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ORIGINAL ARTICLE

LANDSCAPE-DEPENDENT VARIABILITY OF MORPHOMETRIC TRAITS IN *CARABUS GRANULATUS* L., 1758 (COLEOPTERA, CARABIDAE)

Roman Gorbunov*,**♦, Viktor Aleksanov***, Rifgat Shagidullin*,
Sergey Berdnik* and Raisa Sukhodolskaya*,****,*****
* Institute for Problems of Ecology and Mineral Wealth Use of theTatarstan Academy of Sciences, Russian Federation, 420087, Kazan.
** Belogorye State Nature Reserve, Russian Federation, 309342, Borisovka settl.
***State Budgetary Institution of Kaluga Region "Park Directorate", Russian Federation, 248000, Kaluga.
**** Kazan State Medical University, Russian Federation, 420012, Kazan.
***** Volga-Kama State Natural Biosphere Reserve, Russian Federation, 422623, Sadovyi settl.
♦Corresponding author: mailto:xobglor@gmail.com

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ABSTRACT

We examined morphological variations in *Carabus granulatus* L., 1758 (Coleoptera, Carabidae) populations across different habitats in the Kaluga Region. Discriminant analysis revealed subtle but significant morphological differences between populations, with pronotum length being the key discriminating trait. Morphological variability was primarily driven by historical microevolutionary processes rather than direct phenotypic adaptation to specific habitats. Local ecological factors, such as microclimate and resource availability, had a greater influence on morphometric traits than the general habitat type. Populations in the eastern part of the Kaluga Region exhibited smaller body sizes due to intensive forest use. Fragmented forests displayed notable differences in morphometric traits, likely resulting from founder effects. Beetles from various localities showed distinct patterns: populations in the Oka River valley populations were smaller, while park habitats exhibited increased variability. Populations in Kaluga occupied an intermediate position between wild and disturbed forests. The study emphasizes the importance of considering both phylogenetic and ecological factors in understanding morphological differences in ground beetles, highlighting the complex interplay between historical, environmental, and anthropogenic factors shaping population-level morphological variation in *C. granulatus*.

Keywords: Biogeoregion, *Carabus*, Discriminant analysis, Ground beetles, Morphometry.

INTRODUCTION

Studying how organisms respond to ecological factors is essential for developing biomonitoring models and for gaining insights into the phylogenetic pathways of taxa. It is well-established that animals exhibit dynamic adaptive and microevolutionary changes in response to environmental alterations (Newman, 1995; Staton *et al*., 2001; Hauser *et al*., 2003). These transformations can occur independently or in conjunction, forming complex relationships in which the local environment influences their expression (Peiman and Robinson, 2017).

Species-specific traits can be viewed as components of biodiversity, affecting how organisms react to disturbances and shifting environmental conditions, with implications at both population and broader ecological levels (Lavorel and Garnier, 2002). Therefore, selecting particular traits for study is crucial for determining the ecological data obtained.

Body size is a fundamental characteristic of organisms, varying with environmental conditions and subject to selective pressures. In insects, body size is linked to numerous life-history traits, including reproductive rate, dispersal capability, duration of ontogeny, competition, and the number and size of offspring. These factors significantly shape the interactions between insects and their environment (Stearns, 1998).

Current research indicates that the sizes and shapes of individual beetle organs vary across habitats with different vegetation types and levels of anthropogenic impact (Luzyanin, 2023; Khomitskiy *et al*, 2024). For instance, studies on the ground beetle *Poecilus cupreus* (L., 1758) have demonstrated that its body size diminishes in agrocenoses, with both the agrocenosis conditions and the type of vegetation significantly affecting the beetles morphology (Sukhodolskaya *et al*., 2017).

C. granulatus is a transpalaearctic, and hygrophilous eurytopic species with a one-year life cycle. It is a spring breeder species without larval diapause, but with obligatory diapause in adult individuals. Both adults and larvae are predators (Turin *et al*., 2003).

The objective of this study was to identify (i) the differences among *Carabus granulatus* L., 1758 individuals from various localities, (ii) the variations between habitat types within the Kaluga region or specific sites within a given locality, and (iii) how habitat type (defined by dominant tree species) and geomorphological zonation impact these differences.

