Check for updates

Received: 21 July 2021 | Revised: 29 May 2022 | Accepted: 3 June 2022

DOI: 10.1111/jbi.14458

Journal of Biogeography WILEY

RESEARCH ARTICLE

Body size and the urban heat island effect modulate the temperature–size relationship in ground beetles

Gábor L. Lövei[1,2] | **Tibor Magura**[1,2,3]

[1]Department of Agroecology, Flakkebjerg Research Centre, Aarhus University, Slagelse, Denmark

[2]ELKH-DE Anthropocene Ecology Research Group, University of Debrecen, Debrecen, Hungary

[3]Department of Ecology, Faculty of Science and Technology, University of Debrecen, Debrecen, Hungary

Correspondence
Gábor L. Lövei, Department of Agroecology, Aarhus University, Flakkebjerg Research Centre, Slagelse, Denmark.
Email: gabor.lovei@agro.au.dk

Funding information
Aarhus Universitets Forskningsfond; Hungarian National Research, Development and Innovation Fund, Grant/Award Number: OTKA K-131459

Handling Editor: Simone Fattorini

Abstract

Aim: Body size is a key trait linked to other life history traits and influences several individual-, community- and ecosystem-level characteristics, processes, functions and services. Ecological and evolutionary body size responses at the intra- and inter-specific level to thermal geographic gradients (e.g. latitudinal or altitudinal ones) are widely studied. Whether this temperature-size relationship remains true for community-wide body size is still largely unknown.

Location: Northern temperate region.

Taxon: Ground beetles (Carabidae).

Methods: We assessed the temperature-size relationships using data from 11 northern temperate locations, spanning 25 latitudinal degrees. Furthermore, we quantified the effects of potential competing factors, such as body size and habitat preference of carabid assemblages and sub-assemblages along urbanisation gradients, as well as the urban heat island (UHI) effect on this relationship.

Results: We found significant negative relationship between the community-wide mean body size and the geographical latitude (converse Bergmann cline) for the whole ground beetle assemblage and the sub-assemblages of large-bodied species. This relationship was stronger in the urban localities than in rural ones. For the sub-assemblages of small-sized species, the relationship was not significant. We found significant negative relationship between the community-wide mean body size and the latitude for the sub-assemblages of both the non-forest and the forest species, and these became stronger in the urban habitats.

Main Conclusions: Our results highlight the leading role of the individual body size and the UHI effect in determining the community-wide body size–latitude relationship in ground beetles.

KEYWORDS
Bergmann's rule, body size shifts, carabids, habitat preference, rural–urban gradient, urbanisation

1 | INTRODUCTION

Body size is a trait with effects at multiple scales, from individual to ecosystem levels (Hildrew et al., 2007). It influences several individual characteristics, such as the morphology and physiology of organisms with consequences for fitness (Kingsolver & Huey, 2008). In addition, body size correlates with other life history traits, such as life span, and fecundity (Chown & Gaston, 2010), and determines ecological niches and spatial distributions (Davey et al., 2005; Jetz et al., 2004; Magura & Lövei, 2020b). Furthermore, body size influences biotic interactions, thus affecting community dynamics, food webs and ecological networks (Woodward et al., 2005). Consequently, changes in body size have important consequences for ecosystem functioning and related ecosystem services (Ohlberger, 2013; Petchey & Belgrano, 2010).

Larger individuals can potentially produce more offspring, live longer, be superior competitors and better at avoiding predators, have higher dispersal power and larger home range (Brown & Sibly, 2006). Large body size, however, has several drawbacks. Growing larger takes more time and, during this time period, organisms may die or the environment may become unfavourable (Blanckenhorn, 2000). Larger individuals also commonly require more resources per unit time to maintain themselves. Accordingly, there is an optimal size, which depends on the environmental conditions that influence growth (Stearns, 1992).

Ecological and evolutionary body size responses to temperature and associated climatic factors are observed across geographical thermal gradients (e.g. latitude or altitude), where small body size is typically associated with warmer conditions (low latitudes or altitudes) and termed Bergmann's rule for differences within species or among closely related species (Pincheira-Donoso, 2010; Verberk et al., 2021; Watt et al., 2010). Bergmann's rule was originally formulated for endothermic vertebrates (mammals and birds) and costs related to thermoregulation was suggested as an explanatory mechanism, namely that the smaller surface area: volume ratio of larger animals helps to reduce heat loss in cold environments, and vice versa (Shelomi, 2012). The majority of birds and mammals show Bergmann clines (Meiri & Dayan, 2003), but it remains undecided whether Bergmann's rule is also valid for ectotherms (Shelomi, 2012).

The operational body temperature of ectothermic organisms relies on ambient temperature (Atkinson, 1994). Higher ambient temperatures increase the rates of biochemical reactions and of metabolism, causing increased costs associated with developing a given body size (Brown et al., 2004). Based on this relationship, ectothermic species should follow the temperature-size rule, and mature at a smaller size when reared under warmer conditions (Atkinson, 1994). However, theories inspired by temperature-independent mass-specific metabolic rates (Makarieva et al., 2005), temperature-mediated selection on body size (Winterhalter & Mousseau, 2008), and the earlier diapause and shorter growing seasons at high-latitudes/altitudes (Leather et al., 1993) suggest a "converse-Bergmann" cline for ectotherms, in which organisms are smaller in colder climates and vice versa (Shelomi, 2012). Furthermore, the temperature-size pattern in ectotherms can also be influenced by life history and ecological traits (Chown & Gaston, 1999; Tseng & Soleimani Pari, 2019) or habitat preference (Pallarés et al., 2019).

However, anthropogenic influence can modify ambient temperature conditions, potentially influencing the temperature-size relationship. For example, urban areas generally become warmer than their surrounding rural areas due to human activities and the modification of land surfaces (urban heat island [UHI] effect; Arnfield, 2003). Urbanised environments often exert strong selective pressure (Start et al., 2018), and higher temperatures due to the UHI effect can be considered one of the strongest such factor, especially for ectotherms.

In the present study, we aimed to articulate the temperature-size pattern in ectotherms, testing the effects of potential competing factors, such as body size and habitat preference of the given organisms, as well as the UHI effect. For this test, we chose ground beetles (Coleoptera: Carabidae). Among ectothermic groups, ground beetles are frequently used as model organisms to investigate relationship between the individual and community parameters and habitat characteristics (Kotze et al., 2011; Lövei & Sunderland, 1996). Specifically, we hypothesized that (1) the temperature-size relationship of ground beetles shows a converse-Bergmann cline, as it was previously found for beetles (Shelomi, 2012). Further, we assumed (2) a positive relationship between body size and latitude (Bergmann cline) for large-sized beetles, and a negative body size–latitude relationship (converse Bergmann cline) for small-sized beetles, similar to findings along a North American latitudinal gradient (Tseng & Soleimani Pari, 2019). Moreover, we hypothesized that (3) changes in body size along latitudinal gradient are more pronounced for the habitat specialist species (forest species in this study), as they are especially sensitive to modifications in ambient temperature conditions (Magura et al., 2020; Marrec et al., 2021). Finally, it was assumed that (4) the temperature-size relationship is more pronounced in urban habitats compared to rural ones, because the ambient temperature is warmer in urban than in rural habitats (Arnfield, 2003).

Our analysis of published data on ground beetles from 11 countries in the Northern Hemisphere detected a significant negative body size–latitude relationship for ground beetles (H1 supported). Body size of small-sized species, however, did not changed significantly along the latitudinal gradient, while large-sized beetles showed a negative body size–latitude relationship (H2 rejected). Moreover, the negative body size–latitude relationship was not more pronounced for the habitat specialist species compared to the non-habitat specialist species (H3 rejected). All the significant negative body size–latitude relationships were stronger in urban habitats compared to rural ones (H4 supported).

