morphoniches (*r*-CM and *p*-CM, respectively); 1−4, species numbers. The model shaped as a polyhedron (a) shows the realized individual morphoniche of a phenome (*r*-IM) within the convex hull corresponding to the potential individual morphoniche (*p*-IM) in the morphospace of a modular individual formed by axes $\lambda 1 - \lambda 3$.

in the buffer samples, which was confirmed by the results of one-way ANOVA (F = 66.51; d.f. = 284; $p < 0.0001$) and Tukey's pairwise Q test. In other words, birch trees in the impact plot consistently produced small leaves, i.e., the growth processes were depressed.

The results of comparing the average values of canonical variables for trees from the three plots (Fig. 2b) show that the scattering pattern of centroids for individual trees is closely correlated with corresponding cenopopulations: the ordinates of trees from each plots are strictly confirmed to a certain part of the common morphospace. Differences in shape between individual leaves in the control cenopopulation are minimal, while the scattering of centroids reaches the highest level in the group of trees in the buffer plot and is also fairly high in the impact group. Thus, modification shifts in leaf morphogenesis in different plots occur at the level of local tree groups, which is expressed as technogenic variation in leaf shape [20].

POPULATION, SPECIES, AND CENOTIC MORPHONICHES

A multivariate statistical analysis of multiple individuals from the same generation makes it possible to visualize the group morphoniche in the common morphospace. The system of morphogenesis formed in the population on the basis of its epigenetic landscape is invariant for each individual of this population while being generally polyvariant [97]. This system accounts for the formation of a potential morphospace of developmental trajectories characteristic of this population. The population morphospace is historically formed so as to provide the possibility to realize typical modifications of development, i.e., morphogenetic responses to a broad range of fluctuations in local aut- and synecological conditions. On this basis, the population morphoniche (PM) can be identified. The array of individual morphoniches synchronously studied in the local group at a certain stage of species ontogeny
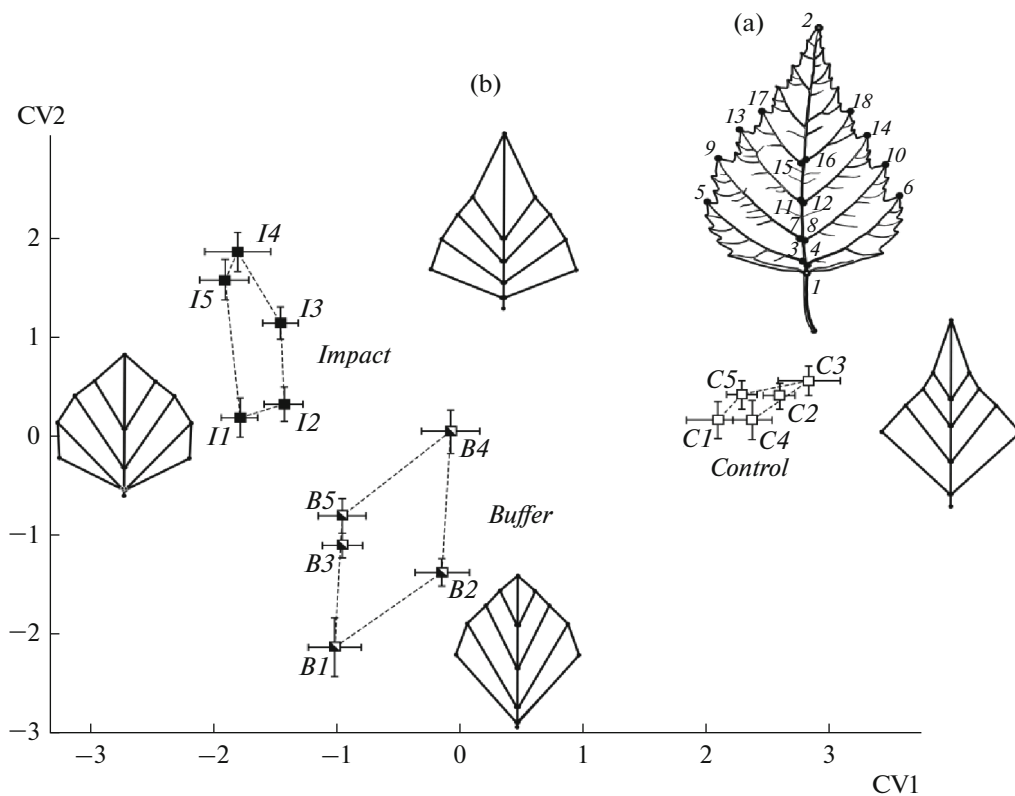
Fig. 2. (a) Locations of 18 landmarks on the upper surface of a silver birch (*Betula pendula* Roth.) leaf and (b) the results of ordination of canonical variable means (± *SE*) for individual birch trees (*1–5*) growing in (C) control, (B) buffer, and (I) impact plots. Schematic configurations of leaves reflect directions of variation in their shape and correspond to the extreme (maximum and minimum) values of ordinates along canonical axes CV1 and CV2.