MATERIAL AND METHODS

Characteristics of the study area: The Kaluga Region is located in the center of the East European Plain, south of Moscow, primarily within the upper basin of the Oka River – the largest right tributary of the Volga. Its northern and western parts belong to the zone of coniferous-broadleaved forests (Lavrenko, 1947), which is classified in Europe as the Boreal biogeoregion (European Environment Agency, 2016). The zonal vegetation is represented by spruce-broadleaf and broadleaf-spruce forests, dominated by European spruce *Picea abies* (L.) H. Karst., 1881, small-leaved linden *Tilia cordata* Mill, 1768, and pedunculate oak *Quercus* *robur* L., 1753. Swamps are common. The relief was formed as a result of the Moscow glaciation (Esipov, 2005). The southern and eastern parts of the Kaluga region belong to the zone of broadleaf forests, also known as the Continental biogeoregion. This area has been influenced by the older Dnieper glaciation and is more distinctly dissected by a network of rivers, with remnants of pre-Quaternary relief preserved in its eastern part. Due to prolonged economic use, the eastern part of the Kaluga region is practically devoid of minimally disturbed forests, while the southern part retains small areas of undisturbed broadleaf forests within the protective belt that defended the southern borders of the Moscow state, where European ash *Fraxinus excelsior* L., 1753 is present in the stand (Bobrovsky and Abatises, 2002).

Characteristics of the sampling sites: The material for this study consisted of specimens of *C. granulatus* collected from 12 sampling sites in 10 localities (Tab. 1.) between 1996 and 2021. A locality is defined as a group of sampling sites located within 5 km of each other and not separated by significant barriers (Map 1). Geographic coordinates are provided in the order of latitude – longitude. High intensity resource use refers to non-forest use of the territory in the recent past or to a significant frequency and intensity of logging. This is identified by: 1) historical maps and satellite images, 2) the current structure of the stand, characterized by young trees or older ones that are regularly planted, with reduced age diversity of trees. Low intensity use: the opposite condition of the same signs, as well as the presence of plant species sensitive to anthropogenic pressure. Medium intensity use: in the recent past, the forest was not completely logged, but deadwood was collected, and there may have been livestock grazing, etc. Forest arrays are classified as follows: small — up to 1.5 sq. km, medium — 10-20 sq. km, large — more than 100 sq. km. Areas with a high perimeter-to-area ratio are also classified as small.

Table (1): Locations of carabid beetle trapping, grouped be vegetation zone and geomorphological zones [by Esipov (2005)].

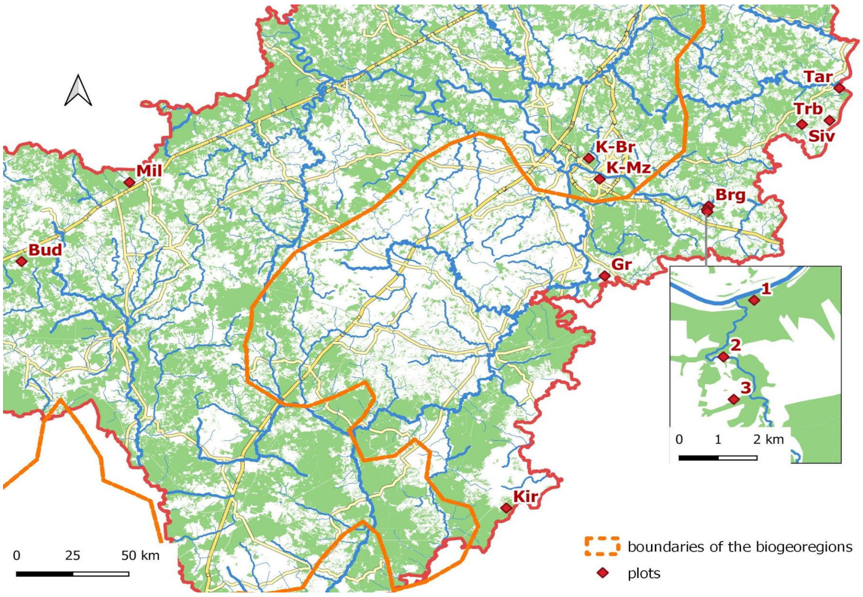
Locality	Type of habitat (by groups of dominant trees)	Position in the landscape	Dominant plant species	Size of forest array	Intensity of resource use over 100 years
Broadleaved forests vegetation zone					
Moraine-glacial gently undulating plain of the Dnieper Glaciation					
Kireykovo (Kir)* 53.6252 35.8647	Broadleaved forests	Watershed	*Q. robur* *F. excelsior* *T. cordata* *Aegopodium podagraria* L. *Allium ursinum* L.	Large	Low
Moraine gently sloping plain of the Dnieper Glaciation with inherited post-Quaternary relief					
Bragino (Brg) See text for details	Small- and broadleaved forest	Big River Valley	See text for details	Small	High
Gremyachevo (Gr) 54.2373 36.2588	Small-leaved forest	Big River Valley	*Alnus glutinosa* (L.) *Urtica dioica* L.	Small	High