2 | MATERIALS AND METHODS

2.1 | Data and study sites

We collected published data through a literature search on Web of Science (all databases option) for the period 1975–2021, using the search terms: TOPIC = (urban*) AND TOPIC = (rural) AND TOPIC = (carabid*). The search was performed on the network of Aarhus University, Denmark. We also checked the references found by this search, and searched the Global Biodiversity Information Facility (https://www.gbif.org) and PREDICTS (Hudson et al., 2017) databases for additional datasets. Our inclusion criteria were: presence of species-level abundance data of ground beetles from at least three forested rural and urban habitats. The urban fragments also had to be remnants of the rural counterpart. We found 11 such datasets, whose locations spanned 25° of latitude, (Table 1) and were in Belgium (Brussels), Bulgaria (Sofia), Canada (Edmonton), Denmark (Sorø), Finland (Helsinki), Germany (Hamburg), Hungary (Debrecen), Japan (Hiroshima), Romania (Sfântu Gheorghe), South Korea (Seoul) and the United Kingdom (Birmingham). In all these studies rural sites had max. 5% built-up area, while urban ones were all >60% within a 1 km radius of the study sites.

2.2 | Statistical analyses

Ecogeographical rules can be analysed at different hierarchical and interacting levels (intraspecific, interspecific and assemblage; Gaston et al., 2008). Body size–latitude relationships are usually tested at the intra- and inter-specific level. Studies at the assemblage level are not common, though processes at the intraspecific, interspecific and assemblage level interact (Gaston et al., 2008). Carabid body size changes at the species level generated by modifications in habitat parameters (like ambient temperature) are usually manifested at the community level, too (Magura & Lövei, 2021). Therefore, we used community-wide body size to test the body size–latitude relationship in ground beetles. Community-wide body size of ground beetles was expressed by community-weighted mean body size (CWMBS) which is a reliable, widely used parameter of community-level body size (Magura et al., 2020; Merckx, Kaiser, et al., 2018; Merckx, Souffreau, et al., 2018). This index is an inherent feature in the assemblage approach for testing ecogeographical rules (Gaston et al., 2008), and is appropriate to measure both the rate of change in community composition in response to environmental changes (sensu the community temperature index: Devictor et al., 2008). Here, we use it to measure the rate of change in community composition in response to geographic thermal gradients. The index reflects the relative composition of large vs. small species in local assemblages and is calculated from species-specific body size data. We obtained minimum and maximum species-specific body length values from a carabid database (Homburg et al., 2014), and geometric means were calculated for body size for all sampled species (Chown & Gaston, 2010). In all 11 studies, the sampling period covered a substantial part of the beetles' activity period (Niemelä et al., 2002). Cumulative species abundance values obtained by continuous pitfall sampling over the full activity period generally provide a good relative measure of species abundance (Baars, 1979), thus the calculation of the CWMBS was done using abundance-weighted means. These are calculated, for a given site, as the average of species-specific body length (mm) weighted by species abundances (CWMBS is, thus, expressed in mm). An increase in CWMBS indicates that the species assemblage is increasingly composed of individuals belonging to larger species and vice versa.

In a recent study, measuring the body size of ground beetle specimens (eight species) collected throughout North America, Tseng and Soleimani Pari (2019) showed that larger-bodied beetles (beetles with elytra >13 mm, which equals body size >21.3 mm; see Hůrka, 1996) show a positive relationship between body size and latitude (Bergmann's rule), while smaller-bodied species were more likely to show a negative body size–latitude relationship (converse Bergmann's rule). Based on this, we calculated site-level CWMBS separately for the whole ground beetle assemblage as well as for the sub-assemblages of large- (body size ≥21.3 mm) and small-bodied (body size <21.3 mm) species. Separately analysing species with different habitat preferences, and thus different sensitivity to environmental changes may provide a more articulate insight into the community-level response (Magura & Lövei, 2020a; Matthews et al., 2014). Therefore, we calculated CWMBS of all sites independently for whole ground beetle assemblages, the sub-assemblages composed of habitat (forest) specialist species, and for non-forest species (habitat generalists and open-habitat specialists). Habitat preferences (forest specialist, habitat generalist, open-habitat specialist) were derived from the original papers; when this information was lacking (in <10% of the species), we consulted the database by Homburg et al. (2014).

TABLE 1 Studies included in this analysis, which sampled ground beetles in at least three spatially replicated, clearly defined, similarly vegetated rural and urban habitats (forests or forest fragments). Study sites are arranged accordingly to their geographical latitude.

Studied city, country	No. of rural (R) and urban (U) sites	Geographical latitude	Reference
Helsinki, Finland	4 R, 4 U	60.16 N	Niemelä et al. (2002)
Sorø, Denmark	4 R, 4 U	55.43 N	Elek and Lövei (2007)
Hamburg, Germany	3 R, 3 U	53.57 N	Weller and Ganzhorn (2004)
Edmonton, Canada	4 R, 4 U	53.55 N	Niemelä et al. (2002)
Birmingham, UK	4 R, 4 U	52.48 N	Sadler et al. (2006)
Brussels, Belgium	3 R, 4 U	50.51 N	Gaublomme et al. (2005)
Debrecen, Hungary	4 R, 4 U	47.53 N	Magura et al. (2004)
Sfântu Gheorghe, Romania	4 R, 4 U	45.86 N	Tóthmérész et al. (2011)
Sofia, Bulgaria	4 R, 4 U	42.69 N	Niemelä et al. (2002)
Seoul, South-Korea	3 R, 3 U	37.57 N	Jung et al. (2018)
Hiroshima, Japan	4 R, 4 U	34.40 N	Ishitani et al. (2003)

As urban areas are generally warmer than their surrounding rural areas (UHI effect; Arnfield, 2003), we analysed the body size–latitude relationships separately for the urban and rural localities. For the selected study locations, the UHI effect was expressed as the difference in the average daytime maximum land surface temperature between the urban and the surrounding rural area. In all locations the UHI effect was notable and ranged from 0.99°C (Sorø) to 5.61°C (Hiroshima) (Center for International Earth Science Information Network - Columbia University, 2016).

We examined whether the identified UHI effect was related to the geographical position (latitude) of the studied locations by linear regression analysis. To analyse the body size–latitude relationships, and to investigate whether this relationship was dependent on the level of urbanisation (rural vs. urban), the site-level CWMBS values (dependent variable) were modelled against the latitude of the study locations (independent variable) and the level of urbanisation (categorical factor) by an analysis of covariance. The strength of the relationships between the CWMBS and the geographical latitude for rural and urban ground beetle assemblages were characterised by the R^2 values. The normal distribution of the data, independence of the latitude of the study locations (independent variable) and the level of urbanisation (categorical factor), and the homogeneity of variance among the categories (rural vs. urban sites) were also verified. All statistical analyses were performed using the R program environment (version 3.5.3; R Core Team, 2017).

3 | RESULTS

The literature search yielded 89 publications, while the additional search in their references provided one additional, relevant study. Of these, 11 studies fulfilled the selection criteria (Table 1). All these studies sampled the same habitat type (forests or forest fragments) in rural (non-urbanised) as well as urbanised sites. The majority of the studies originated from Europe (eight papers), two from Asia and one from North America. At these 11 sites, a total of 207 ground beetle species were collected (supporting information table S1 in Magura et al., 2020).

In all studied locations, well defined, remarkable UHI effects were found, since the ambient surface temperature in urban habitats were warmer by at least ~1°C than their rural counterparts. The difference in the average daytime maximum land surface temperature between the urban and the surrounding rural area, however, significantly decreased with increasing geographical latitude (Figure 1; $F_{1,9} = 7.238$, $R^2 = -0.384$, $p = 0.025$).