forms the realized population morphoniche (*r*-PM) (Fig. 1b). In the case of taxocenes, the same applies to cenopopulations of sympatric species and their PMs.

The realized volumes of particular morphoniches (e.g., those obtained in individual years) may be averaged in order to estimate the mean volume of the realized morphoniche. Long-term monitoring of a population allows rough estimation of its potential PM (*p*-PM), i.e., the hypervolume characterizing the manifestation of its chronographic morphological disparity, which approaches the maximum possible level (Fig. 1c).

Intraspecific chronogeographic analysis of variation makes it theoretically possible to estimate the morphospace of a species, or the species morphoniche (SM), and also to compare between the realized niches of certain infraspecific forms (*r*-SMs) and compare them with the potential species morphoniche (*p*-SM). In practice, such a study within the species range is very difficult and can only be performed on the basis of abundant collection material, producing roughly approximate results.

Another aspect is comparison by means of coupled analysis of morphological disparity in the taxocene at the level of individuals, without dividing them by spe-

cies (taxon-free method) [71, 95]. Cenopopulations of taxonomically close sympatric species in the same taxocene form the cenotic morphoniche (CM) (Figs. 1b, 1c). Comparing the samples of individuals of similar age taken at the same time from cenopopulations of sympatric species, it is possible to estimate the morphospace characterizing the realized cenotic morphoniche (*r*-CM) (Fig. 1b). Similar data on the same set of species over a number of years allows the potential cenotic morphoniche (*p*-CM) to be revealed (Fig. 1c). The diversity of *p*-CM is formed and refined by natural selection over a long time. New constellations of conditions to which the species have never been exposed over their history (in particular, those formed under anthropogenic impact alone or combined with climate change) should lead to rapid depletion of the normal regulatory capacity of morphogenesis, with consequent expansion of the fan of aberrations and morphoses [20].

An abrupt change in environmental conditions causes developmental stress and enhances stress-induced epigenetic variation in impact populations [9, 10, 12]. As noted above, epigenetic changes are often associated with morphogenetic effects and can be inherited transgenerationally. These processes lead to

changes in the region of the morphospace occupied by the potential cenotic morphoniche (*p*-CM).

METHODS USED TO ANALYZE THE DIVERSITY OF MORPHONICHES IN MORPHOSPACE

The notion of morphospace was most completely characterized by McGhee [103] as an element of the concept of theoretical morphology. In multivariate analysis of variation, he regarded the ordinate of each individual as a point in the common morphospace. In our understanding the mutual arrangement and aggregation of the ordinates of phenomes in the morphospace not only characterize their morphogenetic features but also reflect specific features of individual and group morphoniches, provided conditions of morphogenesis for different individuals should be similar (comparable).

