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Suburban Areas Provide Refuge for Carabids in Cities With High Climate Seasonality and Urban Heat Island Effects: A Global Meta-Analysis

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ABSTRACT

Aim: Ground beetles (Coleoptera: Carabidae) are a highly diverse group of soil-associated organisms with varied biological functions, diet preferences and mobility. Their diversity has made them a popular focus in urbanisation research. However, studies on urbanisation's impact on Carabid species richness and abundance have yielded inconsistent results, showing negative, positive, neutral and even non-linear effects. This study aimed to synthesise the existing literature to identify potential non-linear effects of rural-to-urban gradients while accounting for the influence of climatic confounding factors.

Location: Global.

Methods: We conducted hierarchical meta-analyses to evaluate non-linear urbanisation effects on Carabid species richness and abundance. additionally, we examined the moderating roles of climate variables (annual precipitation, precipitation seasonality) and the relative urban heat island (UHI) effect. From 25 relevant studies, we extracted 43 effect sizes for species richness and 46 for assemblage-level abundance.

Results: Our analysis revealed a significant non-linear relationship between urbanisation and carabid abundance, characterised by an increase from rural to suburban areas, followed by a decline towards city centres. Cities with high precipitation seasonality and elevated relative UHI were associated with a suburban peak in both abundance and species richness, likely due to suburban areas mitigating extreme weather, such as harsh winters and heatwaves. Conversely, in climates with low precipitation seasonality and UHI, suburban areas showed a decline, as these conditions do not provide the mitigating benefits, yet the disadvantages of urbanisation remain.

Main Conclusions: Our findings highlight the crucial role of climate as a confounding factor in the non-linear effects of urbanisation, underscoring the importance of integrating these variables into future research. Moreover, the results suggest that suburban environments in regions with high climatic seasonality and elevated UHI may hold conservation potential, supporting higher carabid abundance and species richness compared to urban cores or rural regions.

1 | Introduction

It is estimated that by 2050, 80% of the Earth's population will reside in cities (Bettencourt and West 2010). Urbanisation is a rapidly accelerating process that brings substantial changes, including the fragmentation and destruction of natural habitats, as well as chemical, noise and light pollution (Johnson and Munshi-South 2017; Merckx et al. 2018; Pinho et al. 2021). These transformations typically lead to terrestrial communities exhibiting reduced diversity (species richness) and an increased abundance of generalist species, primarily due to local species extinctions and biotic homogenisation (Piano et al. 2020). This trend arises because only a limited number of generalist species can tolerate or adapt to urbanised environments, whereas many rare or specialist species are unable to survive and go locally extinct (Gray 1989).

Ground beetles (Coleoptera: Carabidae), a highly diverse soil-associated group, exhibit a wide range of biological functions, dietary preferences and mobility (Vanbergen et al. 2005). Specifically, carabids can: (1) be herbivores, omnivores or predators; (2) be flightless or possess flying capabilities; (3) serve as biocontrol agents for weeds and insect pests; and (4) help maintain biodiversity by regulating strong competitors (Korányi et al. 2022; Kromp 1999; Venn et al. 2013). Their sensitivity to environmental changes, such as urbanisation, makes them particularly valuable subjects for urbanisation research (Weller and Ganzhorn 2004). However, the effects of urbanisation on carabid abundance and species richness remain inconsistent (Magura et al. 2010). Some studies report neutral (Alaruikka et al. 2002; Gordienko et al. 2018), positive (Gagne and Fahrig 2011), or negative impacts (Croci et al. 2008; Niemelä and Kotze 2009; Venn et al. 2003; Zelazna and Błazejewicz-Zawadzińska 2003); or suggest non-linear effects of urbanisation (Tóthmérész et al. 2011).

The inconsistent effects of urbanisation on carabids may result from a combination of intertwined ecological mechanisms and methodological challenges. First, urbanisation encompasses and often correlates with multiple environmental gradients, such as the heat island effect, soil compaction and sealing and habitat loss, leading to varying impacts on carabids (Martinson and Raupp 2013). For instance, urbanisation intensifies habitat loss and fragmentation, which reduces species diversity (Martinson and Raupp 2013). At the same time, urban areas often involve increased irrigation and the use of fertilisers, which enhance primary productivity and may promote the abundance and species richness of certain taxa (Blair 1996). Second, different limiting factors along the gradient could explain the observed suburban peak in species richness and/or abundance compared to city centres and rural areas (McDonnell and Pickett 1993; Renaud et al. 2022). Rural areas, characterised by low sealed area and population density, often experience strong biotic limitations (e.g., greater competition, predation), whereas urban areas are characterised by severe physical constraints (McDonnell and Pickett 1993). Additionally, environmental heterogeneity tends to increase with intermediate urbanisation levels, potentially driving suburban diversity peaks (Renaud et al. 2022). A further possibility is that the intermediate disturbance hypothesis could explain the non-linearity observed in the effects of urbanisation on carabid communities (Connell 1978; McKinney 2002). Finally, the definition of urbanisation and the range of the urban gradient vary considerably across studies. These categories are frequently subjective or insufficiently defined, further contributing to inconsistencies in the results (Batáry et al. 2018; McIntyre et al. 2000).

Several meta-analyses have attempted to uncover the mechanisms behind patterns observed along the urban–rural gradient. However, despite numerous field studies reporting impacts on this group, some of these analyses found no significant effect on carabids (Korányi et al. 2022; Szabó et al. 2023). Others detected an overall effect on species richness but could not explain the high variability in assemblage-level abundance (Martinson and Raupp 2013). One possible explanation is that these meta-analyses applied a linear approach, whereas evidence suggests that urbanisation effects on other taxonomic groups may be non-linear (Renaud et al. 2022). Furthermore, previous meta-analyses have shown that climatic factors can interact with urbanisation to modify its effects (Chamberlain et al. 2020; Fenoglio et al. 2020; Szabó et al. 2023). For example, urbanisation can increase rainfall through the urban precipitation effect, as observed in regions like the East Coast of China and the USA (Liu and Niyogi 2019). However, the extensive use of asphalt and concrete in cities can lead to drier soils due to increased runoff and evaporation (Burian and Pomeroy 2010). The urban heat island (UHI) effect, where more urbanised areas, such as city centres, are warmer than less urbanised areas, such as city outskirts (Arnfield 2003), can increase evapotranspiration (mostly by increased surface evaporation) and water runoff, resulting in drier soils in city centres compared to their less urbanised surroundings (Burian and Pomeroy 2010; Nielsen and Ball 2015; Pouyat et al. 2010). Although decreased permeability of the soil can reduce evaporation, combined with increased runoff, it results in drier soil compared to rural areas (Oke et al. 2017). In contrast, urban environments are often enriched with artificial ponds, wetlands and exotic and ornamental plant species that require regular irrigation, increasing soil moisture levels in cities, especially in dry regions, compared to less urbanised areas (Diamant et al. 2025; Ge et al. 2019). Supporting this pattern, a recent meta-analysis found that, with increasing levels of urbanisation, the abundance of soil animals increased in arid regions but declined in wet regions (Szabó et al. 2023).

