

Body size shifts in aquatic and terrestrial urban communities

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Body size is intrinsically linked to metabolic rate and life history features, and central to species interactions such as food web dynamics¹ and ². The increased temperatures associated with the urban-heat-island effect³ result in increased metabolic costs and are expected to drive shifts to smaller body sizes⁴. Urban environments are, however, also characterised by strong habitat fragmentation⁵, favouring mobile species. Here, using a replicated, spatially nested sampling design across ten animal taxonomic groups, we show that urban communities generally consist of smaller species. However, while we show urban warming for three habitat types, and associated reduced community-weighted mean body sizes for four taxa, three taxa display a shift to larger species along the urbanisation gradients. Our results show that the general trend towards smaller-sized species is overruled by filtering for larger species when size positively covaries with dispersal, a process capable of mitigating low connectivity of ecological resources in urban settings⁶. We thus demonstrate that the urban-heat-island effect and urban habitat fragmentation are associated with contrasting community-level body size shifts that critically depend on the association between body size and dispersal. Since body size is key to interspecific relationships¹, such shifts may impact urban ecosystem functioning.

Body size is a central species trait determining key features such as longevity, fecundity, and use of space⁷. It also drives interspecific relationships, thus affecting ecological network dynamics¹. Size-biased species loss has profound impacts on ecosystem functioning^{8,9}. Because higher ambient temperature increases metabolic rates and associated costs for a given body size², global climatic warming is expected to drive shifts to communities consisting of smaller species for ectotherms, which rely largely on ambient conditions to achieve operational body temperatures^{4,10,11}.

Our planet is urbanizing rapidly¹², and urbanisation is a key process of human-induced rapid environmental change. Cities are characterised by urban-heat-islands (UHI) with elevated temperature decades ahead of the global average^{3,13}. Not only are cities warmer than surrounding areas, they also experience extensive fragmentation of (semi-)natural habitats¹⁴. Both habitat fragmentation and the UHI-effect increase with built-up cover (%BU; urbanisation proxy)^{15,16}. This creates an interesting scope to study opposite effects of size-dependent thermal tolerance and dispersal capacity, as larger body size favours dispersal in some but not all taxa.

Here, we test the hypothesis that urbanisation causes shifts in community-level body size, and that these shifts critically depend on the community-specific association between body size and dispersal. We generally expect the UHI-effect to drive shifts to species with smaller body sizes in communities of ectothermic species, in line with Atkinson's temperature-size rule¹⁷. For taxa characterized by a positive association between body size and dispersal, however, we also expect a filtering in favour of larger-bodied species associated with habitat fragmentation^{6,18}. Filtering for increased mobility has been demonstrated for urban ground-beetle communities and plant assemblages^{19,20}. Hence, for taxa characterised by a positive body size-dispersal link, we predict that the general community-level pattern of smaller species with increasing urbanisation may be neutralized or even reversed.

To test our hypothesis, we engaged in an analysis of community-level body size shifts across a broad range of both terrestrial and aquatic taxa along the same and systematically sampled urbanisation gradient. We studied the direction of change of community-level body size in ten taxa using a replicated, highly standardised and nested sampling design covering urbanisation gradients at seven spatial scales (50-3200 m radii; Fig. 1). We sampled each taxon at up to 81 sites, sampling 95001 individuals from 702 species, with species-specific body size varying by a factor 354 (0.226-80 mm; Extended Data Table 1). Three of the ten groups are characterised by a positive association between body size and dispersal capacity (see Methods).

We show that local temperature of pond, grassland and woodland habitats significantly increases with urbanisation. The intensity of these UHI-effects is consistently larger during night and summer, in accordance with slower night-time city cooling and summer's higher irradiation levels²¹ (Fig. 2; Extended Data Fig. 1, Table 2). We also show that increased urbanisation is linked to significant declines in habitat amount and patch size of terrestrial habitats, and significant increases in distances among patches for both terrestrial and aquatic habitats (Extended Data Fig. 2).

Confirming our metabolism-based prediction of interspecific reductions in mean body size with increasing temperature, urban communities for four (ground-spiders, ground-beetles, weevils and cladocerans) out of the seven taxa without a positive size-dispersal link display reduced community-weighted mean body size. For ostracods, bdelloid rotifers and web-spiders, no relationship is found. In contrast, all three taxa with positive size-dispersal links display increased community-weighted mean body size in response to urbanisation (Fig. 3, 4; Extended Data Table 3, Fig. 2). The positive size shifts observed for these taxa are in line with our prediction that increased urbanisation-mediated habitat fragmentation selects for larger species in taxa with positive size-dispersal links.

The Benjamini-Hochberg procedure²², which controls for false positives, confirms all seven significant responses at study-wide level. Contrasting the percentage change in body size over a percentage built-up gradient of 25% shows a marked difference between taxa with a positive size-dispersal link (mean $\pm$ SE: $+13.6\% \pm 8.3\%$ body size increase) versus the other taxa ($-15.6\% \pm 5.3\%$ body size decrease; weighted ANOVA: $F_{1,8} = 12.38$; $P = 0.0079$). These community-level body size shifts happen independently from shifts in species abundance and diversity along the urbanisation gradient. For example, reduced diversity is apparent for both taxa with positive and taxa with negative size shifts, as well as for web-spiders which lack a size shift, while cladocerans show size reduction without diversity change (Extended Data Table 4). For butterflies, macro-moths, and orthopterans (i.e. taxa with a positive size-dispersal link) the increase in the community-weighted size ranges from 7% to 21% depending on the taxon, whereas size reductions of ground-beetles, weevils, and ground-spiders (i.e. terrestrial taxa with non-positive size-dispersal links) range from -18% to -21% over an urbanisation gradient of 0-25%BU (Fig. 3). The cladocerans display the largest size reduction (-44%), which agrees with the temperature-size response generally being stronger in aquatic than in terrestrial species as a result of greater oxygen limitation in water²³. However, the size reduction for the ostracods is much smaller (-13%) and non-significant, while for the rotifers no size shift is found. The absence of a size shift for the microscopic rotifers might indicate that their small size allows for sufficient oxygen exchange between warm, low-oxygen environments and body tissues, so that no community shift to smaller body sizes is induced by increased temperature.