Group samples characterizing specific realized morphoniches are initially standardized to a similar size using the rarefaction procedure and then pooled. For subsequent multivariate analysis, this pooled array should have grouping variables indicating that individuals belong to a certain group (with respect to sex, species, cenopopulation, sampling year, taxocene, etc.). The volumes of morphospaces occupied by morphoniches of individuals, cenopopulations, species, and taxocenes are calculated in the same way. For all these objects, Procrustes coordinates characterizing variation in their shape and the centroid size (CS) reflecting their size are calculated by methods of geometric morphometrics [20]. Procrustes coordinates are usually used for subsequent multivariate analysis of variation and ordination of objects in the morphospace. When necessary, these coordinates may be multiplied by the corresponding natural logarithms of centroid sizes [104, 105], thereby combining the procedures of centering and rotation of landmark configurations and returning them to the actual size of objects. As a result, a "form space" is obtained [104], which allows further ordination of objects in the morphospace. This procedure is performed by multivariate methods (PCA, PCo, RW, CVA, MDS, etc.) based on the Procrustes coordinates of objects or their coordinates in the form space.

Then follows calculation of the volume (area) of morphoniches as the morphospace within a convex hull [38, 92, 93] formed by the set of points corresponding to the outer margin coordinates of object groups. For this purpose, the ordinate values along two (2D) or three variables (3D) are calculated beforehand [92]; e.g., these may be the first three canonical variables (CV1−CV3) or the first three principal components (PC1−PC3). In our studies, the volumes (areas) of the corresponding morphoniches were calculated using the CalculateVolume add-in to Microsoft Office Excel written by A.G. Kursanov on the basis of MatLab's built-in convhull function, which allows calculating the volume of 3D convex hull for a finite set of points. The convex hull volume can also be calculated with the geometry [106] or hypervolume [94] R packages.

The convex hull volume (*Vch*) of realized morphoniche for a group of higher hierarchical level, such as cenopopulation (*r*-PM), will always be greater than the sum of individual realized volumes $\sum_{i=1}^{n} Vch_{ri}$ in the corresponding sample due to the presence of free spaces in it. For example, parameter Vch_{rp} for the entire sample of weeping birch trees from the control cenopopulation (based on the total set of the of the ordinates of leaves) reached 76.11, while its value in the case calculated for the sum of volumes of individual tree morphoniches (IMs) was only 45.83. The proportion of control population morphospace not occupied by the ordinates of leaves of individual trees was about 40%. This proportion in the morphospace of the impact population was slightly higher (52%) indicating that the ellipsoids of ordinates of individual trees increasingly diverge from each other in the impact environment (the effect of provocative background according to [100]).

The value of *Vch* depends on sample size, especially when the number of observations is relatively small, since the positions of marginal ordinates in this case have a strong effect on the convex hull volume. On the other hand, their position may remain unchanged upon a significant increase in the number of objects per sample, and no change in *Vch* occurs in this case. Therefore, it is necessary to use the volumes of morphoniches (*Vch*) calculated for samples randomly standardized to a fixed number of objects (with $n \geq$ 15−20 ind.).

According to the principle of optimal phenotype formulated by Shvarts [107], this term applied to the phenotype that, under given conditions, generates an excess of energy due to its specific tissular and morphophysiological features; i.e., the proportion of its time−energy budget expended for the maintenance of life activities is significantly lower than in other phenotypes, which gives it selective advantage over them. If an individual is able to normally regulate development, its realized individual morphoniche (*r*-IM) will occupy a relatively small volume of morphospace, compared to individuals with disturbed regulation; i.e., the phenotype of such an individual will be close to optimal. Therefore, the volumes of realized morphoniches for each individual (group) within a higher-level group may be used to calculate one more parameter, the index of realized morphoniche optimality (*RMO*):

$$RMO = 2 - \left(Vch_i / \bar{V}ch_i \right),$$

where Vch_i is the volume (3D convex hull) of a particular realized morphoniche, and $\bar{V}ch_i$ is the mean volume of such morphoniches. Note than Vch_i cannot be

