

Original Article

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Relation between the habitat niche breadth and the geographic range size: A case study on palearctic voles (Mammalia: Rodentia: *Arvicolinae*)

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Abstract. Habitat niche breadth for Palearctic *Arvicolinae* species was estimated at both local (α -niche) and global (the entire geographic range, γ -niche) scales using occurrence records of species and environmental (climate, topography, and vegetation) data. Niche breadth was estimated in the space of the first two principal components of environmental variables using kernel smoothing of the densities of species occurrence points. The breadth of α -niches was estimated for a set of random points inside the geographic range in a series of buffers of increasing size around these points. Within each buffer, we calculated the overlap between the distribution of environment values for the kernel smoothed densities of species occurrence points and the distribution of environment values in the background environment. The α -niche breadth was calculated as the slope of the linear regression of the niche breadth for buffers of different size by the \ln area of these buffers with a zero intercept. The γ -niche breadth was calculated as the overlap between the distributions of environmental values for the kernel smoothed densities of species occurrence points over the whole geographic range and the distribution of environmental values in the background environment and also approximated by linear regression of the species' average α -niche to the geographic range area of this species. The results demonstrated that the geographic range size was significantly related with the α - and γ -niche breadth. The γ -niche breadth was significantly positively correlated with the α -niche breadth. Finally, the differences between the γ -niche breadth values that were directly estimated and extrapolated from the α -niche breadth (Δ) values were positively correlated with the geographic range size. Thus, we conclude that the species occupy larger geographic ranges because they have broader niches. Our estimations of the γ -niche breadth increase with the geographic range size not due to a parallel increase of the environmental diversity (spatial autocorrelation in the environment).

Keywords: macro-habitat niche breadth, local niche, global niche, geographic range size, altitudinal distribution, *Arvicolinae*

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INTRODUCTION

The ecological niche is one of the central but at the same time most controversial concepts in current ecology. Initially, the niche was considered as an attribute of the environment, but later, after Hutchinson's (1957) introduction of the concept of multidimensional hyperspace of niche variables, definitions progressively shifted towards the niche as an attribute of the population (or a species) in relation to its environment (Colwell, 1992). The two aspects of the niche concept are usually distinguished based on the original definitions, the Grinnellian and the Eltonian niches. The Grinnellian niche (sometimes referred to as habitat or ecotope – see Whittaker et al., 1973) is defined by environmental variables on a broad (geographic) scale, relevant to understanding coarse-scale ecological and geographic properties of a species (Grinnell, 1917; Vandermeer, 1972; Whittaker et al., 1973; James et al., 1984; Soberon, 2007). The Eltonian niche is defined by biotic interactions and resource variables at a local (intra-community) scale (Elton, 1927; MacArthur, 1968; Vandermeer, 1972; Leibold; 1995, Soberon, 2007).

The ecological niche can be characterized by two parameters, the mean (niche position or centroid) and the variance of the resource use (niche breadth or width) (Hutchinson, 1957; Vandermeer, 1972). Theoretical models of niche evolution consider both, i.e., the evolution of niche width and the niche shifts (Roughgarden, 1972; Holt, Gaines, 1992; Ackermann, Doebeli, 2004; Kawecki, 2008), whereas most empirical studies of niche evolution concentrate on shifts of niche centroids (Pearman et al., 2008).

A positive association between habitat niche breadth and range size across different groups of species seems to be a very common macroecological pattern (Gaston, 2000; Gaston, Spicer, 2001; Slatyer et al., 2013), allowing to understand mechanisms explaining commonness and rarity. Nevertheless, recently it was demonstrated that this pattern might be just an artifact of spatial autocorrelation in the environment (Cardillo et al., 2019).

Niche width, being the estimation of a diversity of resource use, can be decomposed into components analogous to the α , β , and γ components of species diversity (Pickett & Bazzaz, 1978; Silvertown, 2004; Silvertown et al., 2006). From this point of view, the α -component of niche width is a local niche width (as estimated in this paper), the β -component is the rate of niche change across a geographic range, and the γ -component is the overall niche width measured across the entire geographic range. In almost all cases, the association between habitat niche breadth and range size was analyzed at the level of γ -niche (see Slatyer et al., 2013 for review).