Our multi-scale approach allows pinpointing the spatial scales at which urbanisation best explains the observed effects. While during winter the UHI-effect fades with increasing spatial scale during the day but not at night, during summer both diurnal and nocturnal UHI-effects are more pronounced at small scales (Fig. 2; Extended Data Fig. 1, Table 2). The most explicative spatial scale for community-weighted mean body size varied considerably among taxa, with effects for smaller-sized taxa prevailing at small spatial scales (Fig. 3, 4; Extended Data Table 3, Fig. 2).

Urbanisation induces biodiversity loss and biotic homogenisation^{12,14}. Here, we demonstrate that urbanisation also leads to community-wide shifts in body size for the majority of studied species groups, mediated by shifts from larger to smaller species. The size reductions within aquatic and terrestrial taxa follow metabolic rules in line with the UHI-effect. In contrast, urbanisation's increased fragmentation appears to cause size increases for taxa with positive size-dispersal links. Hence, our study documents multi-taxa bi-directional shifts in community body size. In addition to the interspecific patterns reported here, body size shifts can also occur at the intraspecific level, through both phenotypic plasticity and genotypic change^{30,31,32}. Our results open up avenues for mechanistic studies underpinning the observed mixed body size shifts along urban gradients and quantifying their functional effects in urban ecosystems. A better insight into the mechanisms of body size shifts will indeed allow predicting intertwined impacts of climate change and urbanisation on the size-distribution of communities.

The size-biased species loss reported here is expected to strongly impact ecosystem functioning^{8,9}. If taxa are on average represented in urban areas by smaller or larger species, this will affect ecosystem structure and function in multiple ways. Metabolic theory predicts shifted size distributions to affect whole-ecosystem properties such as primary productivity, carbon cycling and decomposition²⁵, and shifts in body size also to smaller species in communities translate into altered life-histories, demographic rates and interspecific relationships^{1,2}. For instance, consumer-resource dynamics are also likely to be affected²⁶. In one example, decreasing availability of large insect prey has driven population declines in Lesser grey shrike, a medium-sized passerine bird²⁷. Indeed, from a predators' viewpoint, it may be difficult maintaining larger sizes if prey decrease in size²⁸. Recently, such dynamics have been modelled for warming-related intraspecific size shifts mediated by phenotypic plasticity²⁹. In another example, we show that urbanisation leads to lower average body size of aerial dipteran prey, although behavioural flexibility in web design helps web-spider communities to partly buffer its negative impact³⁵. A clear-cut impact of body size shifts on ecosystem function can be predicted for zooplankton, where smaller-sized zooplankton communities, typified by reduced densities or even absence of large *Daphnia* species that are highly efficient filter-feeders on phytoplankton, are less able to maintain top-down control on algal blooms than larger-sized communities³³, increasing risks of catastrophic regime shifts towards turbid states³⁴. Also, our observed shifts in hawkmoth body size distributions is likely through pollination functionally linked to flowering plant diversity, as body size of these stout-bodied macro-moths is positively correlated with tongue length, and body size distribution closely matches the distribution of flower depths in hawkmoth-pollinated plants³⁶. Such a tight link between plant and pollinator species is also suggested by the parallel declines in

pollinators and insect-pollinated plants observed across xxxxx³⁷.” In conclusion, the observed shifts in body size will allow to better understand and predict shifts in population resilience, trophic interactions and functioning of urban ecosystems^{38,39,40}. Such insights will be essential to design the biodiversity-friendly towns and cities of the future. For instance, urban planners could mitigate urbanisation’s micro-climatic and fragmentation effects most effectively with measures implemented at multiple spatial scales. Such interventions could for instance involve the creation and/or amending of urban ponds and urban green infrastructure in order to increase the amount and quality of habitats. Our results indicate that the resulting reduction in fragmentation and urban-heat-island effect²⁴ would reduce shifts in body size distributions of urban communities and mitigate its associated impact on ecosystem functioning.

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Author Contributions

T.M., L.D.M and H.V.D. conceived the study's focal points. C.S. and L.D.M. coordinated the consortium. T.M., A.K., L.F.B., D.B., K.B., M.C., M.D., N.D., K.D.W., J.M.T.E., D.F., F.H., J.H., K.M., E.P., R.S. and I.S. contributed to sampling and data collection. T.M. and A.K. performed the analyses. H.M. selected study plots, calculated fragmentation variables and designed the study area map. T.M. wrote the first draft of the manuscript with all authors contributing substantially to revisions.

METHODS

Sampling design

Sampling followed a nested design wherein a local urbanisation gradient (three classes: non-urban/semi-urban/urban) was repeatedly sampled within landscapes distributed along a landscape-scale urbanisation gradient (three classes: non-urban/semi-urban/urban). For each of ten taxa a total of up to 81 local-scale subplots (200x200 m) were sampled within 27 landscape-scale plots (3x3 km) situated in an 8140 km² study area in central Belgium (Fig. 1;

Extended data Table 1). The average human population density of this highly urbanised area amounts to 693 individuals/km², with cities and urban sprawl embedded within an agricultural and semi-natural matrix³⁴¹. As a proxy for urbanisation we used percentage built-up (%BU), which was assessed in a GIS using an object-oriented reference map of Flanders with the precise contours of all buildings, excluding roads and parking infrastructures, as a vectorial layer⁴². Given that only buildings are considered, 15% built-up area can be considered highly urbanised. Within each of the nine urban (%BU>15%), nine semi-urban (5%<%BU<10%) and nine non-urban (%BU<3%) plots, one urban, one semi-urban and one non-urban subplot were chosen, following identical %BU cut-off values, for a total of 81 subplots. As each taxon was sampled in only one of three habitat types (i.e. grassland, woodland or ponds) it was often impossible to sample all taxa within the same 200 x 200 m subplots. As such, independent subplots containing the corresponding habitats were sometimes selected among taxa, but these subplots were always of the same urbanisation level and located within the same 3 x 3 km plot.