In this study, we conducted a systematic review and a series of hierarchical meta-analyses to examine the potential non-linear effects of urbanisation on ground beetle species richness and assemblage-level abundance. Additionally, we aimed to investigate how climate factors and UHI potentially interact with possible non-linear urbanisation responses. On the basis of the findings of a recent global meta-analysis on soil animals (Szabó et al. 2023), we predicted that ground beetles' responses to urbanisation are non-linear. Furthermore, we predicted that climatic parameters and UHI would differentially modify ground beetles' responses in urban-suburban versus suburban-rural comparisons, potentially generating additional non-linearities.

2 | Methods

2.1 | Literature Search

For our literature search, we used the Web of Science Core Collection (Science Citation Index Expanded) from 1975 to November 2023 and the Scopus database (all document types) from 1960 to November 2023 (detailed PICO criteria and search terms are provided in Appendix S1, Section 1). We only included studies that investigated neighbouring urbanisation categories (e.g., urban vs. suburban, suburban vs. rural), as this approach is essential for our planned nonlinear analysis. Specifically, we excluded comparisons that bypass intermediate categories (e.g., urban vs. rural, or urban vs. natural) because such transitions obscure the continuous spatial gradient necessary to accurately model non-linear effects. We accepted both categorical and continuous urbanisation data, provided the continuous data also focused on adjacent areas or gradients that preserved the integrity of this step-wise spatial sequence. The initial search was conducted on 7 May 2022, and the database was closed on 3 November 2023. Titles and abstracts were screened to exclude irrelevant articles. Subsequently, we applied a set of inclusion and exclusion criteria during full-text filtering (Appendix S1, Section 1). Additionally, we incorporated studies meeting our inclusion criteria from a recent meta-analysis (Szabó et al. 2023). Our search initially identified 1029 studies, of which 127 were deemed potentially relevant for testing the interaction effects of urbanisation and climatic parameters on carabids. Ultimately, 25 studies satisfied the inclusion and exclusion criteria (see PRISMA diagram in Appendix S1, Section 2). However, our dataset exhibited a geographical bias. Most studies ($n = 15$; 56%) originated from Europe, while five were from Asia, three from North America and only one from South America (Table 1; Figure 1). In order to increase the robustness of our analyses, we did not control the habitat types from which the carabids were collected; we included studies with all types of habitats.

2.2 | Data Extraction

In two studies, the definition of urbanisation was inconsistent with the criteria used in the rest of the dataset. To address this, we reclassified the urbanisation categories in these two studies to ensure they adhered to roughly the same criteria, based on Batáry et al. (2018). Specifically, the 'rural' category was defined as areas with a very low proportion of buildings and sealed surfaces (< 20% sealed area). The 'suburban' category included residential areas with predominantly single-story houses, lawns and/or gardens (approximately 50% or less sealed area). Finally, the 'urban' category was characterised by a high proportion of sealed surfaces (> 50% sealed area). These percentages were estimated based on the spatial scale the original studies provided using OpenStreetMap (https://www.openstreetmap.org). This could mean district-level percentage in many cases, or if the original study provided sealed area percentage, we used those estimates.

We focused on two main metrics at the assemblage level: abundance data (activity density from pitfall traps) and absolute species richness (number of captured species/alpha diversity). We did not collect population-level abundance data, and other diversity metrics were not considered. In total, we identified 20 relevant studies and extracted 43 observations for species richness, along with 21 studies yielding 46 observations for abundance (Appendix S1, Section 2). Studies excluded during the full-text filtering process are detailed in Appendix S1, Section 3.

After screening each study, we extracted relevant climatic data from the CHELSA database (Climatologies at High Resolution for the Earth's Land Surface Areas) (Karger et al. 2017) using QGIS 3.18 software (QGIS.org 2021). The CHELSA database provides raster-based climatic data for the Earth's land surface conditions (1979–2013) at a resolution of 1 km. For each study city, we created polygons based on OpenStreetMap layers or GADM (Database of Global Administrative Areas) database boundaries if available (GADM 2018). We then extracted the following parameters: total annual precipitation, coefficient of variation (CV) of precipitation and mean annual temperature (used for UHI calculation). Total annual precipitation was expressed in L/m^2, while precipitation seasonality was measured using the CV. A low CV and standard deviation indicate low seasonality, whereas high values reflect high seasonality. Precipitation seasonality was natural-log transformed to achieve a normal distribution. All climatic parameters were used as continuous moderators in the analysis. We also analysed the UHI and the relative UHI effect following the method of Magura et al. (2020), which adjusts for differences in climate zones. Specifically, we extracted daytime UHI data from the Center for International Earth Science Information Network (Center for International Earth Science Information Network—Columbia University 2016). UHI was defined as the maximum daytime land surface temperature difference between the urban area and its rural surroundings. Relative UHI was calculated by dividing daytime UHI by the mean annual temperature. For correlations between the explanatory variables, see Appendix S1, Section 6, Tables S1 and S2.

2.3 | Effect Size Calculation

We used Pearson's correlation coefficient (Pearson's r) as the effect size. Initially, Hedges' g was calculated using the means and standard deviations of abundance or species richness. Hedges' g represents the unbiased standardised mean difference between groups, which can then be converted to Pearson's r to standardise all effect size data onto the same scale (Borenstein et al. 2009). Pearson's r expresses the linear association between two parameters, which can range from 1 (perfect positive association) to −1 (perfect negative association), with zero indicating no connection between the two parameters. In the case of suburban–rural comparison, the positive effect size indicates that the suburban area has higher abundance/species richness than the rural area, while a negative effect size indicates that the suburban area has lower abundance/richness than the rural area. Similarly, in the case of the urban–suburban comparison, the positive effect size suggests that the urban area has higher abundance/species richness than the suburban area, and a negative effect size suggests that the urban area has lower abundance/species richness than the suburban area. Detailed equations used for effect size calculations are provided in Appendix S1, Section 4.