As range size increases, the variability of the environment within it also increases. Consequently, the γ -niche width should increase with the range size, regardless of whether this is the result of functional relations between these two parameters or spatial autocorrelation in the environment. However, the α -niche width, which is measured locally, is independent of the range size. In this paper, we will test the hypothesis that the geographic range size is positively associated with the habitat α -niche width.

MATERIAL AND METHODS

Records of occurrences of rodents of the subfamily Arvicolinae were obtained from the Global Biodiversity Information Facility (GBIF – <https://www.gbif.org>), Finnish

Biodiversity Information Facility (<https://laji.fi>), databases of collections available online separately (mammalogical collection of Department of Biogeography, Faculty of Geography, Moscow State University – <https://www.biogeo.ru/index.php/elektronnyj-katalog/katalog-zoologicheskoy-kollektsii-mlekopitayushchie>; Museum “Archaeology, ethnography and ecology of Siberia”, Kemerovo State University – <http://museum.kemsu.ru/catalog>; Siberian Zoological Museum of the Institute of Animal Systematics and Ecology, Siberian Branch of the Russian Academy of Sciences (Novosibirsk, Russia) – szmn.eco.nsc.ru/Vertebr/Mammalia.htm) and not available online (Natural History Museum Prague, Naturhistorisches Museum Wien, Senckenberg Naturmuseum Frankfurt, Slovenian Museum of Natural History (Ljubljana), Zoological Museum of Moscow State University), and from scientific publications. Most of these data had no original GPS coordinates and were geo-referenced using Geographic Names Gazetteers available at http://earth-info.nga.mil/gns/html/cntry_files.html and checked for suitable habitats using Google Earth. Data that could not be geo-referenced precisely (± 5 km) were excluded from the analysis. Database of occurrence records of analyzed species with geographic coordinates and source information can be obtained upon request from the first author.

Environmental data for niche width estimation and distribution modeling were used as 30 arc-second grids (approximately 1 km resolution) across the distribution range of *Arvicolinae*. These data included climate, relief, and vegetation variables. The climate variables (annual mean temperature, mean daily temperature range, maximal temperature of warmest month, minimal temperature of coldest month, temperature annual range, precipitation of winter, spring, summer and autumn months) were obtained from WORLDCLIM Version 2.0 (Fick, Hijmans, 2017), available at <http://www.worldclim.org/version2>. Altitudes were extracted from GTOPO30 data set available at <https://lta.cr.usgs.gov/GTOPO30>. Slope data were derived from altitude using the Spatial Analyst module of ArcGIS 10.7.1. The data on abundance of green vegetation (NDVI index) were obtained from VEGETATION Programme (<http://free.vgt.vito.be>; data for 1998–2007, each ten days estimations) and averaged for winter, spring, summer, and autumn months.

Habitat niche width refers to the diversity of habitats used by a species' population (Vandermeer, 1972). The measurement of the niche width can be based on estimations of the diversity of quantitative environmental variables using diversity indices. However, this measure is appropriate only if resources are distributed evenly, otherwise, it will produce biased estimates (Hurlbert, 1978; Petraitis, 1979). To consider uneven resource distributions, Feinsinger et al. (1981) proposed quantifying niche width using the Proportional Similarity Index (*PSI*), which measures similarity between the frequency distribution of resources used by individuals of a population and the frequency distribution of resources available to them. However, *PSI* cannot be used directly to compare niche width within and among species in areas differing in the frequency distribution of resources. To estimate the unbiased niche width, we compared the similarity between the frequency distribution of resources used by individuals in a sample and the frequency distribution of resources available across the distribution range of *Arvicolinae*.