This classification of urban, semi-urban and non-urban (sub)plots based on %BU cut-off values was used to establish the nested sampling design, which allowed samples to display a good spread of urbanisation values at both local (subplot) and landscape (plot) scales. To increase precision in the data analysis, however, we moved away from having %BU as a class variable with three levels, and instead quantified %BU as a continuous variable, and this at seven spatial scales, i.e. at 50, 100, 200, 400, 800, 1600, and 3200 m radii around the sampling sites. Due to our nested design, %BU-values at small scales were not correlated with values at large scales, hence allowing pinpointing the scales at which the effects of urbanisation are most pronounced.

Using this highly replicated, nested sampling design, our sampling effort involved counting and identifying 95001 individuals from 702 species from ten taxa: (i) aquatic: cladocerans and ostracods sampled in pond habitats, (ii) limno-terrestrial: aquatic bdelloid rotifers sampled within the water layers of terrestrial *Xanthoria* lichens, and (iii) terrestrial: butterflies, orthopterans (i.e. grasshoppers and bush crickets), macro-moths, ground-beetles, weevils, web-spiders and ground-spiders sampled in grassland and woodland habitats (Extended Data Table 1).

Urban-heat-island-effect

The urban-heat-island effect was quantified using hourly temperature readings that were collected automatically year-round across 63 sampling sites for the three habitat types in which the ten taxa were sampled: ponds, grasslands, and woodlands. Aquatic probes (HOBO, TidbiT v2 UTBI-001; HOBOWare ONSET; resolution: 0.02 °C) were attached to a floating device to log temperatures at 15 cm depth for 15 ponds (27th November 2014–29th November 2015). Terrestrial probes (iButton, Thermochron DS1923, Maxim Integrated; resolution: 0.06 °C) logged air temperature at 20 cm height near 24 pitfall sites (i.e. grassland habitat; 8th May 2014–20th September 2015) and 24 macro-moth sampling sites (i.e. woodland habitat; 1st April 2015–20th March 2016). For each day, temperature averages of twelve diurnal (7am–6pm) and twelve nocturnal (7pm–6am) readings were calculated, which were labelled as summer from 21st March–20th September, and as winter from 21st September–20th March.

Statistical analyses

Temperature averages were analysed in relation to site-specific urbanisation (%BU) values and habitat type (grassland/woodland/pond) using linear mixed regression models (R-package *lme4*). We ran separate models for both seasons (summer/winter) and for both day and night conditions (diurnal/nocturnal). Site ID and date (nested within year) were included as random factors. We used a multi-scale approach, running separate models with %BU-values quantified at seven spatial scales (50-3200 m radii). P-values for the fixed effects were obtained using likelihood-ratio tests of nested models that were fitted with maximum-likelihood and parameter estimates from restricted maximum-likelihood models. Residual plots were always visually inspected to evaluate the fit of models, and we compared maximum-likelihood-based AICc-values (R-package *AICcmodavg*) to select a confidence set of models whose AICc-values did not differ substantially from the value of the best-fitting model, using $\Delta AICc \leq 2$ as a criterion⁴³.

Community-weighted mean body size (CWM-BS) is calculated for a given site as the average of the species-specific body sizes (mm) of all locally sampled species, weighted by species abundance. The raw data for calculating this metric are species-specific count data for all taxa in all sites (based on taxon-specific sampling and identification protocols) and species-specific body size mean values from the literature, or – for web-spiders and cladocerans – from our own measurements (Extended Data Table 1). An increase in CWM-BS with increasing urbanisation implies that the species assemblage of the site is increasingly composed of individuals belonging to larger species as one moves from communities in more rural to communities in more urban sites. Our CWM-BS index hence reflects the relative composition of large versus small species in local communities, and we use it here to quantify community response to urbanisation. Although every sampling method introduces some bias in relative species abundances, the extent of the bias should be similar for non-urban and urban sampling sites. Therefore, using the relative species abundances that we obtained via sampling to calculate the CWM-BS is appropriate to look into relative effects of urbanisation.

CWM-BS was analysed for each taxon in relation to site-specific urbanisation (%BU) values using linear mixed regression models with restricted maximum-likelihood estimation (R-package *lme4*). Plot ID was used as a random variable to account for potential spatial autocorrelation of variables among sites belonging to the same landscape-scale plot. CWM-BS values were $\log_{10}$ -transformed for cladocerans and ostracods. For ostracods, we additionally transformed %BU-values by taking the arcsine of square-rooted %BU-values, which resulted in residual plots with a more homogeneous distribution. Analyses for the other taxa were run with untransformed data as residual plots proved to be homogeneous. The residual plots for orthopterans, ostracods and ground-beetles displayed one outlying data point, and the residual plot for weevils displayed two such points. Because we know that these five data points are legitimate –i.e. not due to measurement, data or sampling errors– we moved forward by assessing their impact on the model output consistency of the regressions.

The filtering out of the data points from the regressions showed (i) that the best-fitting models remained linked to the identical spatial scales, (ii) that the positive slope for orthopterans remained positive and the negative slopes for the other taxa remained negative, and (iii) that the significance levels stayed equal for ground-beetles and ostracods, got stronger for weevils, and decreased but remained significant for orthopterans. Because those five data points are legitimate and do not have a qualitative impact on the output, we opted to retain them in the analyses. We used a multi-scale approach, running separate models with %BU-values quantified at seven spatial scales (50-3200 m radii). For each taxon, we then selected out of the seven models the model, and hence the spatial scale, which fitted the data best using maximum-likelihood-based AICc values (R-package *AICcmodavg*). Also, we retained a confidence set of models whose AICc-values did not differ substantially from the value of the best model using $\Delta AICc \leq 2$ as a criterion⁴³.