Tarusa (Tar) 54.7257 37.1989	Small-leaved forest	Big River Valley	*Salix* sp. *Alnus incana (*L.) Moench *U. dioica*	Small	High
Trubetskoe (Trb) 54.6419 37.1597	Broadleaved forests	Watershed	*T. cordata* *A. podagraria* *Carex pilosa*	Small	High
Sivtsevo (Siv) 54.6316 37.0491	Broadleaved forests	Watershed	*T. cordata* *A. podagraria* *Mercurialis perennis* L.	Small	High
Mixed forests vegetation zone					
Moraine gently undulating plain of the Moscow Glaciation					
Kaluga, Bor (K-Br) 54.5436 36.1955	Spruce forest	Watershed	*Picea abietis* *Pinus sylvestris* *Betula pubescens* *Galeobdolon luteum* Huds. *Oxalis acetosella* L.	Medium	Medium
Kaluga, Ovrag Mozhayka (K-Mz) 54.4876, 36.2402	Small-leaved forest	Small River Valley	*Betula pendula* *P. sylvestris* *Salix* sp. *Á. Incána* *Corylus avellana* L.	Small	Medium
Flat glacial plain of the Moscow Glaciation					
Milyatino (Mil) 54.4811 34.3551	Spruce forest	Watershed	*P. abietis* *A. glutinosa* *Populus tremula* L. *Padus avium* *C. pilosa* *Geum rivale* L.	Medium	Medium
Budnyan-skiy (Bud) 54.2749 33.9226	Spruce forest	Watershed	*P. abietis* *P. tremula* *C. avellana* *C. pilosa* *G. luteum* *M. perennis*	Small	Low

* – Tables and images below use these letter abbreviations.

The locality "Bragino" includes three habitats:

1. Floodplain of the Oka River, willow-gray alder thicket with *Urtica dioica*, 54.4193 36.6749.
2. Valley of a small river (first-order tributary of the Oka), gray alder-thicket with *Padus avium* Mill., 54.4108 36.6678.
3. Gully with a stream (tributary of the small river), linden thicket with *Corylus avellana* and *Carex pilosa* Scop., 54.4044 36.6702.



Map (1): Kaluga region, studied localities.

Research technique: The following morphological traits of the beetles were measured: length and width of the elytra, length and width of the pronotum, head length, and distance between the eyes. A total of 4,252 specimens were measured. After sampling the beetles and determining their species and sex, all individuals were photographed, and their parameters were measured using a custom program written in Python 2.7, utilizing the Num Py and Open CV libraries. (Mukhametnabiev, 2018). The scheme for measuring the beetles is presented in Plate (1). Linear discriminant analysis was performed by STATISTICA 10 software.