To eliminate the influence of factor inter-correlation, original environmental variables were normalized and then ordinated by the Principal Components Analysis (PCA) using the Spatial Analyst module of ArcGIS. The first two principal components had eigenvalues more than 1 and explained cumulatively 70.6% of the observed variation. These principal components were used as environmental variables. Niche breadth was estimated in the space of the first two principal components of environmental variables using kernel smoothing of densities of species occurrence points (Broennimann et al., 2012; Blonder et al., 2014). Breadth of α -niches was estimated for random points inside geographic range in a series of buffers of increasing size around these points. These random focal points were obtained by placing 2,000-10,000 random points (depending on a specie's range size) with a minimal distance 5 km inside the convex hull polygon build around all known points of occurrence of a species. The focal points for the analysis were selected in the three steps. At the first step, we built the 25-km buffers around each of the random points, calculated the number of the specie's occurrence points inside each of these buffers, and removed all random points with less than 5 occurrence points inside the buffer around it. As the second step, we built multiple buffers of increasing size (25, 50, 75, 100, 125, 150, 175, 200, 225 and 250 km) around the rest random points, calculated the number of the specie's occurrence points inside each of these buffers, and selected only random points that were characterized by increase of the number of occurrence points at each step of increase of buffer size around it. At the third step, we selected the first 30 random points from the list of random points remaining after the previous step. Within each buffer, we calculated the overlap between the distribution of environmental values for kernel smoothed densities of species occurrence points and distribution of environment values in background environment using the D metric

(Schoener, 1970) as $D = 1 - \frac{1}{2} \left(\sum_{xy} |\rho_{sxy} - \rho_{esy}| \right)$, where ρ_{sxy} is the proportion of species' records density in the point with coordinates x, y in a two-dimensional space of the first two environmental principal components of the sum of densities of all points of this space and ρ_{esy} is the frequency of environmental conditions in the point with coordinates x, y in a two-dimensional space of the first two environmental principal components. To normalize D metrics, values were arcsin-transformed. The breadth of an α -niche was calculated as the slope of a linear regression of niche breadth for buffers of increasing size by \ln area of these buffers with zero intercepts.

A necessary condition for statistical analysis of geographic variation of habitat niche width is the minimal sample size. A species appropriate for such analysis must have a relatively large and more or less equally well sampled geographic range. We selected for the analysis species that were known from at least 150 geographic points within their geographic ranges.

To estimate the size of geographic ranges, we applied species distribution modeling (SDM) using the set of environmental variables described above. The SDM was built with MAXENT 3.4.0 software (Phillips et al., 2006). The extent of the study area or the "landscape of interest" significantly affects the SDM results (Anderson, Raza, 2010; Elith et al., 2011). To define the study area of a species, we calculated the kernel density of occurrence points of this species with a search radius equal to 4° , reclassified the ob-

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tained raster so that the original kernel density values equal to or more than 0.05 were converted to 1 and values less than 0.05 to “NoData”, and used this reclassified raster as the mask for clipping environmental variables to the study area. Models were constructed with default MAXENT settings as these settings were demonstrated to be the most appropriate for wide-ranging data (Phillips, Dudik, 2008; Warren, Seifert, 2011). We used the MAXENT logistic output, which provides estimates of relative habitat suitability (Elith et al., 2011).

To delineate the areas of real species occurrence, the original model values, ranging continuously from 0 to 1, were transformed to a binary 0 or 1 using a threshold value. The threshold value was chosen to be equal to the “maximum training sensitivity plus specificity”; it was demonstrated experimentally (Liu et al., 2013) that this threshold provides optimal results. After reclassifying the original raster according to the chosen threshold value, the reclassified raster was transformed into polygons. Only polygons containing occurrence records were considered as areas of occurrence. These polygons were converted to the Albers Equal Area Conic projection, and the areas of the polygons were calculated on the map using the command “calculate geometry” in sq. km; the sum of the areas of these polygons was used as an estimation of geographic range size. All map operations were performed using ArcGIS 10.7.1 software.

RESULTS

Estimations of habitat niche breadth were obtained for 30 species of *Arvicolinae*. The results of these estimations together with geographic range size and parameters of the altitudinal distribution of studied species, are presented in Table 1.