For each taxon, and at the spatial scale of the best-fitting model, we calculated the percentage change (with 95% confidence interval) in CWM-BS over a 25%BU-gradient, based on the modelled intercept and slope, or on back-transformed values for ostracods and cladocerans (Fig. 3). These values were then contrasted for taxa with a positive size-dispersal link against all other taxa using ANOVA, with the inverse of the taxon-specific error bars as weights so as to account for the difference among taxa in variance of the estimated percentage change. This weighted ANOVA allows to test whether the percentage change values for taxa with a positive size-dispersal link are significantly different from those from all other taxa.

All analyses were performed using R version 3.2.3⁴⁴.

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Figures

Figure 1

Map of the study area.

Depiction of the configuration of 27 landscape-scale sampling plots –nine urban: magenta; nine semi-urban: yellow; nine non-urban: green– on an urbanisation background (CORINE Land Cover EEA) for North-Belgium (West-Europe; Esri). Solid lines refer to administrative province borders. Three plots are enlarged, showing their within-plot distribution of local subplot types, which allowed sampling following a nested design that covers urbanisation gradients at both the landscape and local scale. Different sets of subplots were selected among taxa, so that subplots always contained the corresponding habitats. Urbanisation was quantified as percentage built-up, assessed using a reference map with building contours (LRD), for each sample site at seven spatial scales (50-3200 m radii), which are depicted around three sample sites of one non-urban plot. Photographs depict sites in an urban and non-urban plot sites, both for terrestrial and aquatic systems.

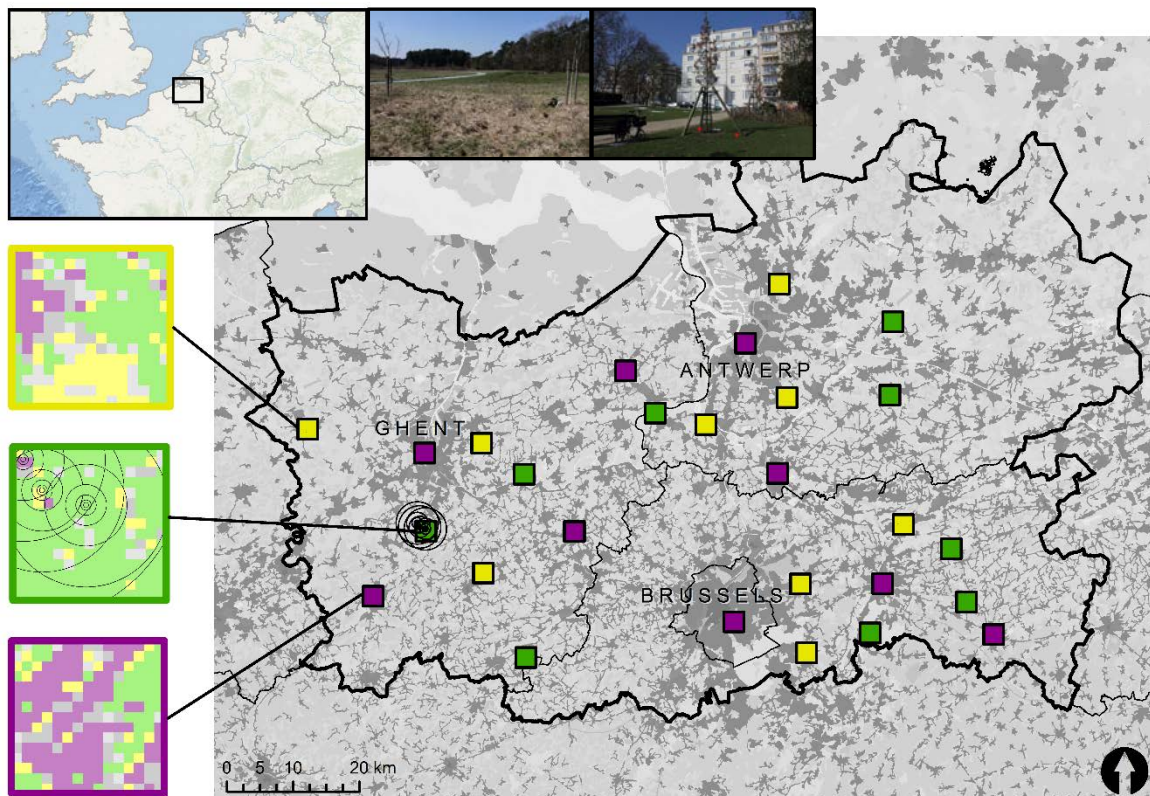


Figure 2

Micro-climatic urban-heat-island-effects.

Temperature increase (°C) when contrasting sites differing 25 units in percentage built-up. Effects are lumped for pond, grassland and woodland habitats, and displayed separately for seven spatial scales (50-3200 m radii at which urbanisation was quantified). a, summer diurnal; b, winter diurnal; c, summer nocturnal; d, winter nocturnal. Error bars depict the range of temperature change based on model-estimated slopes with 95% CI. Symbols depict significance levels ($^{\circ}$ P<0.1/*P<0.05/**P<0.01/**P<0.001).