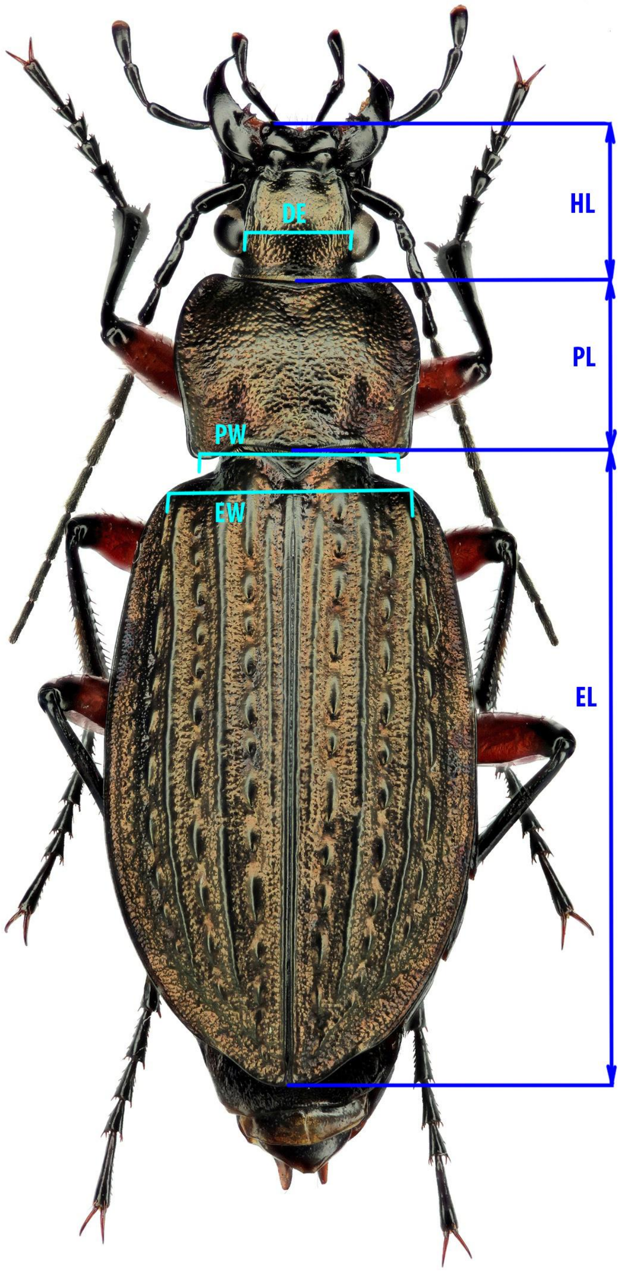


Plate (1): Illustration of measurements: EL – elytra length, EW – elytra width, PL – pronotum length, PW – pronotum width, HL – head length, DE – distance between the eyes.

RESULTS

Discriminant analysis by locality

According to the results, the populations of *C. granulatus* are well-discriminated and differ significantly (Wilks' Lambda: 0.41 approx. F (54.224) = 75.96; $p<0.001$). The coefficients of classification functions show that the length of the pronotum is the most important trait for discrimination. Other characteristics, with the exception of pronotum width, have a smaller and approximately equal contribution. The contribution of pronotum width to discrimination is extremely low.

Squared Mahalanobis Distances (Tab. 2.) vary from 0.20 to 14.70. The largest distances are observed between the pairs Milyatino-Sivtsevo (14.70) and Milyatino-Gremyachevo (12.24). The smallest distances between the values belong to Tarusa and Bragino (0.20) and Tarusa-Trubetskoy (0.22).

Table (2): Squared Mahalanobis distances (locality), $p<0.001$

	Kir	Br	Gr	Tar	Trb	Siv	K-Br	K-Mz	Mil	Bud
Kir	-									
Br	3.41	-								
Gr	4.42	0.53	-							
Tar	3.16	0.20	0.68	-						
Trb	2.45	0.38	1.22	0.22	-					
Siv	5.65	1.52	1.24	1.37	1.53	-				
K-Br	2.63	1.29	2.38	1.29	0.74	3.75	-			
K-Mz	0.58	2.46	2.90	2.37	2.03	5.20	1.80	-		
Mil	3.81	9.35	12.24	8.98	8.28	14.70	8.59	5.07	-	
Bud	0.31	2.68	3.85	2.55	2.07	4.98	2.62	1.03	3.91	-

Comparison of the mean values of measured traits (Diag. 1) shows a high degree of variation depending on the sampling point and significant discreteness. The greatest variation in traits is characteristic of the population from the village of Sivtsevo.

A smaller length of elytra is typical of the ground beetles from points related to small-leaved forests: Gremyachevo, Tarusa, Bragina, and Ovrag Mozhayka in Kaluga, while a greater length is observed in beetles from broadleaf forests: Kireykovo, Trubetskoye, and Sivtsevo. Ground beetles from spruce forests show intermediate values for elytra length. The highest values of elytra length are observed in the village of Sivtsevo, and the lowest in Gremyachevo. The greatest width of elytra is found in the village of Sivtsevo, and the smallest in the village of Milyatino. The width of elytra is also somewhat greater in broadleaf forests.

The greatest length of the pronotum is observed in the Kaluga urban forest, while the smallest is in Gremyachevo. Overall, the length of the pronotum shows higher values for ground beetles from spruce forests (Kaluga urban forest, Milyatino, Budnyansky), lower values for deciduous forests, and average values for broadleaf forests. The greatest width of the pronotum is recorded in the village of Sivtsevo, and the smallest in Budnyansky.

The length of the head of the ground beetles varies significantly; high values are observed in Milyatino, average values in Ovrag Mozhayka in Kaluga, Kireykovo, and Budnyansky, while other localities have uniformly low values. Distance between eyes has the highest values in Milyatino and the lowest in Sivtsevo. In general, ground beetles from spruce forests are characterized by higher values, while those from small-leaved forests have lower values; the values for ground beetles from broadleaf forests vary significantly.

Ground beetles from certain localities show distinct differences. For example, ground beetles from the black alder swamp near Gremyachevo have low values for both elytra and pronotum lengths, while those from the linden forest near Sivtsevo are larger, show greater variation in trait sizes, and have low values for head length and distance between the eyes. Ground beetles from the spruce forest near Milyatino are characterized by a narrower body and greater values for head length and distance between eyes.

