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RESEARCH ARTICLE

Carabus granulatus (Coleoptera, Carabidae) body size becomes less dependent on habitat latitude as soil organic carbon increases across mid-latitude zone

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Abstract

The study examined the relationship between soil quality and the size characteristics of ground beetle *Carabus granulatus* as bioindicators of ecosystem health. Soil quality is defined by its ability to sustain biological productivity, the surrounding environment, and the health of living organisms, with biological (especially soil invertebrates), chemical, and physical soil properties playing a key role. The aim of the research was to identify the influence of soil factors on the size variability of ground beetles. Using regression analysis, we studied the dependence of beetle size on organic carbon content in the soil (0–5 cm layer) and the geographical latitude of the habitat, taking into account the sex of the insects. Carbon content data were extracted from an existing global distribution map generated using machine learning. A total of 8107 specimens from 13 regions (42,9–56,8° N) were examined. The findings revealed a statistically significant influence of both latitude and organic carbon content on beetle size, with an interaction effect identified. It was established that males are 1 mm smaller than females. Additionally, for each degree increase in latitude, the length of the elytra decreases by 0.13 mm, and for each tonne of organic carbon in the 5 cm soil layer, it decreases by 0.14 mm. The results demonstrate a compensatory effect: as organic carbon content increases, the influence of habitat latitude on insect size weakens. These findings expand our understanding of the mechanisms shaping insect size variability in relation to soil conditions and geographical location, which is important for ecological monitoring and bioindication.

Keywords

Carabidae, soil quality, soil organic carbon, latitudinal gradient, bioindicators, body size variability, ecological monitoring

Introduction

Although soil quality is difficult to define precisely, it can be conceptualized as the soil's ability to: sustain biological productivity; maintain environmental quality; promote the health of plants, animals, and humans (Doran and Parkin 1994; Vilkova et al. 2023; Oliveira et al. 2024).

These core soil functions depend on its structural and functional integrity, as well as on the impacts of management practices or unintended disturbances.

Soil is a heterogeneous mixture of living and nonliving components, encompassing a highly complex assemblage of organisms and their byproducts. The living components of soil – including microbes, plant roots, and soil invertebrates – exert profound influences on soil characteristics that affect its quality. Therefore, it is critically important that soil quality assessments incorporate both biological, chemical, and physical soil properties. While most biological measurements to date have focused on microbial populations and activity, there is a growing recognition of the importance of soil invertebrates as vital soil components and potential indicators of soil quality.

Ecological reviews of soil invertebrates confirm that these organisms influence soil structure, alter microbial activity patterns, and affect the dynamics of soil organic matter and nutrient cycling (Heal and Kjoller 1996; Vilkova et al. 2024). Moreover, numerous studies indicate the potential utility of using soil invertebrates as indicators of physical or chemical soil disturbances (Paoletti et al. 1991; Stork and Eggleton 1992; Linden et al. 1994).

Macroinvertebrates have a significant impact on the physical structure of soil, particularly in the formation of stable aggregates. Soil aggregates play a key role in the dynamics of soil organic matter, as they physically protect organic matter from degradation and influence numerous subsurface processes – from microbially mediated nutrient cycling to nutrient sorption and water flow (Six et al. 2004).

Alongside numerous studies on the systematics and taxonomy of soil invertebrates, recent decades have seen growing attention directed towards the functional diversity of this group. Functional traits are measurable characteristics at the individual level (e.g., phenological, morphological, behavioural, or physiological traits) that can be linked to an organism's fitness or its impact on the ecosystem (Blaum et al. 2011; Pey et al. 2014; Brousseau et al. 2018).

In contrast to the taxonomic approach, the functionaltraitbased approach better explains variability in community composition and interspecific effects on ecosystem processes (De Deyn et al. 2008; Mokany et al. 2008; Funk et al. 2017). For example, functional traits can:

- predict species abundance and distribution across environmental gradients (Bernhardt-Römermann et al. 2011; Violle et al. 2011);
- explain the impact of climate change on species range shifts (Lopez-Iglesias et al. 2014; Moor et al. 2015);
- clarify relationships between community structure and ecosystem processes (Lavorel and Garnier 2002; Zirbel et al. 2017; Laigle et al. 2018).