zero, because the calculation of 2D or 3D convex hull is impossible when the values of measurements even along one out of two or three axes are equal. However, the higher the degree of regulation of development within limits of the norm (with consequently lower volume of a particular realized morphoniche), the closer the given phenome(s) to the optimal phenotype. The complete morphological identity of all individuals in a sample is biologically improbable even in the case of monozygotic twins. The RMO in phenotypes approaching the optimum is always greater than 1.0. Unfavorable environmental conditions destabilize the process of development, which leads to a significant increase in the range of variation and within-group morphological disparity. The majority of individuals are incapable of normal regulation of development under such conditions [20, 100], and the volume of morphoniche in the morphospace inevitably increases. A several-fold excess of particular Vch_i over the average volume $\overline{Vch_i}$ indicates significant destabilization of development of an individual or a group, and RMO in such cases may have a negative value. Therefore, characteristics of the group morphoniche volumes under different living conditions for a cenopopulation may be used to calculate RMO and thereby approximately estimate whether these conditions are optimal ($RMO > 1.5$), normal ($1 = RMO < 1.5$), pessimal ($0.5 < RMO < 1$), extreme ($0 = RMO < 0.5$), or critical ($RMO < 0$).

Estimating the ratios between the volumes of realized and potential morphospaces for each morphoniche, it is possible to calculate the adaptive modification potential (AMP) of the morphoniches of corresponding groups:

$$AMP = \left[1 - \left(Vch_r / \left(Vch_p / N\right)\right)\right],$$

where the lowercase indices r and p refer to the realized (particular) and potential (generalized) morphoniches and N is the number of geographically distant populations of a species or of sympatric species populations in a community (taxocene). Such ratios of morphoniches may be calculated for biosystems of different hierarchical levels. Accordingly, the volumes of realized morphoniches may be estimated either individually—e.g., in each elementary sample or in a certain period of time (or in each of several periods)—or on average (e.g., over a number of years). The potential morphoniche is not a sum of volumes but rather the total volume of morphospace occupied by all realized morphoniches. When the numbers of observations in the compared samples are equal and one of them occupies a relatively small volume of morphospace, this indirectly indicates that morphogenesis of the corresponding group is more stable under given environmental conditions; if the occupied volume is relatively greater, this indicates lower capacity for developmental regulation and higher scattering of morphogenetic trajectories in the morphospace. Therefore, the calculated AMP values will be the highest in groups with the smallest volumes of morphoniches in the morphospace.

Using one of resampling methods, e.g., bootstrap with replacement [108] or permutation test, which is less prone to biased estimates [109], it is possible to calculate mean morphoniche volumes with standard errors and corresponding confidence intervals.

A combination of program packages TPS [102], MorphoJ [18], and PAST [105] may be recommended for calculations used in methods of geometric morphometrics and other multivariate methods of ordination and classification.

AN EXAMPLE OF COMPARISON BETWEEN MORPHONICHES OF SYMPATRIC SPECIES AT THE CENOTIC LEVEL

Consider the cenotic model of morphoniche using the example of taxocene of three shrew species: the common shrew *Sorex araneus,* Laxmann's shrew *S. caecutiens*, and pygmy shrew *S. minutus*. We have previously compared variation in the mandible shape on the lingual side in representatives of two local shrew taxocenes from the Il'men reserve (Chelyabinsk oblast, the Southern Urals) and from the vicinity of Kytlym village (Sverdlovsk oblast, the Northern Urals). Since this material has already been published [11], consideration is given below only to new data obtained using the proposed new approach. Using the procedure of random sampling with elimination, we selected for analysis the samples of digitized images of mandibular rami from cenopopulations of each shrew species (with a fixed number of observations per sample) [110]. To describe variation in the mandible shape, 20 landmarks were used (Fig. 3a). Based on the results of canonical analysis of Procrustes coordinates characterizing this variation, ellipsoids of scattering in the common morphospace were plotted for ordinates of the cenopopulations of three sympatric species from the southern and northern taxocenes (Fig. 3b). These ellipsoids, which characterize the realized morphoniches of the corresponding cenopopulations (*r*-PMs) of different shrew species, are located in the morphospace at certain distances from each other. The morphoniches of northern samples of each species are parallel displaced in the morphospace along the CV2 and CV3 axes relative to those of southern samples. We have already noted that geographic variation in the mandible shape manifests itself both in distinct shrew species and in their taxocenes [110].