Significant negative relationship between CWMBS and geographical latitude (converse Bergmann cline) was found for both the whole ground beetle assemblages and the sub-assemblages of large-bodied species, while this relationship was not significant for the sub-assemblages of species with a body size <21.3 mm (Table 2; Figure 2). The relationship was stronger for urban (sub-)assemblages than for the rural ones (whole beetle assemblages: $R^2 = -0.271$ vs. $R^2 = -0.088$; large-bodied species: $R^2 = -0.130$ and $R^2 = -0.073$ for urban and rural, respectively). The effect of urbanisation level (rural vs. urban) was significant for both the whole ground beetle assemblages and the sub-assemblages of small-bodied species (defined as <21.3 mm body size), while it was marginally significant for the sub-assemblages of large-bodied species (Table 2), indicating that the mean CWMBS values of these (sub-)assemblages were higher in rural than urban sites (Figure 2). When a three-class size division (small-sized: <10.5 mm, medium-sized: 10.5–15.0 mm, large-sized: >15.0 mm) was used, the sub-assemblages of both large-sized and the small-sized species showed a significant negative trend, while the sub-assemblages of medium-sized species did not show a trend (see Table S1; Figure S1). The interaction of the geographical latitude and the level of urbanisation (rural vs. urban) was not significantly different from zero for any of the (sub-)assemblages (Table 2), meaning that the geographical latitude has a similar effect on CWMBS for rural and urban assemblages and sub-assemblages (Figure 2).

The relationship between the CWMBS and geographical latitude was significantly negative (converse Bergmann cline) for the sub-assemblages of both the forest and the non-forest species (Table 2; Figure 3). The strengths of these significant relationships were higher for urban sub-assemblages than for rural ones (forest species: $R^2 = -0.203$ and $R^2 = -0.069$; non-forest species: $R^2 = -0.387$ and $R^2 = -0.103$, for urban and rural sub-assemblages, respectively). The effect of urbanisation level (rural vs. urban) was significant for the sub-assemblages of forest species, while it was marginally significant for the sub-assemblages of non-forest species (Table 2), suggesting higher mean CWMBS of these sub-assemblages in rural sites compared to urban ones (Figure 3). The interaction of the geographical latitude and the level of urbanisation (rural vs. urban) was not significant for sub-assemblages of both the forest and the non-forest species (Table 2), indicating that the rate of decline in CWMBS with increasing geographical latitude (slope of the regression lines) was similar for both the rural and urban sub-assemblages (Figure 3).

4 | DISCUSSION

The majority of birds and mammals show Bergmann clines (Meiri & Dayan, 2003), while studies on ectotherms are inconsistent. Fish, amphibians and turtles mostly show Bergmann clines; lizards, snakes, terrestrial turtles, arctic invertebrates mostly show converse clines, and others (benthic invertebrates) show no clinal pattern at all. Furthermore, nonlinear (U-shaped or hump-shaped) cline patterns also exist (Shelomi, 2012). A previous literature review on latitudinal body size variation in arthropods (Blanckenhorn & Demont, 2004) reports 19 species showing Bergmann clines and 29 species with converse Bergmann clines. A systematic review on beetles (Shelomi, 2012) revealed a majority (54 from 97) of converse Bergmann clines, while only a small proportion of the studies (14 out of 97) conformed to Bergmann's rule, and a third of the studies (29 from 97) showed no clines. Our community-level analysis on ground beetles also found converse Bergmann clines, as the CWMBS of the whole ground beetle community significantly decreased with increasing geographical latitude.

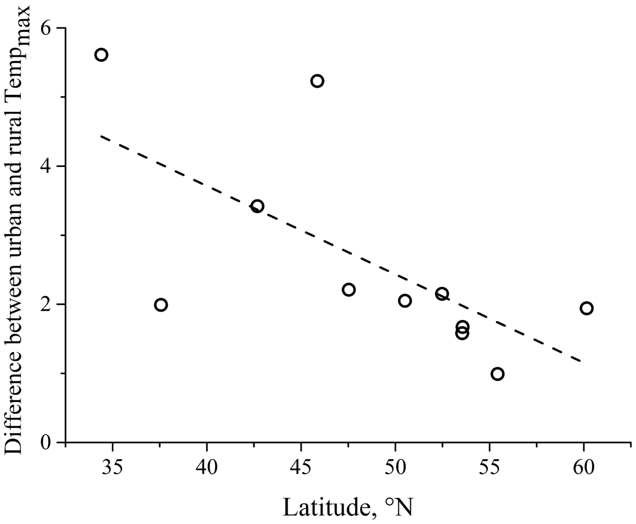

FIGURE 1 The relationship between the difference in the average daytime maximum land surface temperature between the urban and the surrounding rural areas and their geographical latitude.

We set the size limit for large-sized species as 21.3 mm on the basis of a study concentrating on beetles, by Tseng and Soleimani Pari (2019). Naturally, the division of beetles into two size classes is rather simplified, because several studies on this family (Elek & Lövei, 2007; Magura & Lövei, 2020b) use a three-class size division, considered only sizes <10.5 mm as small and sizes >15.0 mm as large. Our two-class size division may mask a more nuanced reaction by ground beetles. Therefore, we re-divided the species into small-sized (≤10.5 mm), medium-sized (10.5–15.0 mm) and large-sized (>15.0 mm) species, and reanalyzed the data (see Appendix S1). Large-sized species (>15.0 mm) showed again a negative body size–latitude relationship (converse Bergmann cline), proving the robust reaction of large-sized species. Small-sized species showed also a negative body size–latitude relationship (converse Bergmann cline), but this pattern was expected, since this trend was proven along a North American latitudinal gradient (Tseng & Soleimani Pari, 2019).

Similar to previous findings (Blanckenhorn & Demont, 2004; Shelomi, 2012), our results also indicate that Bergmann's rule is not a general ecogeographical law for beetles. Bergmann clines, showing increased body size at higher latitudes, and converse Bergmann clines, showing decreased body size at higher latitudes, are about equally common in arthropods. Using ground beetle incidence data for the 79 biogeographic provinces in Northern Europe, mean body

TABLE 2 Summary of ANCOVA results on the relationship between the community-weighted mean body size (CWMBS) and the geographical latitude, moreover on the dependence of this relationship on the level of urbanisation (area; rural vs. urban) for the whole ground beetle assemblage (all species), for the sub-assemblages of differently sized species (small-bodied vs. large-bodied species), as well as for the sub-assemblages of species with different habitat preference (forest vs. non-forest species)

Response variable	Effect	df	SS	MS	*F*	*p*
CWMBS, all species	Latitude	1	174.6	174.59	17.809	**<0.0001**
	Area	1	96.3	96.32	9.825	**0.0024**
	Latitude × Area	1	5.0	4.99	0.509	0.4776
	Residuals	79	774.5	9.80		
CWMBS, small-bodied species	Latitude	1	11.8	11.77	1.748	0.1900
	Area	1	40.4	40.38	5.997	**0.0165**
	Latitude × Area	1	1.3	1.34	0.199	0.6571
	Residuals	79	532.0	6.73		
CWMBS, large-bodied species	Latitude	1	109.4	109.40	9.899	**0.0024**
	Area	1	36.8	36.81	3.331	0.0722
	Latitude × Area	1	6.0	6.00	0.543	0.4636
	Residuals	71	784.6	11.05		
CWMBS, forest species	Latitude	1	149.5	149.5	11.851	**0.0009**
	Area	1	476.1	476.1	37.735	**<0.0001**
	Latitude × Area	1	0.0	0.0	0.001	0.9793
	Residuals	79	996.7	12.6		
CWMBS, non-forest species	Latitude	1	475.0	475.0	26.888	**<0.0001**
	Area	1	66.8	66.8	3.783	0.0553
	Latitude × Area	1	44.9	44.9	2.543	0.1148
	Residuals	79	1395.5	17.7		

Note: Significant effects ($p < 0.05$) are indicated in bold.

Abbreviation: ANCOVA, analysis of covariance.