Thus, the functional traitbased model is currently regarded as a promising approach for identifying patterns in species distribution, community composition, and ecosystem processes (McGill et al. 2006; Violle et al. 2007).

Body size is widely used as a functional trait. It is an integrative characteristic that directly or indirectly affects numerous other morphological traits, as well as physiology, behavior, and biochemical processes (Brown et al. 2004; Baranovská and Knapp 2013; Fitzgerald et al. 2025). The study of body size variability – both within metaanalyses and in the context of clarifying general biological rules – is a priority in modern science. When conducting such studies, it is essential to select an appropriate study organism that is well understood from both biological and ecological perspectives.

Among such suitable organisms are ground beetles (Coleoptera, Carabidae), obligate members of the soil cenosis. As one of the most diverse and economically important beetle families on Earth, carabids are regarded as a valuable bioindicator (Rainio and Niemelä 2003; Meacci et al. 2025).

Recent metaanalyses provide mixed evidence regarding changes in terrestrial insect abundance. Generalisations based on traits (e.g., body size, diet, flight capacity) offer insights into community responses, but generalisations for different Carabidae species have not yet been achieved.

Ecological modelling plays a decisive role in such studies, as extensive databases on a wide range of morphometric traits are available for carabids (Luzyanin et al. 2022; Langraf et al. 2025).

It has been shown that ground beetles exhibit sexual dimorphism, with females being larger; therefore, this factor is highly significant when studying beetle body size (Ananina et al. 2020; Sukhodolskaya et al. 2021).

Latitudinal variation of body size of ectothems is widely explored but shows contradictory results for different species. For example, certain species may increase (Taylor-Cox et al. 2020) or decrease (Fattorini et al. 2013; Marshall et al. 2013) with growing latitude. Interspecific approach reveals great variability which can be treated as absence of trends on that level (Horne et al. 2019; Merwin et al. 2022). Carabid beetles tend to decrease towards the north (Heino et al. 2019; Lövei and Magura 2022).

For the study, we selected the ground beetle species *Carabus granulatus* Linnaeus, 1758, which is widespread in the midlatitude zone and may inhabit diverse biotopes with varying soil characteristics (Thiele 1977). Thus, it can provide reliable representation of environmental conditions, which makes it suitable for our goals.

Previous studies on *C. granulatus* showed that its size decreases towards the north (Sukhodolskaya and Saveliev 2017; Gorbunov et al. 2025).

When planning our study, we took into account previous research and also hypothesised that the amount of organic carbon in the soil – as an indicator of food resource availability for ground beetles – would have a positive effect on their body size.

Based on prior observations and ecological assumptions, we formulated the following hypotheses:

H_0 (no effect):

- Geographic variation in latitude does not affect *C. granulatus* body size;
- Variation in surface soil organic carbon does not correlate with beetle body size;
- No sexual size dimorphism.

H_1 (predicted effect):

- *C. granulatus* body size declines with increasing latitude, according to previous studies.
- Higher soil organic carbon is associated with larger beetles, possibly reflecting improved resource availability.
- Females are larger than males.

Consequently, the study aimed to: develop a regression model that incorporates the latitude of the beetle sampling sites, the amount of organic carbon in the soil, and the sex of the beetles; assess the significance and direction of the effects of these selected factors.

Materials and methods

Carabus granulatus Linnaeus, 1758 is a mesophilous, widespread trans-Palearctic meadow species (Turin et al. 1991), characteristic of forest biotopes in the middle zone of the European part of Russia (Ruchin et al. 2016), but in some regions, for example in Italy, it can occupy both types of biotopes (Allegro 2010).