Discriminant analysis of the beetles from different habitats of the locality "Bragino"

"Bragino" locality is represented by three types of habitats with different vegetation types: willow-gray alder, black alder and linden. Analysis shows significant ($F (12.11) = 23.13$; $p<0.001$) and moderate discrimination (Wilks' Lambda: 0.64). The width of the elytra and pronotum does not make a significant contribution. Classification function coefficients show equally strong influence on discrimination by pronotum length and distance between the eyes. The greatest Mahalanobis distance (Tab. 3) is observed between the linden and black alder forests (small- and broadleaved), while the smallest distance is between the willow and black alder forests (both small-leaved).

Table (3): Squared Mahalanobis distances (habitats in the locality Bragino), $p<0.001$.

	Willow	Black alder	Linden
Willow	-		
Black alder	0.89	-	
Linden	1.67	2.01	-

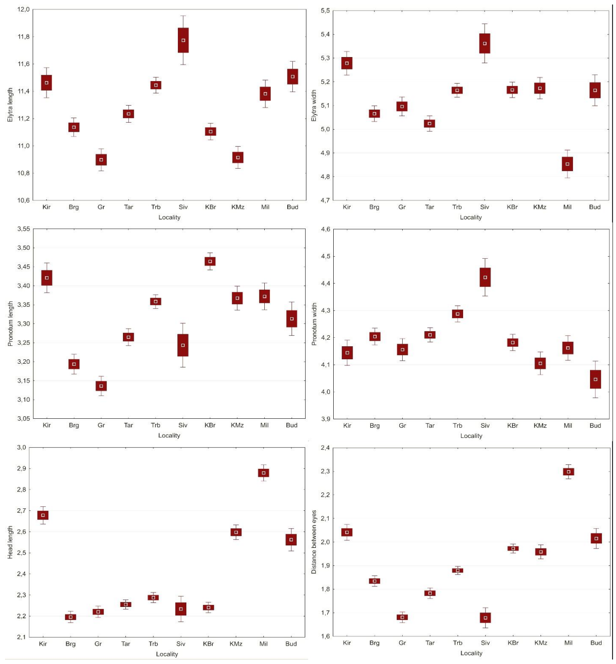


Diagram (1): Compared mean values of the measured traits of the beetle *C. granulatus* from different localities, boxes – mean error, whiskers – 1.96 mean error.

The comparison of mean values (Diag. 2) shows that beetles from the linden forest are smaller in all traits except head length, while beetles from the willow and black alder forests have similar mean values for these traits. Beetles from the black alder stand exhibit greater head length, while the head length of beetles from the linden and willow forests is approximately equal.

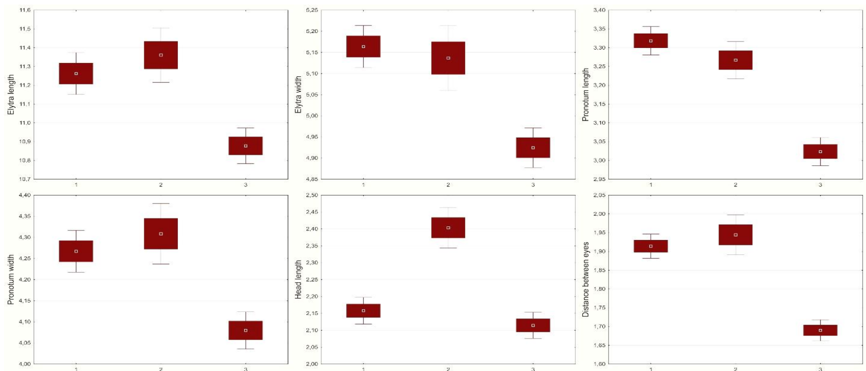


Diagram (2): Compared mean values of the measured traits of the beetle *Carabus granulatus* from different habitats of the locality Bragino; 1 – willow-gray alder, 2 – black alder, 3 – linden. Boxes – mean error, whiskers – 1.96 mean error.

Discriminant analysis by habitat type

The results of the discriminant analysis by habitat type (Tab. 4) show weak (Wilks' Lambda= 0.81), but statistically significant (F (12.85) = 78.05; p < 0.001) differences among the beetles. The coefficients of the classification functions indicate that the parameters with the greatest significance for discrimination are the length of the pronotum, as well as the length and width of the elytra.

Squared Mahalanobis distances are small but statistically significant (Tab. 3.). The maximum distance is observed between the morphometric parameters of ground beetles from spruce forest and small-leaved forest habitats (1.32), while the minimum distance (0.13) is found between beetles from the deciduous and broadleaf forests.