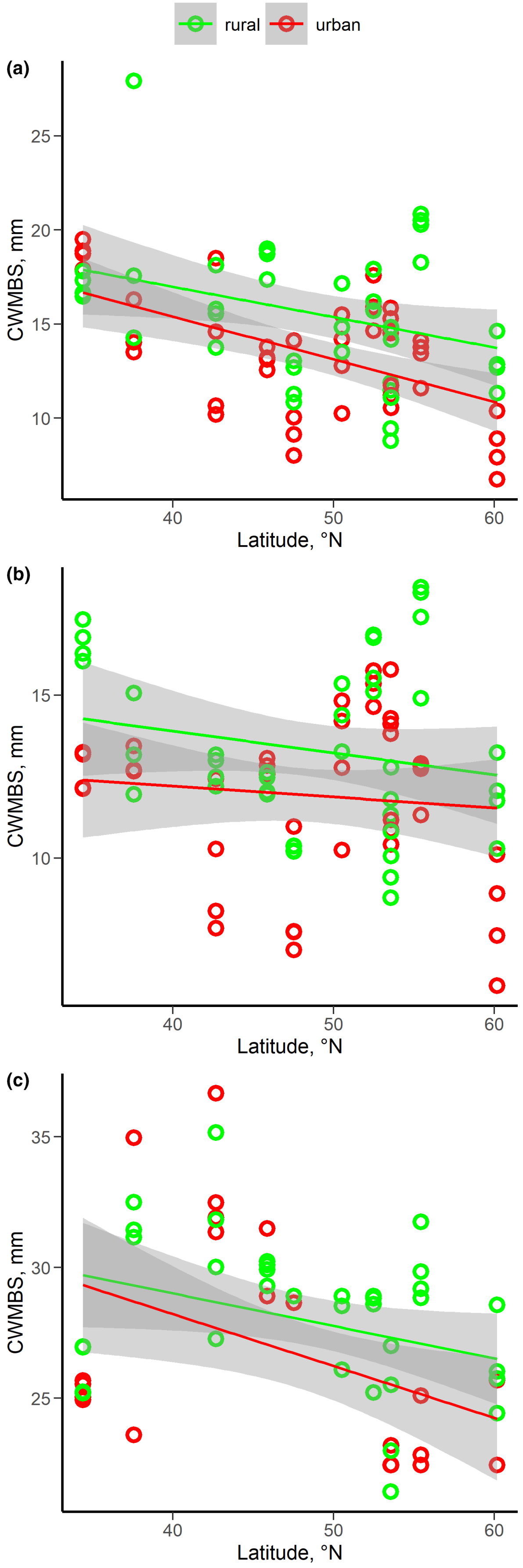

FIGURE 2 The relationship between the community-weighted mean body size and the geographical latitude for the whole ground beetle assemblage (a), for the sub-assemblages of small-bodied species (b), and for the sub-assemblages of large-bodied species (c) in rural (green open circles; medium grey in printed version) and urban habitats (red open circles; dark grey in printed version). Grey shading represents the ±95% confidence bands of the fitted linear regression lines.

size showed a moderately strong quadratic relationship with latitude, first an increasing and then a decreasing trend along the latitudinal gradient (Heino et al., 2019). Similar hump-shaped relationships exist among western Palaearctic ground beetles (Homburg et al., 2013). Body size in four ground beetle species also decreases towards high latitudes in Russia and two others show no clines (Sukhodolskaya & Saveliev, 2016). Such inconsistent body size trends may be caused by non-mutually exclusive mechanisms related to development, thermo-regulatory abilities, life history and ecological traits.

Shorter seasons at higher latitudes progressively limit the time available for foraging, growth and development and hence the attainable body size, resulting in decreasing body size towards the poles (converse Bergmann clines, Blanckenhorn & Demont, 2004). This outcome is predicted by a trade-off between body size (and thus ultimately reproductive success), which increases with the time available to grow, and survival to adulthood, which decreases with the time available to attain maturity (Roff, 1980; Rowe & Ludwig, 1991). In insects, the converse Bergmann clines, are often genetically programmed: smaller sizes and shorter development times of high latitude populations also occur in common-garden laboratory experiments (Blanckenhorn & Demont, 2004; Blanckenhorn & Fairbairn, 1995). In some cases, this problem cannot be solved: several widespread European ground beetle species that normally develop from egg to adult in 1 year, take two or more years to reach adulthood near the northern border of their distribution area (Houston, 1981; Refseth, 1984).

Other potential explanation of the patterns found could be due to the thermo-regulatory abilities of ectotherms. The optimal body temperature may be constant throughout the geographic range of a species, but smaller-sized individuals in cooler environments may be more able to control their body temperature through behaviour, and be active for longer. In warmer climates, thermoregulation may not be so crucial, thereby the selective pressure on an organism's surface area:mass ratio is relaxed, permitting individuals to attain larger sizes and accrue size-related benefits (e.g., competition, predation; Peters, 1983). For squamates smaller body sizes in cooler climates may be the result of selection for increased surface area: volume ratio to allow more rapid heating and cooling, helping digestion and brood care (Ashton & Feldman, 2003).

Of life history traits, body size may be an important characteristic to shape body size–latitude relationships. Larger-bodied insect species are more likely to be affected by changing ambient temperature, than smaller-bodied ones, and such species are better

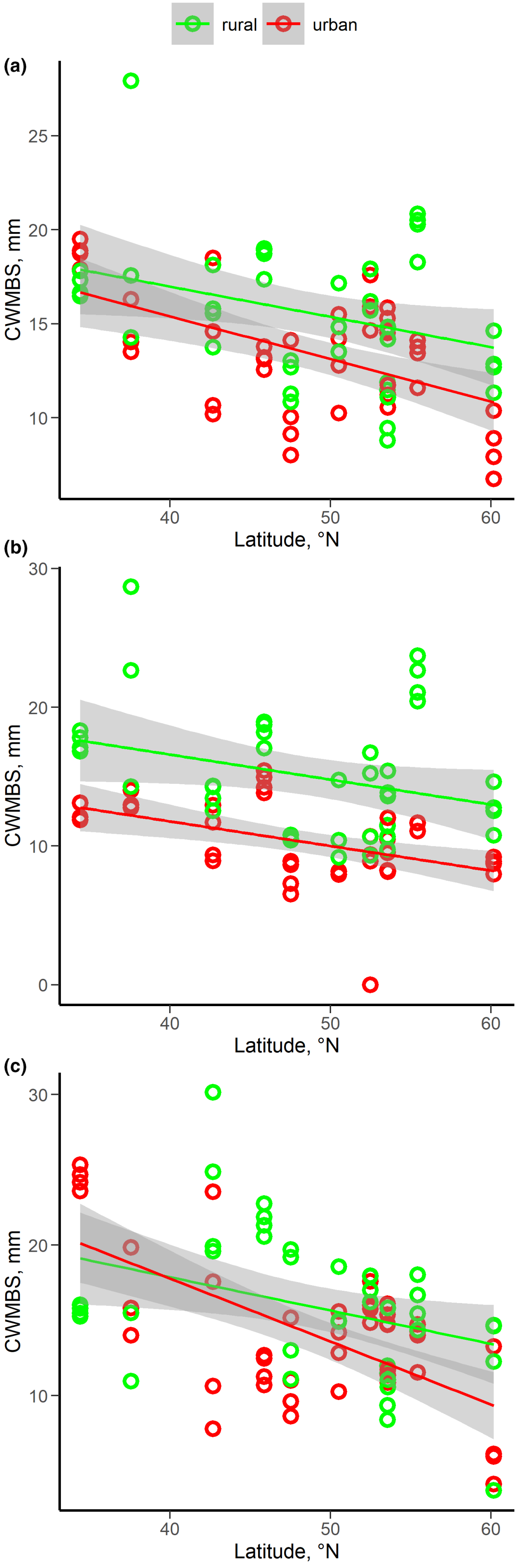

FIGURE 3 The relationship between the community-weighted mean body size and the geographical latitude for the whole ground beetle assemblages (a), for the sub-assemblages of forest species (b), and for the sub-assemblages of non-forest species (c) in rural (green open circles; medium grey in printed version) and urban habitats (red open circles; dark grey in printed version). Grey shading represents the ±95% confidence bands of the fitted linear regression lines.