For two studies, variance measures required to calculate the initial effect size (Hedges' d and subsequently Hedges' g) of categorical data were not reported. To address this, we simulated standard deviation values based on the collected dataset using the R mice package (van Buuren and Groothuis-Oudshoorn 2011). Data points with simulated variances are

TABLE 1 | List of the 25 included studies.

Study	Species richness	Abundance	City(s)	Country (Continent)
Abdel-Dayem et al. (2023)	Y	Y	Wadi Hanifa (Riyadh)	Saudi Arabia (Asia)
Alaruikka et al. (2002)	Y	Y	Helsinki	Finland (Europe)
Castro et al. (2020)	Y	N	General Pueyrrédon	Argentine (S-America)
Croci et al. (2008)	Y	Y	Rennes	France (Europe)
Czechowski (1981)	Y	N	Warsaw	Poland (Europe)
Elek and Lövei (2005)	Y	Y	Sorø	Denmark (Europe)
Fujita et al. (2008)	Y	Y	Hanshin district	Japan (Asia)
Gagne and Fahrig (2010)	Y	Y	Ottawa	Canada (N-America)
Gordienko et al. (2018)	N	Y	Nizhnekamsk	Russia (Asia)
Ishitani et al. (2003)	Y	Y	Hiroshima	Japan (Asia)
Kirichenko-Babko et al. (2017)	N	Y	Lublin	Poland (Europe)
Magura et al. (2008)	Y	Y	Debrecen	Hungary (Europe)
Magura et al. (2010)	Y	Y	Sepsiszentgyörgy	Romania (Europe)
Niemelä et al. (2002)	Y	Y	Sofia, Helsinki, Edmonton	Bulgaria, Finland (Europe), Canada (N-America)
Park and Lee (2021)	Y	Y	Osaka	Japan (Asia)
Perry et al. (2020)	N	Y	Cleavland	USA (N-America)
Piano et al. (2020)	Y	N	Torino	Italy (Europe)
Sadler et al. (2006)	Y	Y	Birmingham	Great Britain (Europe)
Tóthmérész et al. (2011)	Y	Y	Sepsiszentgyörgy	Romania (Europe)
Varet et al. (2014)	Y	Y	Rennes	France (Europe)
Venn et al. (2003)	Y	Y	Helsinki	Finland (Europe)
Venn et al. (2013)	N	Y	Helsinki	Finland (Europe)
Zara et al. (2021)	Y	Y	Triest	Slovenia (Europe)
Zelazna and Błazejewicz-Zawadzińska (2003)	Y	Y	Bydgoszcz	Poland (Europe)

Note: The table shows the data origin at the city and continent level and whether the study contained species richness and/or abundance data.

marked in the dataset provided in the data extraction sheet (Appendix S1, Section 8).

2.4 | Meta-Analysis

We conducted all analyses using the R 4.2.1 statistical environment (R Development Core Team 2022). Prior to analysis, Pearson's r values were converted to Fisher's z to ensure normality (Borenstein et al. 2009). We used meta-analysis models from the *metafor* package (Viechtbauer 2010). For visualisation purposes, Fisher's z values and their 95% confidence intervals were back-transformed to Pearson's r, as this metric is easier to interpret (Batáry et al. 2018). The back-transformed estimates (Pearson's r) reflect the strength and direction of the effect of urbanisation on carabid species richness or abundance, ranging from −1 to 1. Effects were considered significant if the confidence intervals did not overlap with zero. To investigate potential non-linear effects of urbanisation using meta-regression (which employs fundamentally linear models), we adopted a piecewise approach. This means we divided the urbanisation gradient into two distinct comparisons: Urban–Suburban comparison and Suburban–Rural comparison. By treating these two comparisons as separate moderator levels within the meta-analysis, we effectively tested for non-linearity. A significant difference in the direction (positive vs. negative effect) or magnitude of the estimated effect between the urban–suburban and suburban–rural comparisons provides strong evidence for a non-linear (e.g., hump-shaped or *U*-shaped) response across the full urbanisation gradient. Abundance and species richness were analysed using separate hierarchical mixed-effects meta-analysis models (rma.mv function), with continent, study ID and dyad included