1. Object and sample area

Samples were collected from 2006 to 2025 using pitfall traps in the following regions (Table 1):

Table 1. Regions of sampling *C. granulatus*

Region	Number of sampling sites	Mean latitude	Mean longitude	Sample size
Bulgaria	1	42.8911°N	22.9988°E	94
Italy	2	45.4119°N	10.2854°E	105
Slovakia	3	47.8477°N	17.6157°E	143
Czech Republic	2	49.9754°N	32.4301°E	66
Poland	1	52.7314°N	22.8928°E	160
Belarus	1	55.2052°N	30.2933°E	129
Russia:				
Ryazan Oblast	2	53.8701°N	44.2460°E	43
Kaluga Oblast	13	54.45446°N	35.9554°E	3442
Republic of Mordovia	16	54.6811°N	44.4129°E	456
Kemerovo Oblast	4	55.3464°N	86.1041°E	208
Republic of Tatarstan	18	55.8118°N	49.2286°E	2438
Republic of Mariy El	2	56.6489°N	47.6160°E	215
Udmurt Republic	2	56.7769°N	53.1337°E	608

2. Statistical analysis

The sample size comprised 8107 ground beetle specimens. To represent beetle body size, elytra length was selected as the target trait.

To build a model for the variability of elytra length in *C. granulatus*, three predictors were used: latitude (in decimal degrees); soil organic carbon content (in tonnes per hectare; denoted as soil_carbon), as an indicator of habitat resource richness; beetle sex (sex).

The study employed data on the global distribution of organic carbon in the 0–5 cm soil raster layer, with a 250 m spatial resolution. These data were derived using machine learning methods by Hengl et al (2017). The information on soil carbon content at the studied sites was obtained by extracting data from this raster using known coordinates.

To explain the influence of the factors, a standard multiple linear regression model was used. To assess the relationships between predictors, a correlation analysis was performed using Pearson's correlation coefficient (Meshalkina and Samsonova 2008).

To evaluate multicollinearity in the model, the variance inflation factor (VIF) was used:

$$\mathrm{VIF}i = 1 / (1 - R^2 i),$$

where $R^2 i$ is the coefficient of determination from the regression of the i-th independent variable on the others.

The overall model quality was assessed using: the proportion of explained variance (R^2); Akaike's Information Criterion (AIC). A model with a lower AIC value has better explanatory power.

The normality of residuals was tested using the Kolmogorov-Smirnov test with Lilliefors's modification. With large sample sizes, normality tests become overly sensitive to even minor deviations from normality. However, such deviations do not affect the results of parametric tests (Oztuna et al. 2006; Ghasemi and Zahediasl 2012). In cases of significant deviations from normality ($p < 0.05$) we further evaluated distribution visually by quantile-quantile plots and histograms. The quantile-quantile plot of the residuals for the final regression model is shown on Figure 1.

Homogeneity of residual variances across quantitative predictors was assessed using Fisher's test. For quantitative predictors, data were split into two groups based on the median.

Coefficient significance levels were computed with White's correction for heteroscedasticity when residual variances were heterogeneous with respect to any factor (Long and Ervin 2000).

Statistical analyses were conducted in the R programming environment (R Core Team 2025), using the following packages: terra (Hijmans 2025) for raster data extraction; car (Fox and Weisberg 2019) for calculating VIF; nortest (Gross and Ligges 2015) – for normality testing; lmtest (Zeileis and Hothorn 2002) and sandwich (Zeileis 2004; Zeileis et al. 2020) for robust linear regression coefficient estimation.

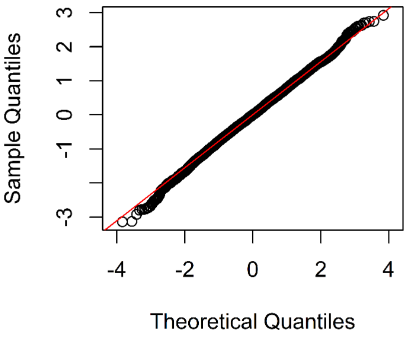

Figure 1. Quantile-quantile plot (QQ-plot) comparing the empirical distribution of model residuals with the normal distribution. Points lying along the straight line indicate that the distribution conforms to normality.