Calculations of the realized morphoniche volume Vch allowed it to be estimated both for individual cenopopulations (*r*-PM) and for each taxocene (*r*-CM). The total volume of the morphospace was $Vch_{rc} = 324.75$. The volume of *r*-CM was significantly smaller in the southern than in the northern taxocene: 110.89 ± 1.63 vs. 125.60 ± 2.91 ($t = 4.41$; $p = 0.0003$). The volume of *r*-PM (Vch_{rp}) was found to be the highest in the south-
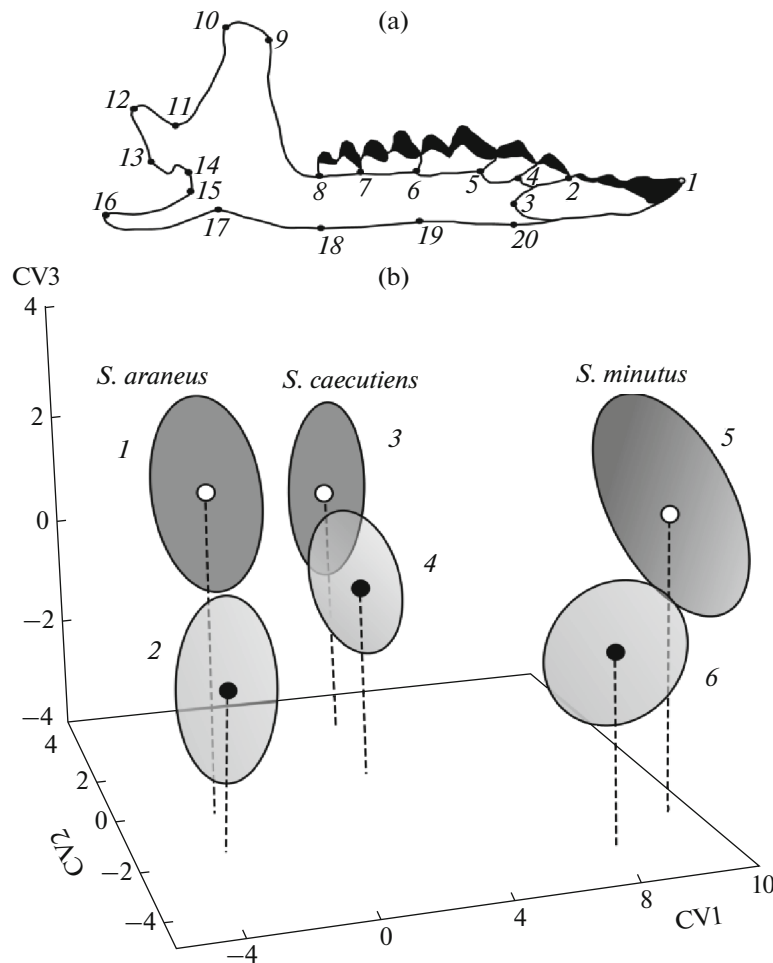
Fig. 3. (a) Locations of 20 landmarks on the lingual side of the common shrew (*Sorex araneus*) mandible and (b) the results of canonical analysis of Procrustes coordinates characterizing the ellipsoids of variation in the mandible shape and the relationships between morphoniches for cenopopulations of sympatric shrew species *Sorex araneus* (*1, 2*), *S. caecutiens* (*3, 4*), and *S. minutus* (*5, 6*) of two local taxocenes: Il'men, the Southern Urals (*1, 3, 5*) and Kytlym, the Northern Urals (*2, 4, 6*).