able to regulate their internal body temperature (Tseng et al., 2018; Tseng & Soleimani Pari, 2019). These findings suggest that size-dependent responses to temperature may be widespread among insects, and that interspecific variation in body size itself may help to explain the inconsistent relationship between body size and latitude. Specifically, if larger-bodied insects are better able to maintain their internal body temperature, then larger-sized insect species may be more likely to show Bergmann's rule than smaller-sized ones. Additionally, if smaller insect species are less able to regulate their internal body temperature, then higher latitudes or lower temperatures and shorter growing seasons may select for shorter larval stages, earlier maturation, leading to smaller size at maturity (Schutze & Clarke, 2008). Indeed, recent studies have shown that larger-bodied insect species are more likely to decrease in size when reared at increased temperature than smaller-sized ones. Overall this would lead to a converse Bergmann's rule in smaller-sized insect species, and larger species would conform to Bergman's rule (Tseng & Soleimani Pari, 2019). Contrary to the predicted positive relationship between body size and latitude in larger-bodied insect species, our results indicated a decrease of the CWMBS with the latitude for the sub-assemblages of large-bodied species. The development of larger-sized insects is generally slower than smaller-sized ones. Based on this, larger-bodied, slower-developing beetles seem to be more affected by limitations due to seasonality, producing converse Bergmann clines (Blanckenhorn & Demont, 2004). Studying ground beetle assemblages along elevational gradients in Alpine regions, Chamberlain et al. (2020) also found that the occurrence of larger species with longer larval development declined steeply from low to high elevation. Furthermore, a systematic review on latitudinal body size variation in arthropods also confirmed that larger species with relatively long development times tend to decrease in size with increasing latitude, that is, follow the converse Bergmann rule (Blanckenhorn & Demont, 2004). Contrary to the expected converse Bergmann clines for smaller-sized insects, we found that the relationship between the CWMBS and the geographical latitude for small-sized species was not significant. A possible explanation for this pattern could be the countergradient variation, also known as the latitudinal compensation hypothesis (Conover & Present, 1990; Levinton & Monahan, 1983). Countergradient variation is exhibited when high latitude (or altitude) populations of a given species compensate for seasonal time constraints by evolving (genetically) faster growth than their lower latitude (or altitude) conspecifics. A common garden experiment of populations of the fly species

Scathophaga stercoraria originating from a latitudinal gradient indeed detected faster growth rates in higher latitude populations, which is a case of adaptive countergradient (Blanckenhorn & Demont, 2004). Smaller ground beetle species with shorter larval development, which enables them to exploit the short snow-free season for reproduction, were more common at higher elevations in Alpine regions (Chamberlain et al., 2020).

Voltinism, the generation time relative to season length can be a crucial parameter in determining temperature–size rules (Zeuss et al., 2017). Species with long development times relative to season length are more prone to experience time constraints than multivoltine species with short generation times and thus exhibit converse Bergmann rule (Blanckenhorn & Demont, 2004; Chown & Gaston, 1999). Ground beetles, however, are typically uni- and bivoltine (Matalin, 2007); therefore, voltinism is unlikely to influence their temperature–size relationship.

Warmer temperatures can also act to increase body size. Females of the univoltine, earthworm-feeding *Carabus japonicus* are larger at locations with warmer ambient temperature in northern Kyushu, Japan (Okuzaki & Sota, 2017). Populations living at cooler sites (high-altitude) use the entire warm season for reproduction and larval development, while in populations living in warmer, low-altitude sites, larval occurrence is shorter, coinciding with seasonal trends in earthworm abundance. At these warmer sites, earthworms also reach larger sizes than at high altitudes. Carabid females at warmer sites lay larger eggs, from which larger first instar larvae hatch that prey more efficiently on the larger earthworms (Okuzaki & Sota, 2017). Consequently, larger adults can develop.

Habitat preference is usually ignored when studying body size patterns along temperature gradients. Habitats, however, may fundamentally determine the patterns in temperature-body size relationships. In 93 species of dytiscid water beetles, significant relationships between size and latitude were found for species with lentic, but not for lotic species, underlining that habitat preference should be considered when exploring latitudinal clines in body size (Pallarés et al., 2019). Habitat preference of ground beetles is also a key characteristic in body size distribution (Magura et al., 2020). Generalist species may be more tolerant than habitat specialists to changes in environmental conditions, such as ambient temperature (Magura et al., 2010). In our study, however, the CWMBS uniformly decreased in the sub-assemblages of both forest (habitat specialist) and non-forest species (not habitat specialists). Based on this, the developmental constraints caused by shorter season, the climate-dependent thermo-regulatory abilities, and the life history traits seem to be more important than ecological traits in modulating the temperature–body size relationship.

The trends were examined on the basis of only 11 locations, mostly in Europe. This is a limited dataset, so our conclusions should be considered with this factor in mind. An additional modifying factor could be the lack of data on within-species geographical variability in size. There could well be a size gradient by geographical latitude within species as well. This calls for caution when we intend to generalise. A third limitation is the accidental correlation between latitude and longitude—both were increasing from north to south, and we cannot exclude that longitude also has an effect on the trends found—but due to the correlation between the two, we could not test this possible effect.

In our dataset, despite the decreasing magnitude of the UHI effect along the latitudinal gradient, the relationships between the CWMBS and geographical latitude were stronger in urban than rural localities, indicating the substantial effect of habitat modification by urbanisation on arthropods (Fenoglio et al., 2020; Magura et al., 2010; Magura et al., 2021a; Niemelä & Kotze, 2009). The UHI effect is one of the most consistent and well-documented change in urban areas (Arnfield, 2003). Warming in urban habitats due to human activities and the modification of land surfaces seem to intensify the temperature-body size relationship. As urbanisation-related environmental changes affect processes at various level of biological organisation, from the population (Magura et al., 2008; Magura et al., 2021b; Sadler et al., 2006) through community (Magura et al., 2018; Niemelä & Kotze, 2009) to ecosystem level (Eötvös et al., 2018; Shochat et al., 2006), holistic, multi-scale green-space planning and management schemes are needed to adequately conserve and restore biodiversity and proper ecosystem functions in urbanised areas (Magura & Lövei, 2021; Norton et al., 2016).

5 | CONCLUSION

In conclusion, our study provides an insight into the community-wide size–temperature pattern in ground beetles, testing the potential factors such as body size and habitat preference, as well as the effect of UHI on this relationship. Our results based on data from 11 countries in the Northern Hemisphere, in line with the majority of previous results on beetles (Shelomi, 2012), detected a significant negative body size–latitude relationship for whole ground beetle assemblages. The negative relationship was not more pronounced for the habitat specialist sub-assemblages than for non-specialists. Contrary to previous results (Tseng & Soleimani Pari, 2019), sub-assemblages of large-sized ground beetles showed a negative body size–latitude relationship, while the sub-assemblages of small species showed no significant changes along the latitudinal gradient. Even though a bigger dataset would allow us more confidence in drawing conclusions, and there were more small-sized than large species, which can also influence the strength of the detected relationships, the detected negative CWMBS–latitude relationship in ground beetles can be explained by development constraints caused by shorter season at higher latitudes (Blanckenhorn & Demont, 2004), climate-dependent thermo-regulatory abilities (Ashton & Feldman, 2003), and/or by laying larger eggs from which larger first instar larvae can hatch (Okuzaki & Sota, 2017).

All the significant negative body size–latitude relationships were stronger in urban than rural areas. As urbanisation affects several community- and ecosystem-level processes and functions, holistic, multi-scale urban landscape planning and management schemes are needed to ensure both the recreational and the diversity preserving functions of urban green spaces (Magura & Lövei, 2021).