Table (4): Squared Mahalanobis distances (habitat type), p<0.001

	Broad-leaved forest	Small-leaved forest	Spruce forest
Broad-leaved forest	-		
Small-leaved forest	0.13	-	
Spruce forest	0.97	1.33	-

Discriminant analysis by geomorphological units

The results show significant and moderate differences between beetles from studied zones (Wilks' Lambda= 0.55, F (18.12) = 153.46, p<0.001). All traits make a statistically significant contribution to discrimination. According to coefficients of the classification functions, pronotum length has the highest discriminative value; other traits contribute to a lesser importance, while the contribution of pronotum width is very minimal. Squared Mahalanobis distances (Tab. 4.) indicate the greatest differences between the Moraine gently sloping plain of the Dnieper Glaciation with inherited post-Quaternary relief and the Flat glacial plain of the Moscow Glaciation. The smallest distance is observed between the Moraine gently sloping plain of the Dnieper Glaciation with inherited post-Quaternary relief and the Moraine gently undulating plain of the Moscow Glaciation.

Table (4): Squared Mahalanobis distances (geomorphological units), p<0,001. I – Moraine-glacial gently undulating plain of the Dnieper Glaciation, II – Moraine gently sloping plain of the Dnieper Glaciation with inherited post-Quaternary relief, III – Moraine gently undulating plain of the Moscow Glaciation, IV – Flat glacial plain of the Moscow Glaciation.

Zones	I	II	III	IV
I	-			
II	2.85	-		
III	1.50	1.06	-	
IV	1.39	5.17	3.73	-

It can be seen (Diag. 3) that Kireykovo (region I, broadleaved forest) is closer to region IV (spruce forest) and region III (spruce and small-leaved forests), than to region II (broadleaved forest as well). Regions II and III are quite similar despite belonging to different vegetation zones, but their geographic coordinates are close. Root 1 is mostly regulated by head length and distance between the eyes; while root 2 is shaped by length and width of the elytra, as well as pronotum length.

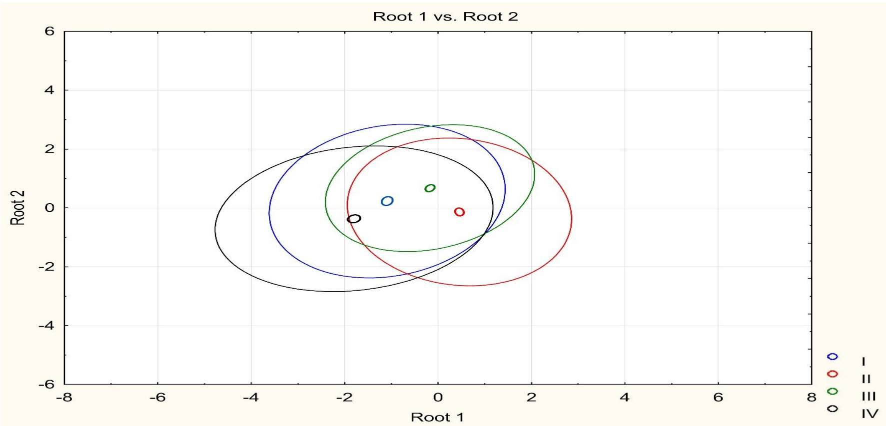


Diagram (3): Ordination of morphometric features in different geomorphological units in the plane of two discriminant axes.

Comparing Mahalanobis distances showed in Diag. (4) denotes the strongest diversification at the localities level; most of the distances fall within the range observed for the geomorphological units. Mahalonobis distances for the habitat type are the smallest, and in some cases, even smaller than the distances between spatially close populations within the Bragino locality.

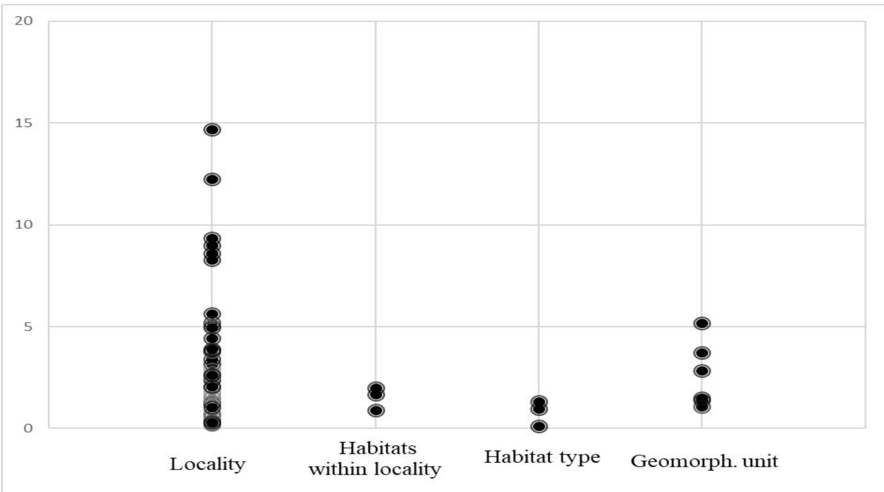


Diagram (4): Compared squared Mahalanobis distances between traits' measures of the *C. granulatus* depending on the grouping variable for the discriminant analysis.