Table 1. Main parameters of geographic ranges and ecological niches estimated for study species

Species	Number of occurrence points	Ln of range area sq. km	α -niche breadth $M \pm SD$	γ -niche breadth direct estimation	γ -niche breadth extrapolated	Altitude of occurrence points $M \pm SD$ m a.s.l.
1	2	3	4	5	6	7
<i>Alexandromys fortis</i>	404	14.44231	0.00798±0.00279	0.35744	0.11519	356.56±417.13
<i>Alexandromys maximowiczii</i>	248	13.93932	0.00760±0.00154	0.18741	0.10591	627.48±456.28
<i>Alexandromys oeconomus</i>	3561	16.39076	0.00779±0.00282	0.47244	0.12774	314.69±430.47
<i>Alticola argentatus</i>	298	13.34424	0.02129±0.00427	0.36269	0.28406	2808.82±811.84
<i>Alticola semicanus</i>	158	12.72636	0.00620±0.00098	0.12296	0.07887	1601.01±470.20
<i>Alticola strelzovi</i>	271	12.87488	0.01116±0.00325	0.22963	0.14374	1406.06±752.03
<i>Arvicola amphibius</i>	13862	16.27532	0.00640±0.00228	0.23182	0.10422	195.04±282.25
<i>Arvicola sapidus</i>	3197	13.77974	0.00655±0.00157	0.12760	0.09020	537.76±447.04
<i>Arvicola scherman</i>	2929	12.79913	0.00544±0.00129	0.09510	0.06966	444.16±371.67
<i>Chionomys gud</i>	183	11.34318	0.01344±0.00157	0.19017	0.15243	1739.20±626.35
<i>Chionomys nivalis</i>	1414	12.91096	0.00563±0.00230	0.22135	0.07269	1650.33±618.14
<i>Clethrionomys glareolus</i>	24146	16.00784	0.00607±0.00154	0.19660	0.09714	313.30±360.99
<i>Clethrionomys rutilus</i>	3611	16.68183	0.01145±0.00317	0.40275	0.19109	415.53±447.44
<i>Craseomys rufocanus</i>	1773	16.44175	0.00876±0.00337	0.42179	0.14396	522.82±559.83
<i>Ellobius talpinus</i>	552	14.52597	0.00377±0.00076	0.22645	0.05479	139.46±168.18
<i>Ellobius tancrei</i>	549	14.62093	0.01073±0.00255	0.26339	0.15693	1160.71±705.75
<i>Eothenomys eleusis</i>	201	12.67009	0.00618±0.00069	0.12235	0.07829	2284.85±653.83
<i>Lagurus lagurus</i>	507	14.81212	0.00392±0.00088	0.22432	0.05804	264.24±467.41
<i>Lasiopodomys brandti</i>	256	13.39001	0.00424±0.00071	0.08535	0.05673	1178.47±498.92
<i>Microtus agrestis</i>	13732	15.94376	0.00606±0.00137	0.20570	0.09656	236.91±277.96

Table 1. Continuation

1	2	3	4	5	6	7
<i>Microtus lavernedii</i>	2816	12.99399	0.00589±0.00123	0.11173	0.07651	503.23±404.19
<i>Microtus juldaschi</i>	177	11.48913	0.01732±0.00402	0.30101	0.19896	2984.87±758.38
<i>Microtus cabrerai</i>	528	11.76286	0.00444±0.00130	0.08573	0.05223	655.08±428.95
<i>Microtus arvalis</i>	16567	15.02672	0.00604±0.00138	0.16778	0.09078	326.14±348.26
<i>Microtus hartingi</i>	204	12.45593	0.00338±0.00070	0.11657	0.04215	508.81±445.84
<i>Microtus mystacinus</i>	1816	14.74934	0.00338±0.00044	0.22558	0.05724	160.80±339.30
<i>Microtus obscurus</i>	628	14.41466	0.00814±0.00371	0.29697	0.11740	769.48±715.26
<i>Microtus socialis</i>	577	13.92379	0.00498±0.00267	0.18991	0.06929	532.89±564.01
<i>Microtus daghestanicus</i>	169	11.55366	0.01174±0.00062	0.18505	0.13562	1671.18±554.98
<i>Microtus duodecimcostatus</i>	2607	13.12763	0.00581±0.00139	0.11343	0.07632	621.29±385.81