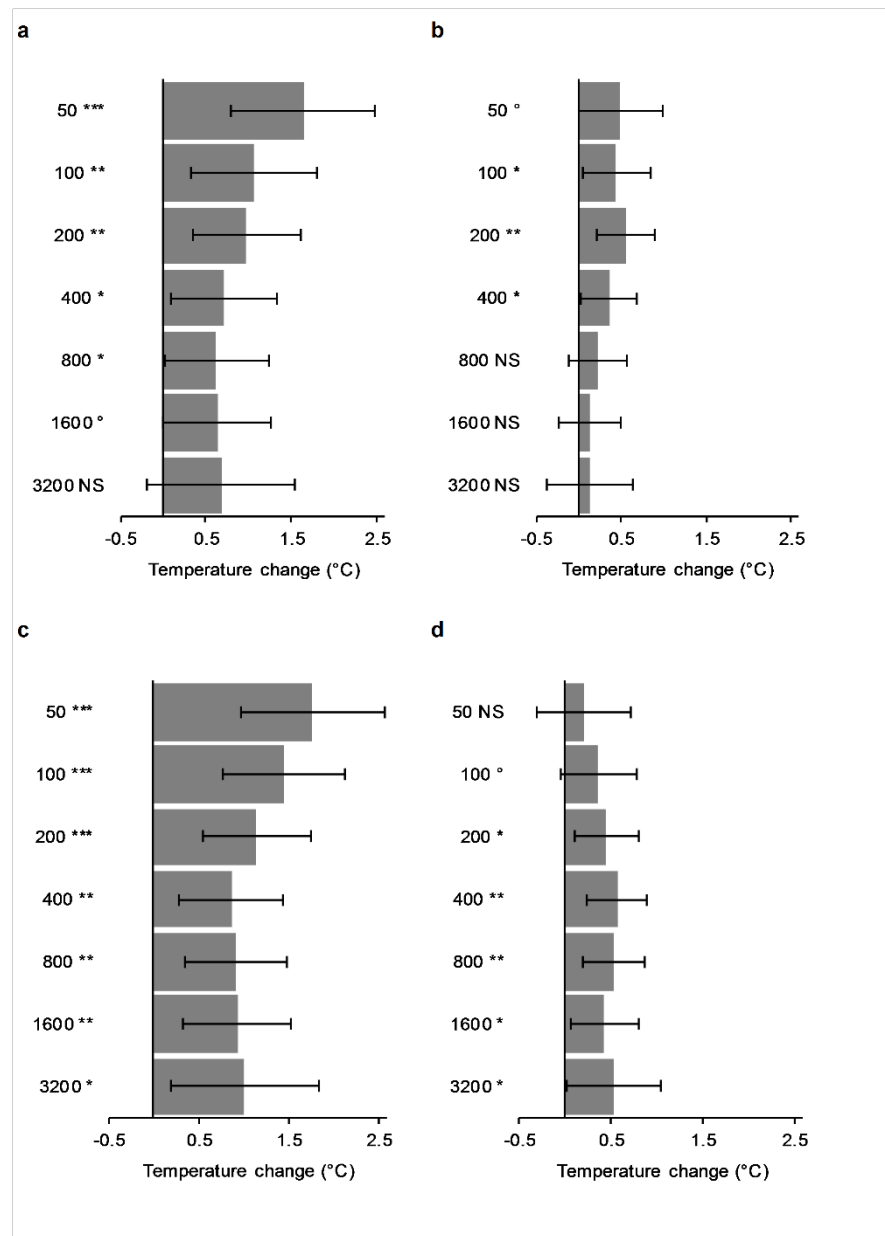


Figure 3

Taxon-specific percentage change in community-weighted mean body size for a 25 percent change in urbanisation.

Overview ordered following the modelled extent of percentage change of community-weighted mean body size (CWM-BS) contrasting sites differing 25 units in percentage built-up. Error bars depict the range in percentage change based on means at 0%BU and on 95% confidence intervals at 25%BU. Symbols depict significance levels (* $P < 0.05$ /** $P < 0.01$ /***/ $P < 0.001$). Numbers indicate the scale (m radius) of the best-fitting model, with the scales of the range of models within the confidence set of models given between brackets. Dark grey bars correspond to taxa with a positive size-dispersal link. Pictograms by Phylopic.org.