DISCUSSION

The fact that discrimination of *C. granulatus* by measured traits is always reliable means that beetles have specific, significant differences in their morphology under various conditions. Although these differences are small and partly overlap with phenotypic variability, they are still consistent.

Discrimination by habitat type based on dominant trees appeared to be very weak, while geographical units as a grouping variable showed much better discrimination. This likely means that the differences in populations of ground beetles are more significantly influenced by historical aspects of microevolutionary changes - caused by mechanisms such as genetic drift and the founder effect, followed by post-glacial changes - rather than by short-term phenotypic adaptation to different habitats. Dominant trees themselves have an indirect and limited effect on the beetle, as it is a generalist predator that requires prey, some shade, humidity, and cover in the form of grass or litter.

Even on single locality level, discrimination based on dominant vegetation shows greater differences between populations than discrimination based on habitat type, which means that specific ecological features (microclimate, level of competition, position in landscape etc.) of each distinct ecosystem affect the morphometric traits more than average differences between habitat types.

Coefficients of classification functions revealed that for both geomorphological and locality predictors, pronotum length has major significance, while pronotum width has very low contribution. This suggests that discrimination by locality type largely inherits the geomorphological patterns. Overall, at the provincial level, pronotum length has the greatest impact on discriminating beetles specimens. The shape of the pronotum is considered to be related to habitat usage and locomotion (Thiele, 1977); it influences forelimb mobility and the way beetles move through their environment (Talarico *et al*., 2007; Laparie *et al*., 2013; Jachertz *et al*., 2019). This is confirmed for different habitat types, where both pronotum length and width play relatively important roles in discrimination. Nevertheless, the low influence of pronotum width for locality and geomorphological grouping variables suggests that it reflects conservative, microevolutionary-based differences or functions as a proxy for body size, as elytra length does (Kaspari and Weiser, 1999).

Overall, higher Wilks' Lambda values for the discrimination by locality suggest that, at the locality level, various environmental and phylogenetic factors combine and provide more pronounced differences in morphological traits.

Differences between populations from the locality Bragino are driven by distance between the eyes as well as pronotum length. It is known, that head width and the positioning of the eyes are correlated with predation behavior and lighting level (Bauer and Kredler, 1993; Bauer *et al*., 1998; Talarico *et al*., 2007). For the habitat-type level, beetles from spruce forests express higher distance between eyes than those from light small-leaved forests.

In terms of the morphometric structure of populations, the central position is occupied by the population from Kireykovo, located in a minimally disturbed area of broadleaf forests on a watershed, which can be considered a reference for the broadleaf forest zone. The population from Budnyansky, which belongs to the coniferous-broadleaf forest zone and is situated within a raised bog, is the closest to it. Formally, it is represented by a spruce forest, which, however, is very rich in broadleaved forest inhabitants (Aleksanov *et al*., 2024a), characteristic of morainic islands. It is interesting to note that despite the reduced abundance of beetles (Aleksanov *et al*., 2024b); a balanced morphometric structure has been preserved here.

Another group is formed by populations in the eastern part of the Kaluga region (broadleaf forest zone), associated with the Oka River valley (Bragino, Gremyachevo, Tarusa), to which a watershed locality (Trubetskoye) is added. Beetles in these localities are smaller in most traits (or lengths). On one hand, this can be explained by the poverty of infertility sediments with a high sand content, which are poor both in terms of moisture and mineral nutrients (compared to morainic deposits). The lower favorability of such habitats for beetles may result from poorer shelter quality (less deadwood for wintering, less dense herbaceous cover) as well as a poorer food base (fewer mollusks, earthworms). On the other hand, a no less important factor could be the prolonged economic use of the forests (agricultural, park, forestry, recreational), leading to their fragmentation and degradation of the soil cover. The negative reaction of the species to recreational load has been demonstrated for this region (Sionova, Alekseev, 2024).

A special case is the park in the village of Sivtsevo, where the beetles are on average the largest, which can be explained by the favorable herbaceous cover, but the variability is very high. Overall, all fragmented forests in the eastern part of the Kaluga region differ significantly from each other in individual morphometric traits. This may be related to selection for specific habitat conditions, but it is more likely a consequence of the small number of individuals that colonized these habitats (likely resulting in reduced genetic diversity).