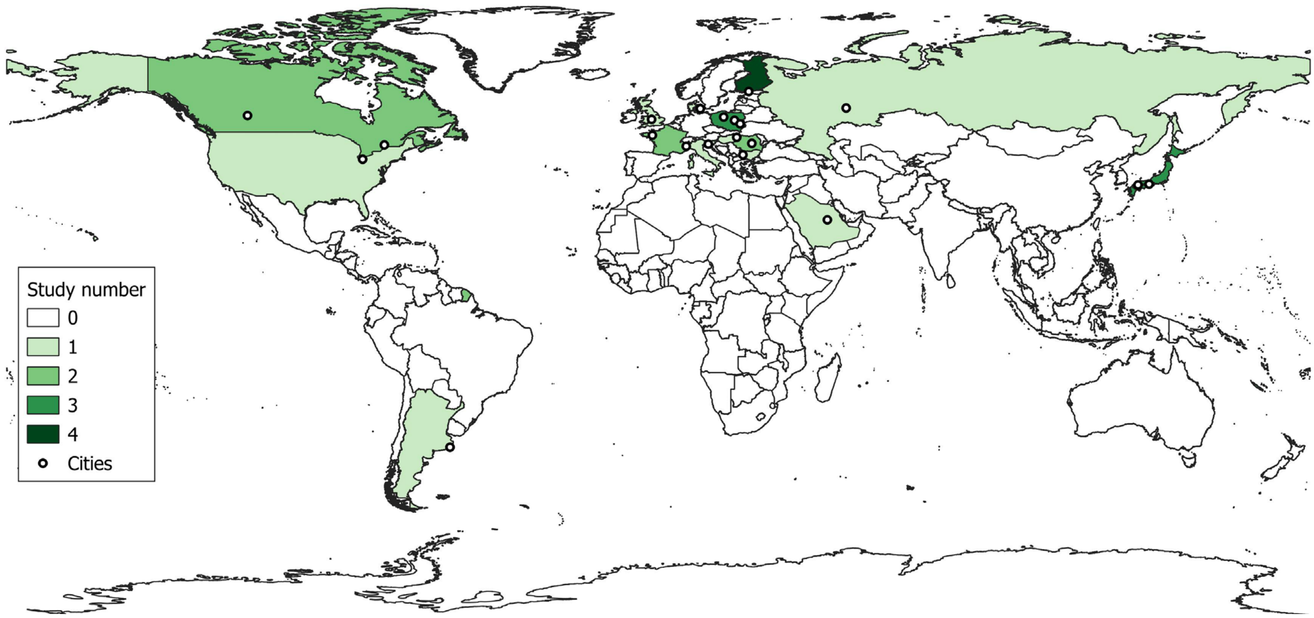

FIGURE 1 | Geographic distribution of studies ($n=25$) in the meta-analysis, with one study was performed in more than one country. Green shading indicates the number of studies originating from each country, and circles with black outlines represent the cities where the studies were conducted.

as nesting factors. The continent was the first nesting factor, as many studies originated from the same region. While it was unclear whether the continent served as an important moderator or nesting factor, we also tested it as a moderator (see Tables S3–S5, Appendix S1, Section 6). Including the continent as a nesting factor ensured that regional heterogeneity did not bias the results. The second nesting factor, study ID, accounted for studies that contributed multiple data points (e.g., data from several cities or years). Lastly, since suburban categories were included twice in the analysis (once for urban–suburban comparisons and once for suburban–rural comparisons), this dyad was incorporated as the third nesting factor to account for this non-independence (Batáry et al. 2018; Borenstein et al. 2009).

We first calculated the overall mean effect size for species richness and abundance, considering the estimated effect size with 95% confidence intervals (CIs) and total heterogeneity statistics (Q) for each analysis. The overall mean effect size, or summary effect size, indicates whether there is a consistent effect across all calculated effect sizes, including both rural–suburban and suburban–urban comparisons. These parameters were extracted from the meta-analysis models. The heterogeneity statistic (Q) represents a weighted sum of squares tested against a χ^2 distribution (Borenstein et al. 2009). Following the summary meta-analysis, we conducted meta-analyses with moderators. Total heterogeneity in these models comprised variance explained by the moderator (between-group heterogeneity) and residual error variance (within-group heterogeneity). χ^2 tests were used to determine significance. A significant between-group heterogeneity indicates that the moderator significantly modifies the effect size of urbanisation (Borenstein et al. 2009).

Due to two climatic extremes in annual precipitation potentially affecting abundance in the suburban–rural comparison, we conducted a sensitivity analysis by excluding these two points. This did not alter the overall trends but significantly decreased the p-values. As a precaution, we chose to retain these data points in the analysis and interpret the original results.

2.5 | Publication Bias

To identify potential publication bias, we employed funnel plots (Figure S1), Egger's test and Kendall's rank correlation test (see Appendix S1, Section 5). Funnel plots graphically represent the relationship between effect sizes and their sample size (i.e., variance or standard error). Symmetry in the funnel plot typically indicates the absence of publication bias, while asymmetry might suggest the opposite. Egger's and Kendall's rank correlation tests provide statistical verification of this symmetry. Both tests confirmed that the data for species richness and abundance were free from publication bias, supporting the reliability of our dataset (see Appendix S1, Section 5).

3 | Results

We did not detect an overall effect of urbanisation on species richness or assemblage-level abundance. However, the effects significantly differed between suburban–rural and urban–suburban comparisons for both species richness and abundance, confirming a non-linear relationship (Figure 2a; Table 2, Table S6). Compared to rural areas, suburban areas had a higher assemblage-level abundance of carabids but tended to have lower species richness (Figure 2a–c; Table 2, Table S6).

When considering climate parameters as single moderators, direct moderation was detected only for the UHI on urbanisation effects on species richness (Figure 2a; Table 2, Table S7). However, interactions between climate parameters and urbanisation category (urban-suburban vs. suburban-rural) were evident in all cases. These interactions affected abundance and,

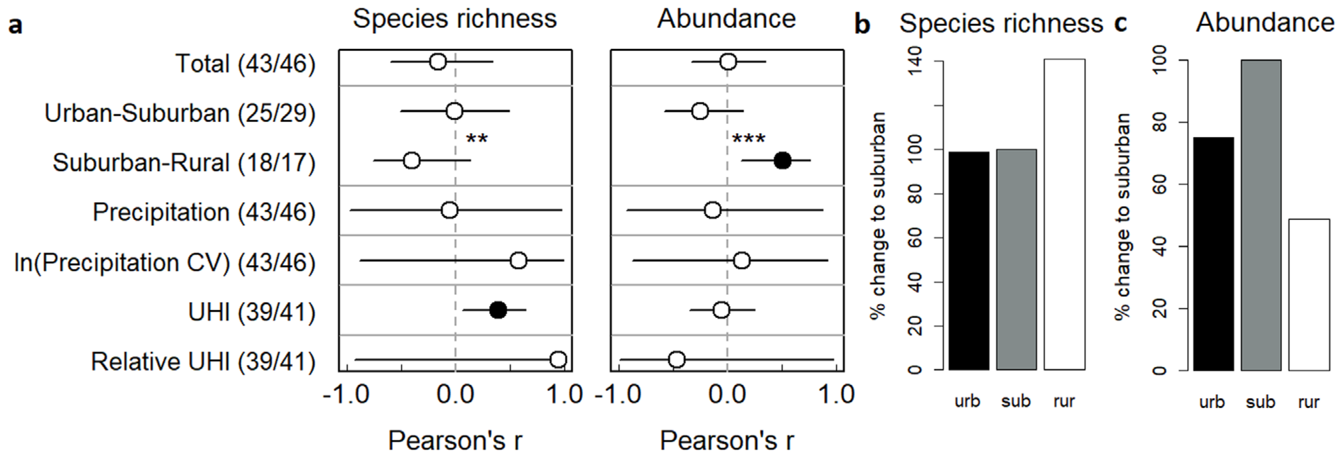

FIGURE 2 | Forest plot about the effects of urbanisation on species richness and abundance of carabids with different urbanisation categories or climate variables as moderators (a) and the percentage of change in (b) species richness or (c) abundance compared to suburban. On the forest plots, the mean effect sizes (Pearson's *r*) with 95% CIs are shown. UHI, Urban heat island; Relative UHI means the urban heat island effect corrected for the mean annual temperature. Black circle indicates a significant effect size. The asterisks show significant differences between comparison levels (** < 0.01, *** < 0.001). Numbers in parentheses indicate sample sizes (first number for species richness, second for abundance analyses). Urb: urban, sub: suburban, rur: rural. Colours at b and c are for contrast between categories.