ACKNOWLEDGEMENTS

We thank the Aarhus University Forskningsfond (Guest Professorship to TM) and the Hungarian National Research, Development and Innovation Fund (grant number: OTKA K-131459) for supporting this research, two anonymous reviewers and Handling Editor Prof. S. Fattorini for helpful comments. No permits were necessary for this work. This is publication no. 1 of the ELKH-DE Anthropocene Ecology Research Group. Open access funding enabled and organized by ProjektDEAL.

CONFLICTS OF INTEREST

The authors declare that they do not have any conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supplementary material of this article.

ORCID

Gábor L. Lövei https://orcid.org/0000-0002-6467-9812

Tibor Magura https://orcid.org/0000-0002-9130-6122

REFERENCES

Arnfield, A. J. (2003). Two decades of urban climate research: A review of turbulence, exchanges of energy and water, and the urban heat Island. *International Journal of Climatology*, *23*(1), 1–26. https://doi.org/10.1002/joc.859

Ashton, K. G., & Feldman, C. R. (2003). Bergmann's rule in nonavian reptiles: Turtles follow it, lizards and snakes reverse it. *Evolution*, *57*(5), 1151–1163. https://doi.org/10.1111/j.0014-3820.2003.tb00324.x

Atkinson, D. (1994). Temperature and organism size - a biological law for ectotherms? *Advances in Ecological Research*, *25*, 1–58. https://doi.org/10.1016/S0065-2504(08)60212-3

Baars, M. A. (1979). Catches in pitfall traps in relation to mean densities of carabid beetles. *Oecologia*, *41*(1), 25–46. https://doi.org/10.1007/BF00344835

Blanckenhorn, W. U. (2000). The evolution of body size: What keeps organisms small? *The Quarterly Review of Biology*, *75*(4), 385–407. https://doi.org/10.1086/393620

Blanckenhorn, W. U., & Demont, M. (2004). Bergmann and converse Bergmann latitudinal clines in arthropods: Two ends of a continuum? *Integrative and Comparative Biology*, *44*(6), 413–424. https://doi.org/10.1093/icb/44.6.413

Blanckenhorn, W. U., & Fairbairn, D. J. (1995). Life history adaptation along a latitudinal cline in the water strider *Aquarius remigis* (Heteroptera: Gerridae). *Journal of Evolutionary Biology*, *8*(1), 21–41. https://doi.org/10.1046/j.1420-9101.1995.8010021.x

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, *85*(7), 1771–1789. https://doi.org/10.1890/03-9000

Brown, J. H., & Sibly, R. M. (2006). Life-history evolution under a production constraint. *Proceedings of the National Academy of Sciences*, *103*(47), 17595–17599. https://doi.org/10.1073/pnas.0608522103

Center for International Earth Science Information Network - Columbia University. (2016). *Global urban Heat Island (UHI) data set, 2013*. NASA Socioeconomic Data and Applications Center. https://doi.org/10.7927/H4H70CRF

Chamberlain, D., Gobbi, M., Negro, M., Caprio, E., Palestrini, C., Pedrotti, L., Brandmayr, P., Pizzolotto, R., & Rolando, A. (2020). Trait-modulated decline of carabid beetle occurrence along elevational gradients across the European Alps. *Journal of Biogeography*, *47*(5), 1030–1040. https://doi.org/10.1111/jbi.13792

Chown, S. L., & Gaston, K. J. (1999). Exploring links between physiology and ecology at macro-scales: The role of respiratory metabolism in insects. *Biological Reviews*, *74*(1), 87–120. https://doi.org/10.1111/j.1469-185X.1999.tb00182.x

Chown, S. L., & Gaston, K. J. (2010). Body size variation in insects: A macroecological perspective. *Biological Reviews*, *85*(1), 139–169. https://doi.org/10.1111/j.1469-185X.2009.00097.x

Conover, D. O., & Present, T. M. C. (1990). Countergradient variation in growth rate: Compensation for length of the growing season among Atlantic silversides from different latitudes. *Oecologia*, *83*(3), 316–324. https://doi.org/10.1007/BF00317554

Davey, A. J. H., Hawkins, S. J., Turner, G. F., & Doncaster, C. P. (2005). Size-dependent microhabitat use and intraspecific competition in *Cottus gobio*. *Journal of Fish Biology*, *67*(2), 428–443. https://doi.org/10.1111/j.0022-1112.2005.00736.x

Devictor, V., Julliard, R., Couvet, D., & Jiguet, F. (2008). Birds are tracking climate warming, but not fast enough. *Proceedings of the Royal Society B*, *275*(1652), 2743–2748. https://doi.org/10.1098/rspb.2008.0878

Elek, Z., & Lövei, G. L. (2007). Patterns in ground beetle (Coleoptera: Carabidae) assemblages along an urbanisation gradient in Denmark. *Acta Oecologica*, *32*(1), 104–111. https://doi.org/10.1016/j.actao.2007.03.008

Eötvös, C. B., Magura, T., & Lövei, G. L. (2018). A meta-analysis indicates reduced predation pressure with increasing urbanization. *Landscape and Urban Planning*, *180*, 54–59. https://doi.org/10.1016/j.landurbplan.2018.08.010

Fenoglio, M. S., Rossetti, M. R., & Videla, M. (2020). Negative effects of urbanization on terrestrial arthropod communities: A meta-analysis. *Global Ecology and Biogeography*, *29*, 1412–1429. https://doi.org/10.1111/geb.13107

Gaston, K. J., Chown, S. L., & Evans, K. L. (2008). Ecogeographical rules: Elements of a synthesis. *Journal of Biogeography*, *35*(3), 483–500. https://doi.org/10.1111/j.1365-2699.2007.01772.x

Gaublomme, E., Dhuyvetter, H., Verdyck, P., & Desender, K. (2005). Effects of urbanisation on carabid beetles in old beech forests. *DIAS Report*, *114*, 111–123.

Heino, J., Alahuhta, J., & Fattorini, S. (2019). Macroecology of ground beetles: Species richness, range size and body size show different geographical patterns across a climatically heterogeneous area. *Journal of Biogeography*, *46*(11), 2548–2557. https://doi.org/10.1111/jbi.13693

Hildrew, A., Raffaelli, D., & Edmonds-Brown, R. (2007). *Body size: The structure and function of aquatic ecosystems*. Cambridge University Press. https://doi.org/10.1017/CBO9780511611223

Homburg, K., Homburg, N., Schäfer, F., Schuldt, A., & Assmann, T. (2014). Carabids.org – A dynamic online database of ground beetle species traits (Coleoptera: Carabidae). *Insect Conservation and Diversity*, *7*(3), 195–205. https://doi.org/10.1111/icad.12045

Homburg, K., Schuldt, A., Drees, C., & Assmann, T. (2013). Broad-scale geographic patterns in body size and hind wing development of western Palaearctic carabid beetles (Coleoptera: Carabidae). *Ecography*, *36*(2), 166–177. https://doi.org/10.1111/j.1600-0587.2012.07488.x

Houston, W. W. K. (1981). The life cycles and age of *Carabus glabratus* Paykull and *C. problematicus* Herbst (Col.: Carabidae) on moorland in northern England. *Ecological Entomology*, *6*(3), 263–271. https://doi.org/10.1111/j.1365-2311.1981.tb00613.x

Hudson, L. N., Newbold, T., Contu, S., Hill, S. L. L., Lysenko, I., De Palma, A., Phillips, H. R. P., Alhusseini, T. I., Bedford, F. E., Bennett, D. J., Booth, H., Burton, V. J., Chng, C. W. T., Choimes, A., Correia, D. L. P., Day, J., Echeverría-Londono, S., Emerson, S. R., Gao, D., … Purvis, A. (2017). The database of the PREDICTS (projecting responses of ecological diversity in changing terrestrial systems) project. *Ecology and Evolution*, *7*, 145–188. https://doi.org/10.1002/ece3.2579

Hůrka, K. (1996). *Carabidae of the Czech and Slovak republics*. Kabourek.