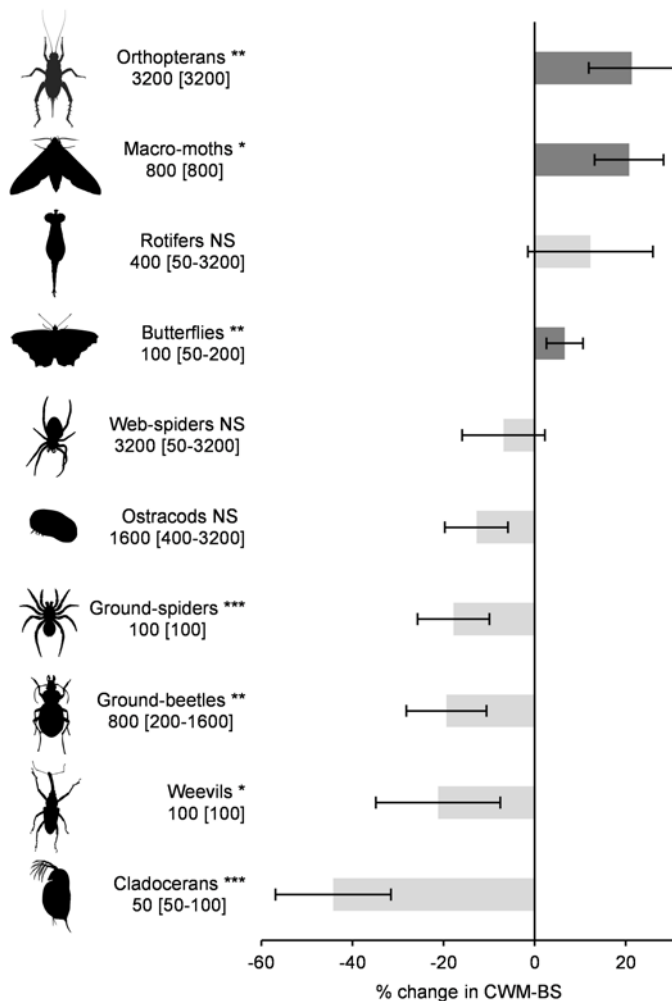
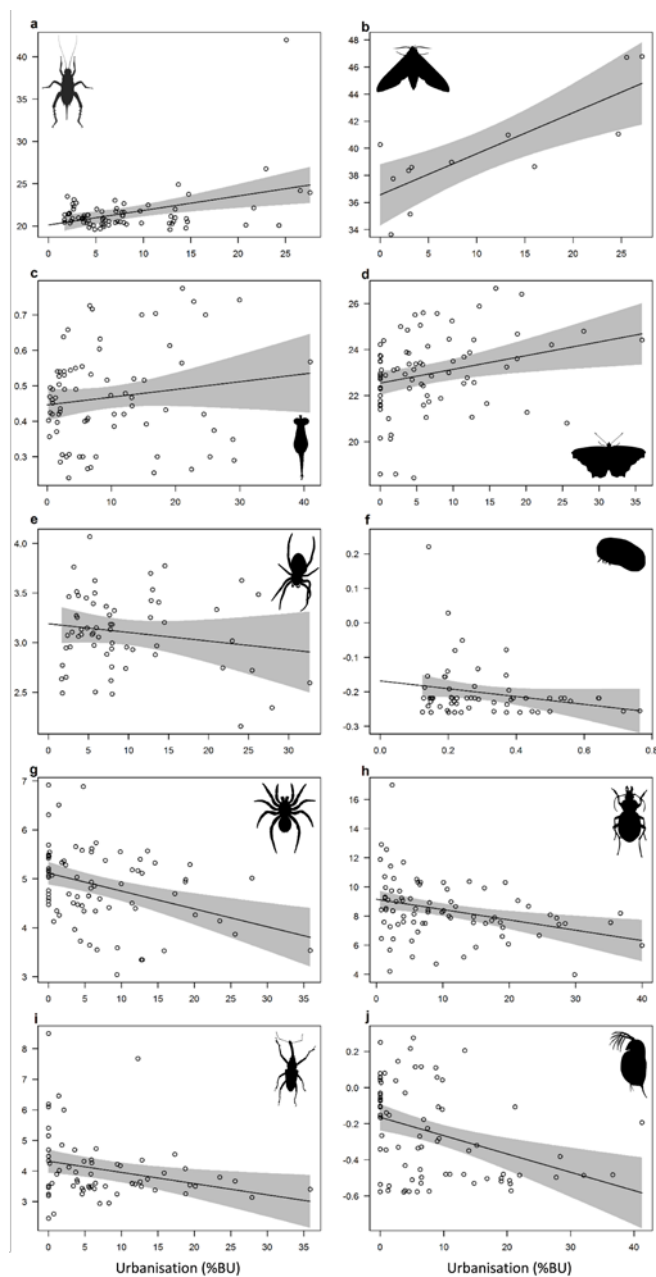


Figure 4

Taxon-specific plots of community-weighted mean body size (CWM-BS) as a function of urbanisation.

Modelled CWM-BS (mm) values of all taxa are depicted against percentage built-up (%BU) at the spatial scale (m radius) providing the best-fitting model. a, orthopterans (3200); b, macro-moths (800); c, rotifers (400); d, butterflies (100); e, web-spiders (3200); f, ostracods (1600); g, ground-spiders (100); h, ground-beetles (800); i, weevils (100); j, cladocerans (50). CWM-BS values are log-transformed for ostracods and cladocerans (depicted range: 0.55–1.66 and 0.26–1.89 mm, respectively), while for the former also the %BU-values are transformed (depicted range: 1.5–47.8%BU). Modelled linear regression slopes with 95% CI are provided. Plots are ordered in line with Fig. 3.



Extended Data Table 1

Taxon-specific details of sampling procedures, body size data and size-dispersal links.

Number of sampled sites (Sites), counted individuals (N) and cumulative species richness (S) are provided.