The forests of Kaluga occupy an intermediate position between wild, quasi-climax forests and economically disturbed forests in terms of morphometric structure. They are smaller, but maintain the morphological proportions of beetles from quasi-climax forests. Despite being within the boundaries of a present-day city, they have remained forests for a long time, with moderate anthropogenic impact. Compared to broadleaf forests, they are less fertile—both climatically and in terms of soil-forming rocks.

At the opposite end of the virtual morphometric space is the wet spruce forest in the western part of the Kaluga region (Milyatino), it is wet, with moderate disturbance (apparently, it began to overgrow after World War II), but the glacial sediments from the Moscow glaciation are less fertile than those in Kireykovo.

Landscape-dependent variability

At the locality level, the linden forest in the ravine is harsher because it is a dry, young forest with hairy sedge, where beetles show reasonably smaller morphometric traits.

CONCLUSIONS

The study showed that *C. granulatus* beetles classified by various grouping factors have significant but relatively weak differences in their morphological traits. Pronotum length is a key trait for distinguishing populations, while pronotum width has low significance. Morphological differences in populations of *C. granulatus* are primarily influenced by historical microevolutionary processes, such as genetic drift, rather than being solely the result of phenotypic adaptation to habitats. Differences between beetles from various ecosystems depend on local ecological factors, such as microclimate, rather than just habitat type. At both spatial levels, similarity in morphometric structure does not directly correlate with geographic distance. between points on the ground.

Populations from the eastern part of the Kaluga region are smaller, which may be related to poor soil quality and intensive use of forests. Fragmented forests exhibit significant differences in morphometric traits, likely due to the small number of colonizing individuals.

Overall, the results highlight the importance of considering phylogenetic and ecological factors when studying morphological differences.

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CONFLICT OF INTEREST STATEMENT

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التغاير المورفومتري المرتبط بالأنماط البيئية للنوع *Carabus granulatus* L., 1758 (Coleoptera, Carabidae)

رومان غوربونوف*، فيكتور ألكسانوف**، ريفغات شاجيدولين*، سيرجي بيردنيك*، و ورايسا سوخودولسكايا*

*معهد مشاكل البيئة واستخدام الثروة المعدنية التابع لأكاديمية تتارستان للعلوم، الاتحاد الروسي، 420087، قازان.

**محمية بيلوجوربي الطبيعية الحكومية، الاتحاد الروسي، 309342، قرية بوريسوفكا.

***مؤسسة الميزانية الحكومية لمنطقة كالوغا "مديرية الحدائق"، الاتحاد الروسي، 248000، كالوغا.

****جامعة قازان الطبية الحكومية، الاتحاد الروسي، 420012، قازان.

*****محمية فولغا-كاما الحكومية للمحيط الحيوي الطبيعي، الاتحاد الروسي، 422623، قرية سادوفي.

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الخلاصة

هدفت هذه الدراسة إلى استقصاء مظاهر التغاير الشكلي في جماعات *Carabus granulatus* L., 1758 من رتبة Coleoptera و عائلة Carabidae المنتشرة ضمن بيئات متباينة في إقليم كالوغا، وذلك في إطار فهم ديناميات التكيف المورفولوجي على المستوى المحلي. وقد أفضى التحليل التمييزي متعدد المتغيرات إلى الكشف عن فروق شكلية ذات دلالة إحصائية، وإن كانت دقيقة، بين الجماعات المدروسة، حيث تبيّن أن طول الصدر الأمامي (البرونوتوم) يُعد السمة الأكثر تمييزًا بينها.

لقد أظهرت النتائج أن التغاير المورفومتري لا يُعزى في المقام الأول إلى التكيف الفينوتيبي المباشر مع نوع الموئل، بل يرتبط إلى حدّ بعيد بالعمليات التطورية الدقيقة التي نشأت عبر التاريخ الميكروتطوري للسلالات المحلية. كما بيّنت المعطيات أن العوامل البيئية

الموضعية، كالتغيرات الدقيقة في المناخ المحلي وتفاوت وفرة الموارد، تمتلك تأثيرًا أكثر فاعلية في تشكيل السمات الشكلية مقارنةً بتصنيف الموائل على نحوٍ عام.

أما من حيث التوزيع الجغرافي، فقد اتّسمت الجماعات الواقعة في شرق الإقليم بانخفاض في الحجم الكلي، ويرجّح أن ذلك يعود إلى الضغط الناتج عن الاستغلال الحراجي المكثّف. كما كشفت الدراسة أن الجماعات القاطنة في الغابات المجزأة أظهرت تمايزًا مورفومتريًا واضحًا، يُحتمل أنه ناجم عن "تأثير المؤسس" الناتج عن تأسيس جماعات جديدة من عدد محدود من الأفراد.