Ishitani, M., Kotze, D. J., & Niemelä, J. (2003). Changes in carabid beetle assemblages across an urban-rural gradient in Japan. *Ecography*, *26*(4), 481–489. https://doi.org/10.1034/j.1600-0587.2003.03436.x

Jetz, W., Carbone, C., Fulford, J., & Brown, J. H. (2004). The scaling of animal space use. *Science*, *306*(5694), 266–268. https://doi.org/10.1126/science.1102138

Jung, J.-K., Lee, S. K., Lee, S.-I., & Lee, J.-H. (2018). Trait-specific response of ground beetles (Coleoptera: Carabidae) to forest fragmentation in the temperate region in Korea. *Biodiversity and Conservation*, *27*(1), 53–68. https://doi.org/10.1007/s10531-017-1421-x

Kingsolver, J. G., & Huey, R. B. (2008). Size, temperature, and fitness: Three rules. *Evolutionary Ecology Research*, *10*(2), 251–268.

Kotze, D. J., Brandmayr, P., Casale, A., Dauffy-Richard, E., Dekoninck, W., Koivula, M., Lövei, G. L., Mossakowski, D., Noordijk, J., Paarmann, W., Pizzoloto, R., Saska, P., Schwerk, A., Serrano, J., Szyszko, J., Taboada, A., Turin, H., Venn, S., Vermeulen, R., & Brandmayr, T. Z. (2011). Forty years of carabid beetle research in Europe – From taxonomy, biology, ecology and population studies to bioindication, habitat assessment and conservation. *ZooKeys*, *100*, 55–148. https://doi.org/10.3897/zookeys.100.1523

Leather, S. R., Walters, K. F. A., & Bale, J. S. (1993). *The ecology of insect overwintering*. Cambridge University Press. https://doi.org/10.1017/CBO9780511525834

Levinton, J. S., & Monahan, R. K. (1983). The latitudinal compensation hypothesis: Growth data and a model of latitudinal growth differentiation based upon energy budgets. II. Intraspecific comparisons between subspecies of *Ophryotrocha puerilis* (Polychaeta: Dorvilleidae). *The Biological Bulletin*, *165*(3), 699–707. https://doi.org/10.2307/1541472

Lövei, G. L., & Sunderland, K. D. (1996). Ecology and behavior of ground beetles (Coleoptera: Carabidae). *Annual Review of Entomology*, *41*, 231–256. https://doi.org/10.1146/annurev.en.41.010196.001311

Magura, T., Ferrante, M., & Lövei, G. L. (2020). Only habitat specialists become smaller with advancing urbanisation. *Global Ecology and Biogeography*, *29*(11), 1978–1987. https://doi.org/10.1111/geb.13168

Magura, T., & Lövei, G. L. (2020a). The permeability of natural versus anthropogenic forest edges modulates the abundance of ground beetles of different dispersal power and habitat affinity. *Diversity*, *12*(9), 320. https://doi.org/10.3390/d12090320

Magura, T., & Lövei, G. L. (2020b). The type of forest edge governs the spatial distribution of different-sized ground beetles. *Acta Zoologica Academiae Scientiarum Hungaricae*, *66*(Suppl), 69–96. https://doi.org/10.17109/AZH.66

Magura, T., & Lövei, G. L. (2021). Consequences of urban living: Urbanization and ground beetles. *Current Landscape Ecology Reports*, *6*(1), 9–21. https://doi.org/10.1007/s40823-020-00060-x

Magura, T., Lövei, G. L., & Tóthmérész, B. (2010). Does urbanization decrease diversity in ground beetle (Carabidae) assemblages? *Global Ecology and Biogeography*, *19*(1), 16–26. https://doi.org/10.1111/j.1466-8238.2009.00499.x

Magura, T., Lövei, G. L., & Tóthmérész, B. (2018). Conversion from environmental filtering to randomness as assembly rule of ground beetle assemblages along an urbanization gradient. *Scientific Reports*, *8*(1), 16992. https://doi.org/10.1038/s41598-018-35293-8

Magura, T., Mizser, S., Horváth, R., Nagy, D. D., Tóth, M., Csicsek, R., & Lövei, G. L. (2021a). Are there personality differences between rural vs. urban-living individuals of a specialist ground beetle, *Carabus convexus*? *Insects*, *12*(7), 646. https://doi.org/10.3390/insects12070646

Magura, T., Mizser, S., Horváth, R., Nagy, D. D., Tóth, M., Csicsek, R., & Lövei, G. L. (2021b). Differences in life history traits in rural vs. urban populations of a specialist ground beetle, *Carabus convexus*. *Insects*, *12*, 540. https://doi.org/10.3390/insects12060540

Magura, T., Tóthmérész, B., & Molnár, T. (2004). Changes in carabid beetle assemblages along an urbanisation gradient in the city of Debrecen, Hungary. *Landscape Ecology*, *19*(7), 747–759. https://doi.org/10.1007/s10980-005-1128-4

Magura, T., Tóthmérész, B., & Molnár, T. (2008). A species-level comparison of occurrence patterns in carabids along an urbanisation gradient. *Landscape and Urban Planning*, *86*(2), 134–140. https://doi.org/10.1016/j.landurbplan.2008.01.005

Makarieva, A. M., Gorshkov, V. G., & Li, B.-L. (2005). Temperature-associated upper limits to body size in terrestrial poikilotherms. *Oikos*, *111*(3), 425–436. https://doi.org/10.1111/j.1600-0706.2005.14095.x

Marrec, R., Le Roux, V., Martin, L., Lenoir, J., Brunet, J., Cousins, S. A. O., De Smedt, P., Deconchat, M., Diekmann, M., Ehrmann, S., Gallet-Moron, E., Giffard, B., Liira, J., Lindgren, J., Valdes, A., Verheyen, K., Wulf, M., & Decocq, G. (2021). Multiscale drivers of carabid beetle (Coleoptera: Carabidae) assemblages in small European woodlands. *Global Ecology and Biogeography*, *30*(1), 165–182. https://doi.org/10.1111/geb.13208

Matalin, A. V. (2007). Typology of life cycles of ground beetles (Coleoptera, Carabidae) in Western Palaearctic. *Entomological Review*, *87*(8), 947–972. https://doi.org/10.1134/S0013873807080027

Matthews, T. J., Borges, P. A. V., & Whittaker, R. J. (2014). Multimodal species abundance distributions: A deconstruction approach reveals the processes behind the pattern. *Oikos*, *123*(5), 533–544. https://doi.org/10.1111/j.1600-0706.2013.00829.x

Meiri, S., & Dayan, T. (2003). On the validity of Bergmann's rule. *Journal of Biogeography*, *30*(3), 331–351. https://doi.org/10.1046/j.1365-2699.2003.00837.x

Merckx, T., Kaiser, A., & Van Dyck, H. (2018). Increased body size along urbanization gradients at both community and intraspecific level in macro-moths. *Global Change Biology*, *24*(8), 3837–3848. https://doi.org/10.1111/gcb.14151

Merckx, T., Souffreau, C., Kaiser, A., Baardsen, L. F., Backeljau, T., Bonte, D., Brans, K. I., Cours, M., Dahirel, M., Debortoli, N., De Wolf, K., Engelen, J. M. T., Fontaneto, D., Gianuca, A. T., Govaert, L., Hendrickx, F., Higuti, J., Lens, L., Martens, K., … Van Dyck, H. (2018). Body-size shifts in aquatic and terrestrial urban communities. *Nature*, *558*(7708), 113–116. https://doi.org/10.1038/s41586-018-0140-0

Niemelä, J., & Kotze, D. J. (2009). Carabid beetle assemblages along urban to rural gradients: A review. *Landscape and Urban Planning*, *92*(2), 65–71. https://doi.org/10.1016/j.landurbplan.2009.05.016