Taxon	Sampling method	Sites	N	S	Body size (proxy) (mm)	Body size data	Size-dispersal link
Butterflies	Visual counts while walking 20 minutes ("Pollard walk") / subplot, with occasional netting and visual inspections; each site sampled three times during July till early September 2014; up to 18 sites/day	81	4413	23	Forewing length	Means from Bink (1992), with means for sexually and seasonally dimorphic species	Positive: Sekar (2012); Stevens <i>et al.</i> (2012; 2014)
Macro-moths	Full-night light-trapping (Heath, 6W) at woody sites; each site sampled 11 times during August till early September 2014 and during April, July and August 2015; four sites simultaneously/night; identification of within-trap samples during early mornings down to species-level, except for <i>Hoplodrina</i> and <i>Mesapamea</i> sp.	12	3067	202	Wing span	Means from Manley (2010) and on www.lepidoptera.eu for non-UK species. Means of both sexes for sexually dimorphic species; except male values only for three species with flightless females	Positive: Nieminen <i>et al.</i> (1999); Slade <i>et al.</i> (2013); Stevens <i>et al.</i> (2014)
Orthopterans	Auditive counts of male grasshoppers and bush crickets while walking 20 minutes/subplot, with occasional visual inspections; each site sampled three times during July till early September 2014; up to 18 sites/day	81	10302	8	Body length	Means (without wings nor appendages) taken from Reinhardt <i>et al.</i> (2005)	Positive: Reinhardt <i>et al.</i> (2005) (our subset)
Web-spiders	Visual and complete exploration of subplots to collect and store every individual in 70% ethanol until identification via a microscope of all adult specimens; three sites sampled/day during September 2014	62	2456	18	Cephalo-thorax width	Means of all captured adult spiders; microscope measured	Neutral (bell-shaped): Stevens <i>et al.</i> (2014)
Ground-spiders	Pitfall trapping, simultaneously at all sites with two pitfalls/site placed in grassy, open habitats from April till August 2013. Identification via microscope of all adult specimens, stored in 70% ethanol	81	27763	184	Body length	Values of females from Roberts (2009) and on www.araneae.unibe.ch	Neutral (bell-shaped): Stevens <i>et al.</i> (2014)
Ground-beetles	Identical to ground-spider sampling	81	7604	128	Body length	Means from Turin (2000)	Neutral: Stevens <i>et al.</i> (2014)
Weevils	Identical to ground-spider sampling	78	2600	73	Body length	Means of minimum and maximum values from Duff <i>et al.</i> (2016)	Neutral
Rotifers	Community sampling of bdelloid rotifers recovered from dormancy four hours after hydration of <i>Xanthoria</i> lichen thalli of 2.5 cm ² in a petri dish, a period known to recover all dormant individuals; each site sampled once during July 2013; up to 18 sites/day	81	4936	21	Body length	Maximum recorded lengths in literature; mostly from original species descriptions and Donner (1965)	Neutral: Fontaneto (2011)
Ostracods	Handnet sampling of up to 9 sites/day from mid-August till mid-September 2014. Individual ostracods were sorted from the bulk sample under a microscope to a minimum of 50 individuals, in cases where ostracods were present. Rarefaction analyses showed that the samples were representative for the ostracod communities.	81	3111	17	Body length	Values of females taken from Meisch (2000)	Negative / Neutral: Bilton <i>et al.</i> (2001); De Bie <i>et al.</i> (2012)
Cladocerans	Zooplankton sampling with tube sampler, collecting 5L water at each of eight locations/pond, integrating the entire water column from close to bottom till surface; crustacean zooplankton for density assessment is filtered through a 64 µm conical net; samples are collected in 60 ml vials and fixed with formalin (2 ml in 48 ml of sample); min. 300 individuals were identified per sample (<i>Daphnia longispina</i> , <i>D. galeata</i> and <i>D. hyalina</i> were combined in the <i>D. longispina</i> complex); individual counts were volume-corrected for each sample; 15 random individuals per species occurring in each sample were measured (if less individuals present per species, all were measured). Sampling was conducted from 29 May till 10 July 2013. Three ponds (one plot) were sampled/day, with plot sampling randomized over the sampling period. Detailed information in Brans <i>et al.</i> (2017) and Gianuca <i>et al.</i> (2017)	81	28749	28	Body length	Means (eye top till tail spine base) of up to 15 individuals per species per sample, with <i>Ceriodaphnia</i> values combined into one category. Means from all ponds were then further averaged	Negative / Neutral: Bilton <i>et al.</i> (2001); De Bie <i>et al.</i> (2012)

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Extended Data Table 2

Model output of average temperature in relation to urbanisation and habitat type.

Output of linear mixed models testing the relationship between ambient local average temperatures and the interaction between percentage built-up (%BU) and habitat type (pond/grassland/woodland). Only the output for the confidence set of models ($\Delta\text{AICc} \leq 2$) is given, with scale referring to the associated m radius scale of %BU. P-value symbols indicate significance levels ($^{\circ}P < 0.1$ /** $P < 0.01$ /**P < 0.001). Model estimates ($\pm$ SE) for %BU regression coefficients are provided. Model output consistently shows clear temperature differences among habitats and a clear positive effect of urbanisation on temperature, irrespective of habitat type (*cfr.* non-significant interactions).

Diurnal summer

Scale	ΔAICc	Fixed effect	Chi-square test	P-value	Estimate $\pm$ SE
50	0.00	%BU x Habitat %BU Habitat	$\chi^2_2 = 4.05$ $\chi^2_1 = 13.96$ $\chi^2_2 = 39.67$	P = 0.13 (NS) P = 0.0001 (**) P < 0.0001 (***)	0.0655 $\pm$ 0.0172

Nocturnal summer

Scale	ΔAICc	Fixed effect	Chi-square test	P-value	Estimate $\pm$ SE
50	0.00	%BU x Habitat %BU Habitat	$\chi^2_2 = 2.73$ $\chi^2_1 = 17.66$ $\chi^2_2 = 82.37$	P = 0.25 (NS) P < 0.0001 (***) P < 0.0001 (***)	0.0706 $\pm$ 0.0163
100	0.91	%BU x Habitat %BU Habitat	$\chi^2_2 = 0.14$ $\chi^2_1 = 16.76$ $\chi^2_2 = 83.19$	P = 0.93 (NS) P < 0.0001 (***) P < 0.0001 (***)	0.0579 $\pm$ 0.0138

Diurnal winter

Scale	ΔAICc	Fixed effect	Chi-square test	P-value	Estimate $\pm$ SE
200	0.00	%BU x Habitat %BU Habitat	$\chi^2_2 = 0.21$ $\chi^2_1 = 10.15$ $\chi^2_2 = 5.45$	P = 0.89 (NS) P = 0.001 (**) P = 0.06 ($^{\circ}$)	0.0221 $\pm$ 0.0069

Nocturnal winter

Scale	ΔAICc	Fixed effect	Chi-square test	P-value	Estimate $\pm$ SE
400	0.00	%BU x Habitat %BU Habitat	$\chi^2_2 = 0.21$ $\chi^2_1 = 10.94$ $\chi^2_2 = 76.57$	P = 0.89 (NS) P = 0.0009 (***) P < 0.0001 (***)	0.0227 $\pm$ 0.0068
800	1.33	%BU x Habitat %BU Habitat	$\chi^2_2 = 0.39$ $\chi^2_1 = 9.61$ $\chi^2_2 = 77.55$	P = 0.82 (NS) P = 0.0019 (**) P < 0.0001 (***)	0.0213 $\pm$ 0.0068

Extended Data Table 3

Model output of community-weighted mean body size (CWM-BS) in relation to urbanisation.

Output of linear mixed models testing the relationship between CWM-BS and percentage built-up (%BU) at multiple scales. Confidence sets of models ($\Delta AIC_c \leq 2$) have grey shading. The best-fitting model output is given in bold. P-value symbols indicate significance levels ($^{\circ}P < 0.1$ / $^*P < 0.05$ / $^{**}P < 0.01$ / $^{***}P < 0.001$). Modelled intercepts and slopes ($\pm$ SE) are given.