TABLE 2 | Summary of meta-analysis models with an intercept on abundance and species richness showing total heterogeneity and heterogeneities explained by moderators with corresponding residual heterogeneities.

		Species richness				Abundance			
Moderator		***Q***	**df**	***p***	**AIC**	***Q***	**df**	***p***	**AIC**
Total	Residual	447.65	42	< 0.001	201.4	545.2	45	< 0.001	428.2
Urbanisation	Moderator	**7.447**	**2**	**0.006**	**195.5**	**28.31**	**1**	**< 0.001**	**401.8**
	Residual	443.3	41	< 0.001		543.1	44	< 0.001	
Precipitation	Moderator	0.002	1	0.964	200.6	0.032	1	0.858	428.2
	Residual	447.1	41	< 0.001		544.8	44	< 0.001	
Precipitation × Urbanisation	Moderator	7.596	3	0.055	196.1	**34.11**	**3**	**< 0.001**	**397.4**
	Residual	435.4	39	< 0.001		530.6	42	< 0.001	
ln(Precipitation CV)	Moderator	0.398	1	0.528	200.0	0.032	1	0.859	428.0
	Residual	441.0	41	< 0.001		544.9	44	< 0.001	
ln(Precipitation CV) × Urbanisation	Moderator	**18.03**	**1**	**< 0.001**	**185.6**	**65.66**	**3**	**< 0.001**	**366.1**
	Residual	404.8	41	< 0.001		502.4	42	< 0.001	
UHI	Moderator	**5.349**	**1**	**0.021**	**185.1**	0.105	1	0.746	419.3
	Residual	326.5	371	< 0.001		538.1	39	< 0.001	
UHI × Urbanisation	Moderator	**21.67**	**3**	**< 0.001**	**171.9**	**221.0**	**4**	**< 0.001**	**202.3**
	Residual	319.8	35	< 0.001		377.7	37	< 0.001	
Relative UHI	Moderator	1.024	1	0.312	188.6	0.140	1	0.708	419.2
	Residual	395.5	37	< 0.001		540.3	39	< 0.001	
Relative UHI × Urbanisation	Moderator	**38.14**	**3**	**< 0.001**	**154.6**	**244.7**	**3**	**< 0.001**	**178.1**
	Residual	361.4	35	< 0.001		290.3	37	< 0.001	

Note: Significant moderator effects are bolded.
Abbreviation: UHI, urban heat island.