Niemelä, J., Kotze, D. J., Venn, S., Penev, L., Stoyanov, I., Spence, J., Hartley, D., & de Oca, E. M. (2002). Carabid beetle assemblages (Coleoptera, Carabidae) across urban-rural gradients: An international comparison. *Landscape Ecology*, *17*(5), 387–401. https://doi.org/10.1023/A:1021270121630

Norton, B. A., Evans, K. L., & Warren, P. H. (2016). Urban biodiversity and landscape ecology: Patterns, processes and planning. *Current Landscape Ecology Reports*, *1*(4), 178–192. https://doi.org/10.1007/s40823-016-0018-5

Ohlberger, J. (2013). Climate warming and ectotherm body size - from individual physiology to community ecology. *Functional Ecology*, *27*(4), 991–1001. https://doi.org/10.1111/1365-2435.12098

Okuzaki, Y., & Sota, T. (2017). Factors related to altitudinal body size variation in the earthworm-eating ground beetle *Carabus japonicus*. *Zoological Science*, *34*(3), 229–234. https://doi.org/10.2108/zs160182

Pallarés, S., Lai, M., Abellán, P., Ribera, I., & Sánchez-Fernández, D. (2019). An interspecific test of Bergmann's rule reveals inconsistent body size patterns across several lineages of water beetles (Coleoptera: Dytiscidae). *Ecological Entomology*, *44*(2), 249–254. https://doi.org/10.1111/een.12701

Petchey, O. L., & Belgrano, A. (2010). Body-size distributions and size-spectra: Universal indicators of ecological status? *Biology Letters*, *6*(4), 434–437. https://doi.org/10.1098/rsbl.2010.0240

Peters, R. H. (1983). *The ecological implications of body size*. Cambridge University Press. https://doi.org/10.1017/CBO9780511608551

Pincheira-Donoso, D. (2010). The balance between predictions and evidence and the search for universal macroecological patterns: Taking Bergmann's rule back to its endothermic origin. *Theory in Biosciences*, *129*(4), 247–253. https://doi.org/10.1007/s12064-010-0101-0

R Core Team. (2017). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. http://www.R-project.org

Refseth, D. (1984). The life cycles and growth of *Carabus glabratus* and *C. violaceus* in Budalen, Central Norway. *Ecological Entomology*, *9*(4), 449–455. https://doi.org/10.1111/j.1365-2311.1984.tb00843.x

Roff, D. (1980). Optimizing development time in a seasonal environment: The 'ups and downs' of clinal variation. *Oecologia*, *45*(2), 202–208. https://doi.org/10.1007/BF00346461

Rowe, L., & Ludwig, D. (1991). Size and timing of metamorphosis in complex life cycles: Time constraints and variation. *Ecology*, *72*(2), 413–427. https://doi.org/10.2307/2937184

Sadler, J. P., Small, E. C., Fiszpan, H., Telfer, M. G., & Niemelä, J. (2006). Investigating environmental variation and landscape characteristics of an urban–rural gradient using woodland carabid assemblages. *Journal of Biogeography*, *33*(6), 1126–1138. https://doi.org/10.1111/j.1365-2699.2006.01476.x

Schutze, M. K., & Clarke, A. R. (2008). Converse Bergmann cline in a *eucalyptus* herbivore, *Paropsis atomaria* Olivier (Coleoptera: Chrysomelidae): Phenotypic plasticity or local adaptation? *Global Ecology and Biogeography*, *17*(3), 424–431. https://doi.org/10.1111/j.1466-8238.2007.00374.x

Shelomi, M. (2012). Where are we now? Bergmann's rule sensu lato in insects. *American Naturalist*, *180*(4), 511–519. https://doi.org/10.1086/667595

Shochat, E., Warren, P. S., Faeth, S. H., McIntyre, N. E., & Hope, D. (2006). From patterns to emerging processes in mechanistic urban ecology. *Trends in Ecology & Evolution*, *21*(4), 186–191. https://doi.org/10.1016/j.tree.2005.11.019

Start, D., Bonner, C., Weis, A. E., & Gilbert, B. (2018). Consumer-resource interactions along urbanization gradients drive natural selection. *Evolution*, *72*(9), 1863–1873. https://doi.org/10.1111/evo.13544

Stearns, S. C. (1992). *The evolution of life histories*. Oxford University Press.

Sukhodolskaya, R., & Saveliev, A. (2016). Body size variation of ground beetles (Coleoptera: Carabidae) in latitudinal gradient. *Periodicum Biologorum*, *118*(3), 273–280. https://doi.org/10.18054/pb.2016.118.3.3918

Tóthmérész, B., Máthé, I., Balázs, E., & Magura, T. (2011). Responses of carabid beetles to urbanization in Transylvania (Romania). *Landscape and Urban Planning*, *101*(4), 330–337. https://doi.org/10.1016/j.landurbplan.2011.02.038

Tseng, M., Kaur, K. M., Soleimani Pari, S., Sarai, K., Chan, D., Yao, C. H., Porto, P., Toor, A., Toor, H. S., & Fograscher, K. (2018). Decreases in beetle body size linked to climate change and warming temperatures. *Journal of Animal Ecology*, *87*(3), 647–659. https://doi.org/10.1111/1365-2656.12789

Tseng, M., & Soleimani Pari, S. (2019). Body size explains interspecific variation in size–latitude relationships in geographically widespread beetle species. *Ecological Entomology*, *44*(1), 151–156. https://doi.org/10.1111/een.12684

Verberk, W. C. E. P., Atkinson, D., Hoefnagel, K. N., Hirst, A. G., Horne, C. R., & Siepel, H. (2021). Shrinking body sizes in response to warming: Explanations for the temperature–size rule with special emphasis on the role of oxygen. *Biological Reviews*, *96*(1), 247–268. https://doi.org/10.1111/brv.12653

Watt, C., Mitchell, S., & Salewski, V. (2010). Bergmann's rule; a concept cluster? *Oikos*, *119*(1), 89–100. https://doi.org/10.1111/j.1600-0706.2009.17959.x

Weller, B., & Ganzhorn, J. U. (2004). Carabid beetle community composition, body size, and fluctuating asymmetry along an urban-rural gradient. *Basic and Applied Ecology*, *5*(2), 193–201. https://doi.org/10.1078/1439-1791-00220

Winterhalter, W. E., & Mousseau, T. A. (2008). The strength of temperature-mediated selection on body size in a wild insect population. *Journal of Orthoptera Research*, *17*(2), 347–351. https://doi.org/10.1665/1082-6467-17.2.347

Woodward, G., Ebenman, B., Emmerson, M., Montoya, J. M., Olesen, J. M., Valido, A., & Warren, P. H. (2005). Body size in ecological networks. *Trends in Ecology & Evolution*, *20*(7), 402–409. https://doi.org/10.1016/j.tree.2005.04.005

Zeuss, D., Brunzel, S., & Brandl, R. (2017). Environmental drivers of voltinism and body size in insect assemblages across Europe. *Global Ecology and Biogeography*, *26*(2), 154–165. https://doi.org/10.1111/geb.12525

BIOSKETCHES

Gábor L. Lövei is a Senior Scientist Emeritus at Aarhus University, Denmark and Professor at the Hungarian University of Agriculture and Life Sciences, Godollo, Hungary. His research covers agroecology, biosafety and invasion biology.

Tibor Magura is a Professor at the Department of Ecology, University of Debrecen. His main research interests include urban ecology, forest ecology, agroecology and conservation biology, with special emphasis on ground beetles.

Author contributions: Both authors contributed to all phases of research, data evaluation and writing.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Lövei, G. L., & Magura, T. (2022). Body size and the urban heat island effect modulate the temperature–size relationship in ground beetles. *Journal of Biogeography*, *49*, 1618–1628. https://doi.org/10.1111/jbi.14458