Results

The correlation coefficient between latitude and soil organic carbon was 0.33, which falls within acceptable limits for conducting regression analysis. This correlation aligns with known data indicating that soil carbon content increases at higher latitudes (Holden 2005; Ahmedin and Elias 2022).

Simple linear regression of elytra length on latitude has R^2 = 0.25, and latitude coefficient = -0.05 (Fig. 1). Simple regression on organic carbon has R^2 = 0.26 and coefficient = -0.01 (Fig. 2). All p-levels < 0.001. Beetle sex was included in these models without interactions. Thus, elytra length statistically significantly decreases along sole factors for both males and females.

A model including interactions among all three predictors (R^2 = 0.275, AIC = 19292) revealed a significant effect of latitude, organic carbon, and their interaction. Beetle sex was not identified as a significant factor influencing size, which contradicts biological evidence; therefore, this model was rejected.

A model with interactions between organic carbon and latitude, and between organic carbon and sex (R^2 = 0.276, AIC = 19289) showed that organic carbon significantly affects female size, with a coefficient of −0.13. However, no significant carbon effect was detected for males, so this interaction was excluded from further consideration.

The final model (R^2 = 0.276, AIC = 19287, *F*-statistic = 771.7) included beetle sex, latitude, soil organic carbon level, and the interaction between latitude and carbon (Table 2). According to the R^2 and AIC values, this model exhibits slightly greater explanatory power. ANOVA results for the selected set of predictors indicate their significant influence on beetle size (Table 3).

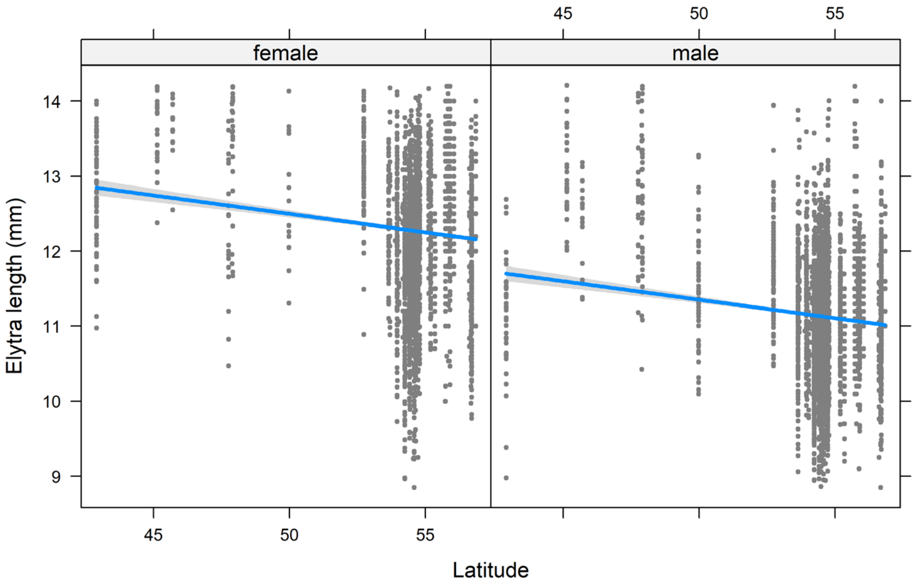

Figure 2. Linear regression plot of elytra length of *C. granulatus* on latitude.