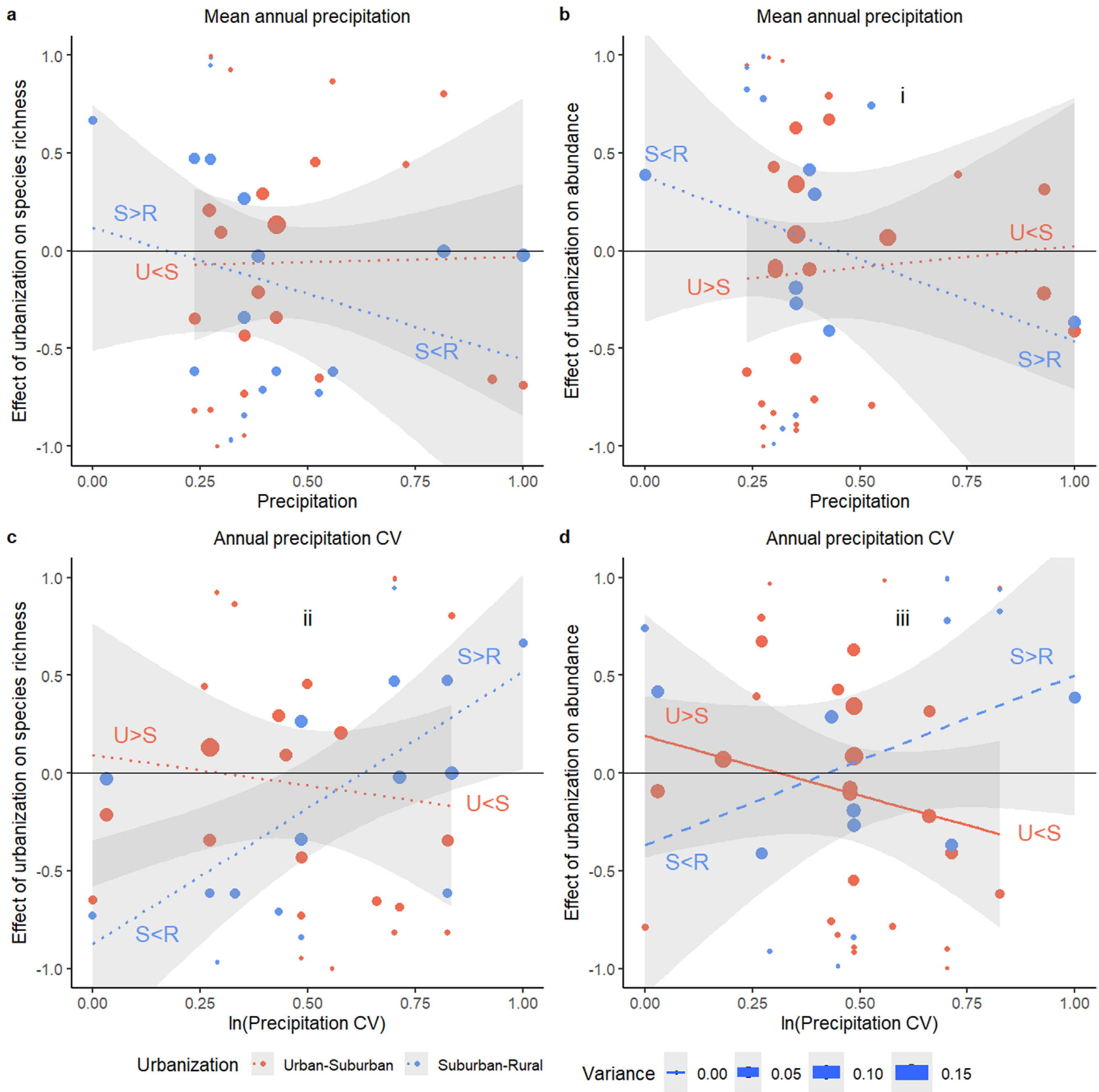

FIGURE 3 | Moderation effect of (a) annual precipitation on urbanisation effect size for abundance and (b) species richness and moderation effect of annual precipitation coefficient of variation (CV) (c) on urbanisation effect size for abundance and (d) species richness (Pearson's r). Both variables are normalised between 0 and 1; the range of the precipitation is 109.8–1576.7 mm, and the range of the precipitation CV is 9.91–99.03. Point size is proportional to the variance associated with the given effect size. Grey areas indicate ±95% confidence intervals. The blue dots and lines are for suburban-rural categories, and the red ones are for urban-suburban categories. A solid line indicates a significant slope ($p < 0.05$), a dashed line indicates a marginally significant slope ($p < 0.1$), and a dotted line indicates a non-significant slope. Significant interaction between urbanisation levels and climate is marked with i: $p < 0.5$, ii: $p < 0.01$ or iii: $p < 0.001$. The solid black line indicates zero effect. R: rural, S: suburban, U: urban, R, S, U indicate which area has higher abundance or species richness.

in some instances, both abundance and species richness simultaneously (Figures 3 and 4; Table 2, Table S7). Annual precipitation and its interaction with urbanisation significantly and marginally significantly influenced abundance and species richness, respectively. Specifically, in the suburban–rural comparison, abundance tended to be higher in suburban areas of drier cities but lower in wetter cities. No such moderation effect was observed in the urban–suburban comparison (Figure 3a,b; Table S7).

Precipitation seasonality, represented by its coefficient of variation, significantly influenced how urbanisation affected species richness and abundance (Figure 3c,d; Table 2, Table S7). In cities with low precipitation seasonality, suburban areas

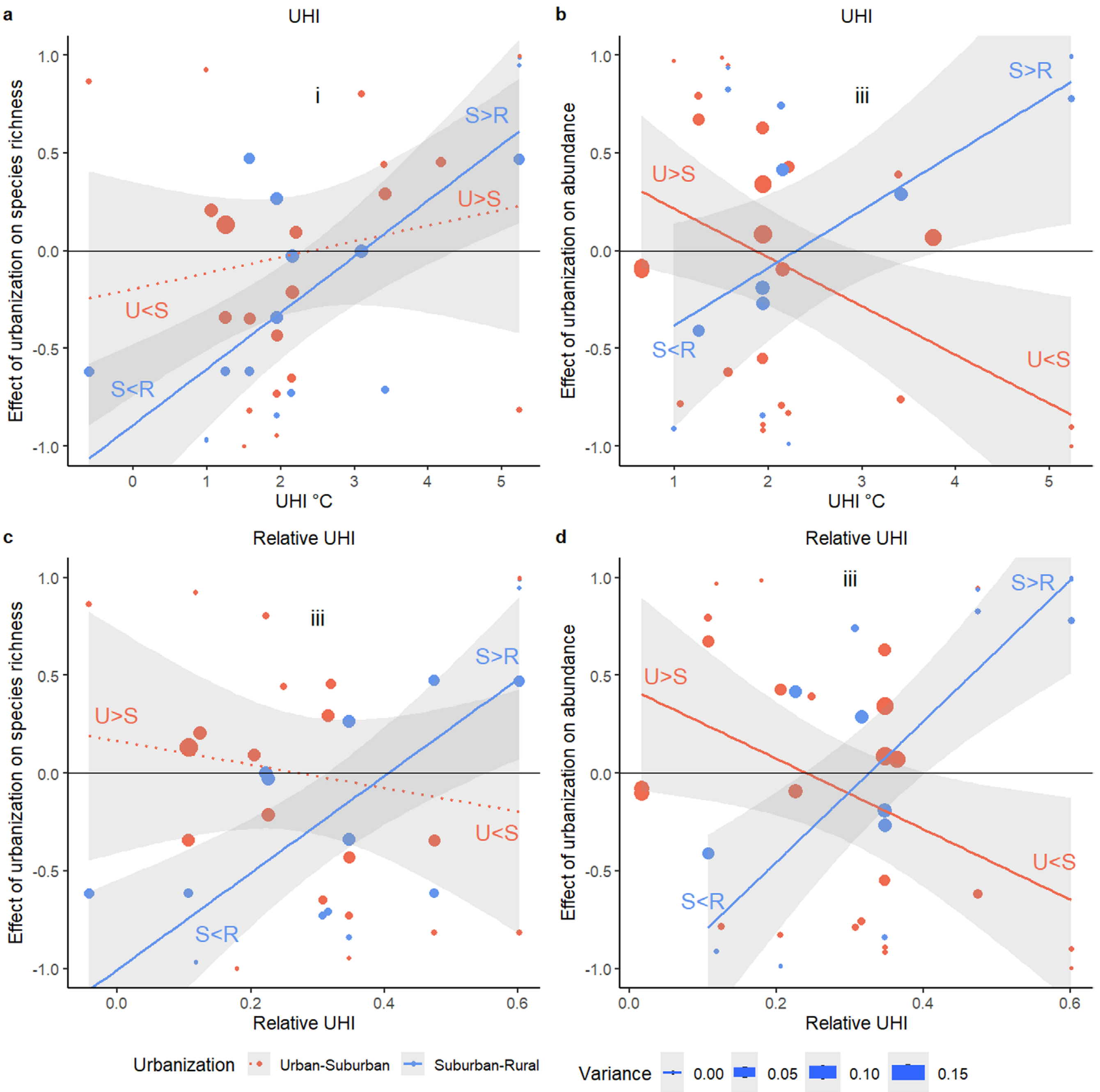

FIGURE 4 | Moderation effect of urban heat island (UHI) on (a) urbanisation effect size for abundance, and (b) species richness, and moderation effect of relative UHI on (c) urbanisation effect size for abundance and (d) species richness (Pearson's *r*). Point size is proportional to the variance associated with the given effect size. Grey areas indicate ±95% confidence intervals. Blue dots and lines represent the suburban-rural categories, whereas red ones represent the urban-suburban categories. A solid line indicates a significant slope ($p < 0.05$), a dashed line indicates a marginally significant slope ($p < 0.1$) and a dotted line indicates a non-significant slope. Significant interaction between urbanisation levels and UHI is marked with i: $p < 0.5$, ii: $p < 0.01$ or iii: $p < 0.001$. The solid black line indicates zero effect. R, S, U indicate which area has higher abundance or species richness.