We found that the breadth of α -niche was not correlated with geographic range size ($r = -0.21$; $p = 0.270$), but was strongly correlated with mean altitude of species' occurrence points ($r = +0.71$; $p < 0.0001$) and with standard deviation of altitude of species' occurrence points ($r = +0.68$; $p < 0.0001$). Directly estimated breadth of γ -niche was positively correlated with log-transformed size of geographic range ($r = +0.56$; $p = 0.001$) and with the breadth of α -niche ($r = +0.50$; $p = 0.005$); there were no correlations of directly estimated γ -niche breadth with mean altitude of species' occurrence points ($r = +0.024$; $p = 0.899$) and with standard deviation of altitude of species' occurrence points ($r = +0.27$; $p = 0.155$). Estimations of γ -niche breadth extrapolated from values of α -niche breadth to log-transformed size of geographic range were not correlated with log-transformed geographic range size ($r = +0.043$; $p = 0.822$) but was positively correlated with directly estimated γ -niche breadth ($r = +0.65$; $p < 0.0001$), mean altitude of species' occurrence points ($r = +0.56$; $p = 0.001$) and with standard deviation of altitude of species' occurrence points ($r = +0.60$; $p < 0.0001$). Differences between values of directly estimated γ -niche breadth and extrapolated from values of α -niche breadth (Δ) were positively correlated with the log-transformed size of the geographic range ($r = +0.69$; $p < 0.0001$). Multiple forward stepwise linear regression analysis demonstrated that log-transformed size of the geographic range was significantly related to niche breadth and mean altitude of species' occurrence points in the cases of both α - and γ -niches (Table 2).

Table 2. Results of linear multiple regression analyses dependence on altitudinal range size and niche breadth

N = 30	Beta	Std. Err. of Beta	B	Std. Err. of B	t(22)	p-level
Dependent Variable: LnArea; $R = 0.71938558$; $R^2 = 51751561$; Adjusted $R^2 = 0.48177603$; F(2,27) = 14.480, $p < 0.00005$; Std. Error of estimate: 1.1314						
Intercept	–	–	14.2296	0.45097	31.55366	0.000000
NBr(α)	0.494737	0.190011	189.5774	73.19311	2.59010	0.015280
Mean Altitude	-0.98397	0.190011	-0.0020	0.00038	-5.15138	0.000020
Dependent Variable: LnArea; $R = 0.85177441$; $R^2 = 0.72551964$; Adjusted $R^2 = 0.70518776$; F(2,27) = 35.684, $p < 0.0000001$; Std. Error of estimate: 0.85338						
Intercept	–	–	13.18823	0.407350	32.37571	0.000000
NBr(γ)	0.572782	0.100856	8.66001	1.524864	5.67920	0.000005
Mean Altitude	-0.64449	0.100856	-0.00130	0.000203	-6.39016	0.000001

DISCUSSION

In agreement with previously published results on a number of different taxa (Gaston, 2000; Gaston, Spicer, 2001; Slatyer et al., 2013; Kambach et al., 2019), we found that γ -niche breadth in *Arvicolinae* rodents was strongly correlated with geographic range size. The problem is that this result may be just an artifact of spatial autocorrelation in the environment (Cardillo et al., 2019). In other words, diversity of environmental conditions that a species meets within its geographic range increases geographic range size. Thus, we formulate two alternative hypotheses: 1) species occupy larger geographic ranges because they have wider niches or 2) estimations of γ -niche breadth increase with geographic range size due to parallel increase of environmental diversity.

In the case of the first hypothesis, one can expect a positive correlation between α -niche breadth and range size; one can also assume that species distributions are limited mainly by their physiological or behavioral tolerances and that the observed γ -niches are close to fundamental niches. In this case, α -niche breadth and γ -niche breadth should be positively correlated.

In the case of the second hypothesis, one can expect no correlation between α -niche breadth and range size; one can also assume that species distributions are limited mainly by their dispersal abilities and that the observed γ -niches represent relatively small part of their fundamental niches. In this case, α -niche breadth and γ -niche breadth should not correlate. Moreover, one can expect that γ -niche breadth can be correctly estimated from extrapolation of α -niche breadth to the size of the geographic range. Differences between γ -niche breadth estimated directly and extrapolated from α -niche breadth (Δ) should be minimal in this case.