ern cenopopulation of *S. minutus* (7.98 ± 0.49) and the lowest in southern cenopopulations of *S. caecutiens* (1.72 ± 0.23) and *S. araneus* (2.13 ± 0.18). The Vch_{rp} value in the northern populations of these species, compared to southern ones, was the lowest in *S. minutus*, being higher in *S. araneus* and reaching a maximum in *S. caecutiens* (3.86 ± 0.33, 3.76 ± 0.32, and 4.64 ± 0.39, respectively). The *AMP* value proved to be the lowest in the southern population of *S. minutus*, but that in the northern population of this species was the highest among others (0.792 ± 0.013 and 0.926 ± 0.007, respectively). This parameter in *S. caecutiens* was the highest in the south and the lowest in the north (0.955 ± 0.006 vs. 0.899 ± 0.008). The *AMP* values in *S. araneus* were intermediate both in the south (0.945 ± 0.005) and in the north (0.918 ± 0.007). Judging from the index of realized morphoniche optimality (*RMO*), conditions of development in the Southern Ural mountains were

favorable, normal to optimal (*RMO* > 1.0), for *S. caecutiens* (1.468 ± 0.043) and *S. araneus* (1.577 ± 0.050), but extreme (0 = *RMO* < 0.5) for *S. minutus* (0.004 ± 0.122). However, conditions in the Northern Urals were suitable for normal development (*RMO* ~ 1.0) of *S. araneus* and *S. minutus* (1.070 ± 0.059 and 1.040 ± 0.073) but proved to be pessimal (0.5 < *RMO* < 1.0) for *S. caecutiens* (0.841 ± 0.093). Unfortunately, many other examples of the analysis of morphoniches cannot be considered here because of space limitations.

Thus, the concept of morphoniche applied to different model situations can provide the possibility to quantitatively evaluate and verify both population-ecological and evolutionary-ecological hypotheses based on the relationship between the realized and potential limits of phenotypic plasticity of individuals, cenopopulations, and taxocenes in the morphospace.

CONCLUSIONS

The concept of morphoniche is in line with the rapidly developing fields of functional and trait-based ecology. It may be used in research on population ecology and morphology of individual species as well as in evolutionary ecological and synecological studies on cenopopulations of sympatric species within taxocenes. This concept offers a theoretical perspective of indirectly estimating the ratio of Ricklefsian niches, or morphoniches (morphological components of ecological niches) of certain groups in the common morphospace. Analysis of the relationship between realized and potential morphoniches allows estimation of the limits of phenotypic plasticity, and it appears promising to use these estimates for solving various ecological problems with assessing the degree of tolerance for changes in the environment at different levels of biological organization.

The main direction of research involving the concept of morphoniche is to evaluate the stability of development and adaptive potential of biological systems upon changes of environmental conditions in space and time. Our approach applied to a sample of modular organisms may allow identification of individuals whose phenomes most closely approach the "optimal" phenotypic state under given conditions (i.e., individuals with a low level of destabilization of development). In groups of individuals, including cenopopulations, morphogenetic reactions (patterns of variation in shape) make it possible to estimate the degree of favorability of conditions that have an effect on the process of development. Comparing populations of a species within its range, regions may be revealed where conditions are more favorable and close to optimal. Finally, studies on taxocenes provide the possibility to identify populations of ecologically vulnerable species and to estimate the stability and tolerance of communities (taxocenes) themselves in the changing environment. Convergence in size between the volumes of morphospace occupied by realized and potential morphoniches of the compared objects may be indicative of reduction or depletion of their adaptive modification potential. Such a situation makes it possible to identify vulnerable species and communities and reveal the first symptoms of local critical evolutionary-ecological phenomena in biocenoses. The proposed approach may be used as a specific toolkit for monitoring the state and stability of natural populations and communities and for solving problems in nature conservation.

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