exhibited lower species richness and abundance than rural areas. This pattern was reversed in cities with high precipitation seasonality, where suburban areas supported higher species richness and abundance than rural areas, although the slope for abundance was only marginally significant. For urban-to-suburban comparisons, the pattern flipped entirely: in low-seasonality cities, urban areas had higher species richness and abundance than suburban areas, whereas in high-seasonality cities, suburban areas exhibited higher species richness and abundance than urban areas (Figure 3c,d, Figure S3; Table S7).

UHI and relative UHI intensity similarly moderated the effects of urbanisation on species richness and abundance (Figure 4; Table 2, Table S7). In suburban-to-rural comparisons, low UHI and relative UHI intensity were associated with reduced species richness and abundance in suburban areas compared to rural ones. As UHI intensity increased, this trend reversed, with suburban areas showing higher species richness and abundance than rural areas. For urban-to-suburban comparisons, species richness and abundance were higher in urban areas than in suburban areas under low relative UHI conditions. This pattern was also observed for carabid abundance under low UHI conditions, except for species richness which showed an opposite pattern. At higher relative UHI levels, however, both species richness and abundance were higher in suburban areas than in urban ones, while with high UHI, species richness was higher in urban areas.

4 | Discussion

Several theoretical studies and meta-analyses have already explored the effects of urbanisation on carabids. However, our study is unique in several respects as it is the first study to consistently analyse the non-linear effect of urbanisation on both abundance and species richness of carabids, while investigating its interactive effect with climatic conditions. Consistent with our first hypothesis, our study reports for the first time a non-linear effect of urbanisation on carabid abundance. However, our analyses also indicate a consistent reduction of species richness in both urban and suburban areas compared to rural areas, confirming previous findings (reviewed by Martinson and Raupp 2013). Our analyses further revealed that several climatic factors, including precipitation seasonality and UHI intensity, moderated this non-linear effect of urbanisation. For example, under conditions of higher precipitation seasonality and greater UHI intensity, we could observe a suburban peak in both abundance and species richness. These findings align with our second hypothesis, which posited that climatic conditions influence the effect of urbanisation on carabid communities. Overall, our results suggest that suburban environments may buffer the impacts of climatic extremes on carabids (e.g., mitigating winter and heatwaves), highlighting the role of climatic context in shaping carabid responses to urbanisation. Our study, therefore, provides novel insights to explain the strong context dependency observed in previous research on the effects of urbanisation on carabids.

Several theoretical studies and meta-analyses considered the effects of urbanisation on carabids; however, there are considerable differences compared to our study. Some studies concentrated on how the body size of the carabids changes because of urbanisation, UHI and temperature (Lövei and Magura 2022; Magura et al. 2020). Martinson and Raupp (2013) also analysed the abundance and the species richness among other variables; however, they did not analyse the interaction with climate. Magura et al. (2010) provide valuable analysis of species richness and abundance but are restricted to the GLOBENET project sites, whereas our study is a global-level meta-analysis. An earlier meta-analysis of the effects of urbanisation on soil animals analysed similar variables, but it did not analyse the interacting effect of climate and urbanisation on individual taxa, such as carabids (Szabó et al. 2023). Furthermore, unlike our meta-analysis considering responses at suburban-rural and urban-suburban scales, none of the above-mentioned studies analysed the non-linear effects of urbanisation.

The observed decrease in species richness from rural to suburban areas can likely be attributed to the loss of specialist species and the dominance of generalist species in more urbanised regions (Alaruikka et al. 2002; Diamant et al. 2025; Knop 2016). Our findings can be explained by the findings of previous studies showing that they document a decline in forest-specialist carabid species and individuals with increasing urbanisation, alongside an increase in open-habitat and generalist species (Alaruikka et al. 2002; Gaublomme et al. 2008; Magura et al. 2008).

Urbanisation frequently leads to suburban peaks in both species richness and abundance (Diamant et al. 2025; Fattorini et al. 2020; Grade et al. 2022; Kowarik 2011). Several hypotheses have been proposed to explain this pattern. The most plausible explanation for the peak in suburban abundance is the relatively stable micro- and macroclimatic conditions in suburban environments. These areas can provide more enriched resources compared to city centres or rural regions (Alberti 2015; Arnfield 2003; Oke 1997; Parris 2016; Philpott et al. 2014). Suburban areas benefit from more stable temperatures, and irrigation often mitigates dry periods, while negative urbanisation impacts, such as habitat fragmentation, pollution and soil compaction, are less severe compared to highly urbanised areas (Alberti 2015; Oke 1997). Another hypothesis suggests that heterogeneity in physical parameters, such as the heat island effect, impervious surfaces, soil compaction and water availability, contributes to suburban peaks in both abundance and species richness (McKinney 2002; Renaud et al. 2022), which could support diverse carabid populations. Alternatively, the results may be explained by the intermediate disturbance hypothesis, where suburban areas would represent an intermediate level of disturbance (Connell 1978; McKinney 2002). Interestingly, our study found a peak only in abundance, which may be explained by suburban areas' unique management practices and vegetation compositions, including private gardens and parks, that enhance landscape heterogeneity (Alberti 2015; Tscharntke et al. 2012). Such heterogeneity may promote high carabid abundance (Fahrig et al. 2011; Kotze et al. 2011). Additionally, suburban environments may provide supplemental resources, such as garbage and higher plant productivity, contributing to increased abundance (McKinney 2002). In city centres, predation pressure tends to decrease, but resource competition increases (Alberti 2015; Eötvös et al. 2018; Korányi et al. 2021, 2022). Conversely, suburban areas strike a balance where resources remain abundant, while predation pressures diminish, potentially fostering both species richness and abundance.