Our results clearly support the first hypothesis. The size of the geographic range was significantly related to the α -niche breadth. The breadth of γ -niche was significantly positively correlated with the breadth of α -niche. Finally, differences between the γ -niche breadth values which were directly estimated and extrapolated from values of α -niche breadth (Δ) positively correlated with the size of geographic ranges. Similar results, in the part of correlation between α -niche (local or microhabitat niche in the terms used by authors) breadth and geographic range size, were obtained by Kambach et al., (2019) in the study of plant species of the European Alps and by Ficetola et al. (2020) in the study of European plethodontid salamanders; in both studies, the correlation was weaker for α -niche than for γ -niche. Thus, we conclude that species occupy larger geographic ranges because they have wider niches.

Another fundamental problem arises in the second hypothesis, namely the problem of adaptation to environmental conditions that species never experience. According to the model of Roughgarden (1972), each population contains a variety of ecologically specialized phenotypes. Individuals of each phenotype are specialized to a specific part of a resource (habitat) axis present in the environment where their fitness is maximal. If a species contains a set of different narrow-specialized phenotypes, those phenotypes which are adapted to environmental conditions currently not occupied by the species will be eliminated. If a species is composed by a set of similar generalized phenotypes, these will maintain adaptations to unused environmental conditions only if such adaptations have no extra cost. As shown by Vacher et al. (2005), such adaptations may involve high

cost. Thus, significant differences between γ -niches and fundamental niches seem unrealistic.

We also found that the breadth of α -niche was strongly positively correlated with a mean altitude of species' occurrence points and with a standard deviation of altitude of species' occurrence points. This can be explained by higher habitat variability in the mountains than in plain areas, especially due to a high variation in slope exposition in the mountains.

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**СВЯЗЬ ШИРИНЫ БИОТОПИЧЕСКОЙ НИШИ
С РАЗМЕРОМ АРЕАЛА: НА ПРИМЕРЕ ПАЛЕАРКТИЧЕСКИХ ВИДОВ ПОЛЁВОК
(MAMMALIA: RODENTIA: ARVICOLINAE)**

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Аннотация. Оценивали ширину биотопической ниши у палеарктических видов *Arvicolinae* в локальном (α -ниша) и глобальном (весь ареал, γ -ниша) масштабах с использованием данных о встречаемости видов и параметров окружающей среды (климат, топография и растительность). Использовали первые две основные компоненты переменных среды с центральным сглаживанием плотностей точек встречаемости видов. Для α -ниши это был набор случайных точек внутри ареала в серии буферов увеличивающегося размера вокруг этих точек. В каждом буфере рассчитывали перекрытие между распределением значений среды для сглаженных плотностей точек встречаемости видов и распределением значений среды в фоновой среде. Ширину α -ниши рассчитывали как наклон линейной регрессии ширины ниши для буферов разного размера на \ln площади этих буферов с пересечением координатных осей в точках нулевых значений. Ширина γ -ниши рассчитывалась как перекрытие между распределением значений среды для сглаженных по ядру плотностей встречаемости видов по всему ареалу и распределением значений в фоновой среде, а также аппроксимировалось линейной регрессией средней α -ниши вида. Показано, что размер ареала в значительной степени связан с шириной α - и γ -ниш. Ширина γ -ниши положительно коррелировала с шириной α -ниши. Наконец, различия между значениями ширины γ -ниши, которые были непосредственно оценены и экстраполированы из значений ширины α -ниши (Δ), положительно коррелировали с размером ареалов. Таким образом, можно сделать вывод, что более широкие ареалы имеют виды с более широкими пространственными нишами. При этом оценки ширины γ -ниши увеличиваются с увеличением размера ареала не за счет параллельного увеличения экологического разнообразия (пространственная автокорреляция в среде).

Ключевые слова: ширина биотопической ниши, локальная ниша, глобальная ниша, размер ареала, высотное распределение, *Arvicolinae*

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