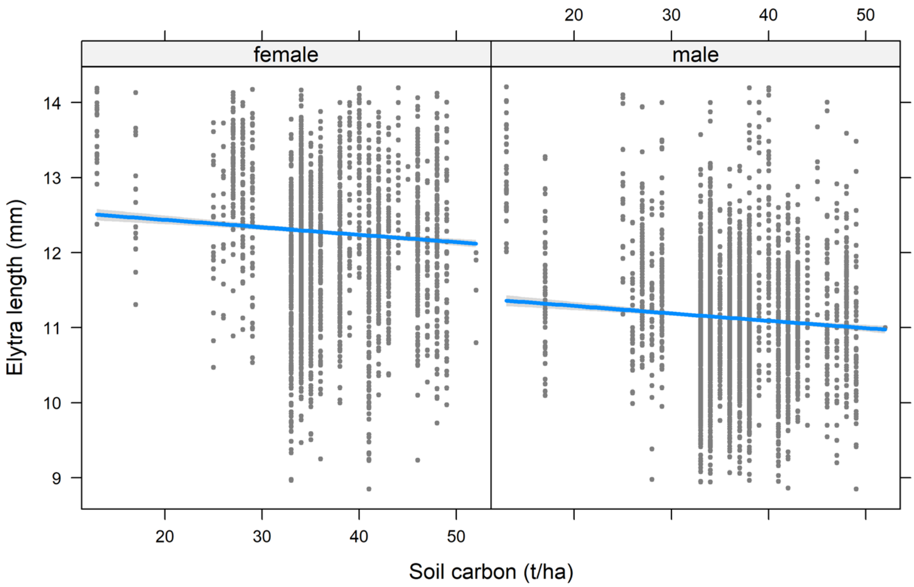

Figure 3. Linear regression plot of elytra length of *C. granulatus* on soil organic carbon content.

Table 2. Results of regression analysis of the relationship between elytra length in *C. granulatus* and the predictors: latitude, soil carbon content, and sex. All p-levels < 0.001

	Estimate	Std. Error	t value
Intercept	19.466	0.913	21.32
latitude	-0.129	0.017	-7.536
soil_carbon	-0.136	0.030	-4.498
sex2*	-0.986	0.019	-52.475
latitude×soil_carbon	0.002	0.0005	4.115

Note: *Males compared to females.

The degree of multicollinearity (as measured by VIF) among the variables was low, not exceeding 1.002. The significance level (*p*-level) of the normality test for residuals was 0.014 (with $D = 0.01$). The *p*-levels from Fisher's test for residual variance across predictors were: 0.065 for latitude; < 0.001 for sex.

Table 3. Results of the factorial analysis of variance (ANOVA) for elytra length in *C. granulatus*, by factors: latitude, soil organic carbon, and sex

	Df	Sum of Squares	Mean Square	*F*-value	*p*-level
latitude	1	174.11	174.11	275.56	< 0.001
soil_carbon	1	2.86	2.86	4.53	0.033
sex	1	1726.78	1762.78	2789.84	< 0.001
latitude× soil_carbon	1	10.7	10.7	16.93	< 0.001
Residuals	8100	5118	0.63	–	–

According to the estimated coefficients, male elytra are 1 mm shorter than female elytra. For every degree increase in latitude, elytra length decreases by 0.13 mm, and for every increase in tonne of soil carbon/ha, decreases by 0.14 mm. When both organic carbon and latitude increase simultaneously, elytra length increases by 0.002 mm.

Scatter plots with regression line for sole factors and their combination displayed on Figures 2–4. Since beetles sex wasn't included in the interactions, both females and males displayed on the plots. In Figure 4 displayed regression lines for both sexes in order to visualize sexual dimorphism of *C. granulatus*.