Our findings reveal that suburban areas increased carabid abundance and species richness compared to rural areas in drier climates. However, this trend reversed in wetter climates, where suburban areas reduced these metrics. Although these effect sizes were not significant, with more included data from future field studies, their direction could be validated in a later meta-analysis. This divergence likely stems from irrigation practices in suburban areas, which enhance soil water availability in dry climates, contrasting with the increased runoff from sealed surfaces that exacerbate water loss in wetter climates (Alberti 2015; Diamant et al. 2025; Nielsen and Ball 2015). These results align with a prior meta-analysis showing that soil animal abundance is increased by urbanisation in dry climates but decreased in wet climates (Szabó et al. 2023). Additionally, urban core areas slightly reduced abundance compared to suburban areas in drier climates, whereas no such effect was observed in wetter climates. This could be due to the presence of some generalist carabid species that thrive in wetter habitats (Alaruikka et al. 2002). Furthermore, in drier climates, the urban cores can be more suitable to local dryland species than to broadly adaptable generalist species (Diamant et al. 2025), which also explains why the decrease in abundance is only slight. Their increased abundance in urban cores might offset the typically negative impacts of urbanisation in these regions.

Regarding precipitation seasonality, similar trends were observed for both species richness and abundance. In cities with low precipitation seasonality, species richness and abundance in suburban areas declined compared to rural areas. Conversely, in cities with high seasonality, suburban areas increased both species richness and abundance compared to rural and urban core areas. This can likely be explained by the net positive effect of the more stable micro- and macroclimatic conditions in suburban areas that buffer climatic extremes (e.g., harsh winters, heatwaves), where the negative effects of urbanisation-related stressors, such as pollution and habitat fragmentation, are less pronounced (Alberti 2015; Arnfield 2003; Oke 1997).

Our analysis of the urban heat island (UHI) effect revealed a robust and significant suburban peak in both species richness and abundance in cities with high relative UHI, in contrast to cities with low UHI. UHI is a relative measure of temperature increase in the cities compared to their surrounding rural areas (Oke et al. 2017). Due to its correlation with sealed surfaces, UHI is typically stronger in urban cores than in suburban areas (Oke et al. 2017). Although an earlier analysis found that UHI decreases carabid body size, it did not find an interaction of UHI with urbanisation (Lövei and Magura 2022). The differences in results compared to our study can be explained by the different variables we used. Our result suggests that UHI might mitigate seasonal temperature extremes in winter (Macintyre et al. 2021), creating a more favourable overwintering microenvironment in suburban areas (Bale and Hayward 2010). Suburban environments likely offer better access to resources and warmer, well-insulated overwintering spots around residential areas compared to rural regions. Additionally, habitat edges—that might be abundant in heterogeneous suburban landscapes—are particularly suitable for carabid overwintering (Knapp et al. 2019). This pattern may not only arise from UHI's ability to moderate temperature seasonality in suburban zones, but also due to the more severe effects of UHI in urban cores. For example, the increased frequency and intensity of heatwaves in urban centres (Perkins-Kirkpatrick and Lewis 2020) can exacerbate thermal stress, negatively impacting biodiversity (Wei et al. 2022). Although ectothermic organisms like carabids in temperate and cold climates possess broad tolerance to temperature fluctuations, this tolerance is typically biased towards cold rather than heat extremes (Chown and Duffy 2015; Youngsteadt et al. 2017). Moreover, the urban environment has been shown to reduce insects' warming tolerance (the difference between a population's critical thermal maximum and habitat temperature) (Chown and Duffy 2015), making heat waves and high UHI levels exceed the tolerance range of many species. However, in the case of ants, an increase in upper thermal tolerance was found (Chown and Duffy 2015; Roeder et al. 2021). Consequently, urban cores become dominated by generalist, synanthropic and heat-tolerant species, further reducing biodiversity (Piano et al. 2017). In summary, UHI improves overwintering temperatures in cities, but habitat limitations render suburban areas more favourable. This positive winter effect may be offset by summer's negative impacts, like intense heatwaves.

5 | Conclusion

Our study demonstrates a non-linear effect of urbanisation on carabid communities and highlights the pivotal role of climatic context in shaping these patterns. The decline in species richness towards suburban and urban cores could be attributed to the loss of specialist species, while the hump-shaped response of the abundance might be caused by the net positive effect of suburban resource richness and habitat heterogeneity coupled with the increased urban stressors in city centres. In cities with high precipitation seasonality and pronounced urban heat island (UHI) effects, suburban areas emerge as refuges for carabids, positively influencing their abundance. Suburban environments provide more stable micro- and macroclimates compared to rural areas, buffering against harsh winters and mitigating the amplified heatwave impacts common in urban cores. However, this suburban advantage diminishes in cities with low seasonality and weak UHI, where climatic conditions are relatively stable. This response pattern underscores the need for climate-specific mitigation strategies. These should include increasing the number, size and ecological quality of green spaces (or so-called yellow spaces in dry climates; Diamant et al. 2025), as well as enhancing their connectivity at a landscape scale. It is also important to consider which species are supported by such measures and preferably support the local species instead of alien ones or urban generalists (Diamant et al. 2025). Future research should focus on the role of resource quantity and quality along the urbanisation gradient on community structure to better understand and address these challenges. Furthermore, a better geographical representation of the tropical areas and the global south is necessary for future studies to strengthen the generalisability of the findings.

Author Contributions

Borbála Szabó: conceptualisation, data curation, formal analysis, investigation, methodology, software, visualisation, writing – original draft preparation; **Dávid Korányi:** conceptualisation, validation, writing – reviewing and editing; **Adrien Rusch:** conceptualisation, validation, writing – reviewing and editing; **Péter Batáry:** conceptualisation, funding acquisition, methodology, project administration, resources, supervision, validation, writing – reviewing and editing.

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Disclosure

The main focus of the authors lies in the field of ecology with conservation biologically oriented research, such as the biological effectiveness of agri-environment schemes, habitat fragmentation, urbanisation and edge effect on a wide range of terrestrial taxa and ecosystem functions and services.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data are available at Zenodo Data repository at https://zenodo.org/records/17328575 or https://doi.org/10.5281/zenodo.17328574.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** Supporting Information.