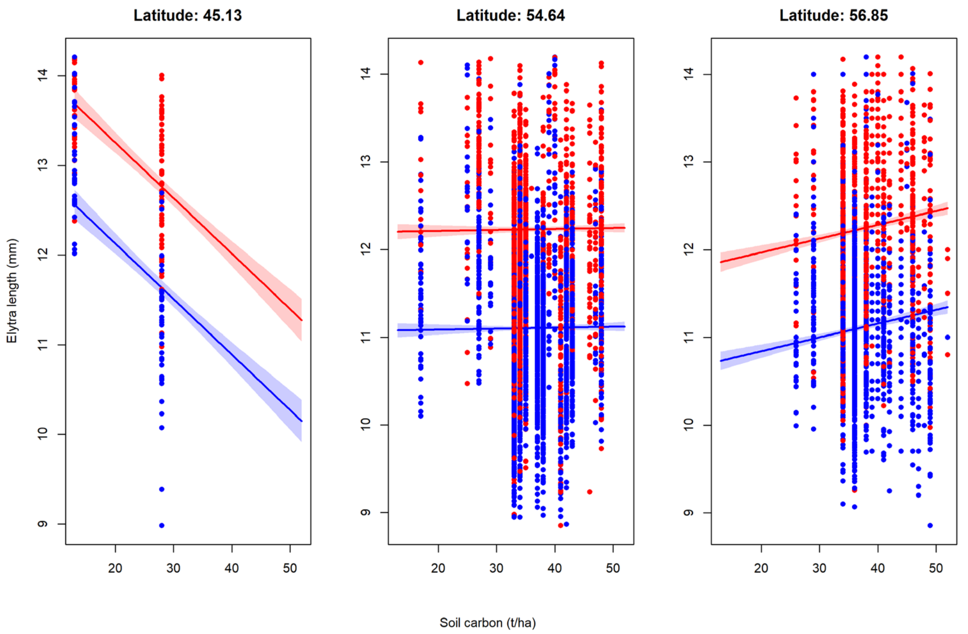

Figure 4. Regression plots of elytra length of *C. granulatus* on soil carbon for the 1st, 50th and 99th percentiles of latitude factor. Females colored in red, males in blue. The first, fiftieth, and ninety-ninth percentiles of latitude were used. They do not correspond to the beginning, middle, and end of the latitudinal gradient. We believe this is correct, as the «sampling gap» between the starting point and the 55th degree of latitude does not yield a representative graph.

Discussion

A significant effect of sex, latitude, and soil organic carbon level on the elytra length of *C. granulatus* was detected. Both females and males responded to these factors in the same way, showing a decrease in size. Consequently, the null hypothesis was rejected, although not all results matched the initial assumptions.

The reduction in insect body size within a species at higher latitudes has been documented in the literature and is consistent with the socalled "inverse Bergmann's rule" (Van Voorhies 1996; Mousseau 1997; Sota et al. 2000). It was expected that soil organic carbon content reflects the richness of the food base for predatory ground beetles, which would promote larger body sizes. However, this assumption was not confirmed.

Probably, within the model, this indicator – without interactions – is associated with habitat conditions where beetles face food limitations, or smallersized beetles gain a competitive advantage. Thus, at the same latitude, a more abundant food supply may favor increased population densities both of the same ground beetle species and of other predators.

Under conditions of competition and high population density, the amount of food available per individual beetle decreases, and high fecundity – linked to female abdominal size – loses its adaptive value. This conclusion aligns with one of the intermediate models, where only females show a negative coefficient for soil organic carbon.

Increasing numbers of predators promote selection for smaller body sizes, regardless of sex (Shmalgauzen 1946). The positive coefficient of the joint effect of carbon and latitude may indicate that in higher latitudes – where environmental conditions are harsher – greater organic richness contributes to better nutrition and, consequently, larger body size in ground beetles. We hypothesize that in colder climates, the utilization of organic carbon in soil within food chains involving ground beetle larvae is more efficient, leading to an increase in the body size of adult animals.

Conclusion

Regression modeling showed that body size of *C. granulatus* decreases with increasing both latitude and soil organic carbon as sole factors. But combined influence of these factors reveals that with growing latitude negative effect of soil carbon content weakens up to changing its direction. *C. granulatus*, belongs to Carabidae family – valuable monitoring object and important part of ecosystems, which reflects its health and stability. Their role as both predators and prey in food webs indirectly affects soil processes, including nutrient cycling. Modelling the influence of external factors on functional traits of carabids opens up opportunities for predicting the dynamics of soil communities both under anthropogenic transformation and in the context of contemporary climate change.

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