Taxon	Scale	ΔAIC_c	F-test	P-value	Intercept	Slope
	50	9.24	$F_{1,61.0} = 0.14$	$P = 0.71$ (NS)	21.458 ± 0.436	0.015 ± 0.040
	100	8.91	$F_{1,53.8} = 0.48$	$P = 0.49$ (NS)	21.370 ± 0.457	0.024 ± 0.035
	200	6.83	$F_{1,59.9} = 2.49$	$P = 0.12$ (NS)	21.104 ± 0.476	0.052 ± 0.033
	400	8.29	$F_{1,73.9} = 1.01$	$P = 0.32$ (NS)	21.203 ± 0.502	0.035 ± 0.034
	800	7.85	$F_{1,55.0} = 1.43$	$P = 0.24$ (NS)	21.084 ± 0.527	0.047 ± 0.038
	1600	5.67	$F_{1,34.1} = 3.64$	$P = 0.065$ ($^{\circ}$)	20.752 ± 0.548	0.081 ± 0.042
	3200	0.00	$F_{1,26.7} = 10.46$	$P = 0.0032$ (**)	20.122 ± 0.549	0.171 ± 0.053
	50	10.14	$F_{1,8.6} = 1.72$	$P = 0.22$ (NS)	38.883 ± 1.293	0.227 ± 0.148
	100	7.70	$F_{1,7.0} = 4.26$	$P = 0.078$ ($^{\circ}$)	37.949 ± 1.336	0.282 ± 0.123
	200	3.98	$F_{1,9.1} = 7.64$	$P = 0.022$ (*)	36.721 ± 1.245	0.335 ± 0.103
	400	3.04	$F_{1,7.4} = 8.96$	$P = 0.019$ (*)	36.886 ± 1.140	0.306 ± 0.087
	800	0.00	$F_{1,4.6} = 16.84$	$P = 0.011$ (*)	36.566 ± 1.016	0.303 ± 0.070
	1600	2.78	$F_{1,4.1} = 12.41$	$P = 0.023$ (*)	36.889 ± 1.122	0.273 ± 0.076
	3200	4.57	$F_{1,4.0} = 9.57$	$P = 0.036$ (*)	36.996 ± 1.227	0.319 ± 0.103
	50	1.08	$F_{1,70.9} = 0.55$	$P = 0.46$ (NS)	0.456 ± 0.021	0.002 ± 0.002
	100	1.24	$F_{1,67.5} = 0.41$	$P = 0.52$ (NS)	0.457 ± 0.022	0.001 ± 0.002
	200	0.23	$F_{1,72.1} = 1.35$	$P = 0.25$ (NS)	0.447 ± 0.023	0.002 ± 0.002
	400	0.00	$F_{1,53.9} = 1.55$	$P = 0.22$ (NS)	0.446 ± 0.022	0.002 ± 0.002
	800	0.69	$F_{1,37.2} = 0.92$	$P = 0.34$ (NS)	0.450 ± 0.023	0.002 ± 0.002
	1600	0.36	$F_{1,27.5} = 1.26$	$P = 0.27$ (NS)	0.447 ± 0.024	0.002 ± 0.002
	3200	0.81	$F_{1,23.2} = 0.84$	$P = 0.37$ (NS)	0.449 ± 0.025	0.002 ± 0.002
	50	0.41	$F_{1,71.2} = 7.25$	$P = 0.0088$ (**)	22.637 ± 0.230	0.068 ± 0.025
	100	0.00	$F_{1,59.6} = 7.53$	$P = 0.0080$ (**)	22.546 ± 0.257	0.060 ± 0.022
	200	1.49	$F_{1,66.2} = 6.27$	$P = 0.015$ (*)	22.511 ± 0.285	0.050 ± 0.020
	400	6.50	$F_{1,77.5} = 1.10$	$P = 0.30$ (NS)	22.720 ± 0.308	0.022 ± 0.020
	800	7.45	$F_{1,53.8} = 0.05$	$P = 0.82$ (NS)	22.885 ± 0.318	0.005 ± 0.022
	1600	7.17	$F_{1,33.4} = 0.27$	$P = 0.61$ (NS)	23.063 ± 0.332	-0.013 ± 0.024
	3200	7.39	$F_{1,27.7} = 0.07$	$P = 0.80$ (NS)	23.007 ± 0.360	-0.008 ± 0.032
	50	0.14	$F_{1,46.5} = 0.96$	$P = 0.33$ (NS)	3.133 ± 0.067	-0.003 ± 0.003
	100	0.83	$F_{1,42.7} = 0.32$	$P = 0.58$ (NS)	3.128 ± 0.073	-0.002 ± 0.004
	200	0.83	$F_{1,47.2} = 0.31$	$P = 0.58$ (NS)	3.131 ± 0.076	-0.003 ± 0.005
	400	0.76	$F_{1,59.6} = 0.35$	$P = 0.56$ (NS)	3.138 ± 0.081	-0.003 ± 0.005
	800	0.93	$F_{1,48.7} = 0.19$	$P = 0.66$ (NS)	3.134 ± 0.087	-0.002 ± 0.005
	1600	1.08	$F_{1,28.7} = 0.05$	$P = 0.82$ (NS)	3.124 ± 0.093	-0.002 ± 0.006
	3200	0.00	$F_{1,22.3} = 1.06$	$P = 0.31$ (NS)	3.190 ± 0.101	-0.009 ± 0.008
	50	3.03	$F_{1,57.0} = 0.00$	$P = 0.97$ (NS)	-0.202 ± 0.016	-0.002 ± 0.062
	100	2.72	$F_{1,57.2} = 0.27$	$P = 0.60$ (NS)	-0.194 ± 0.019	-0.031 ± 0.058
	200	2.09	$F_{1,58.0} = 0.88$	$P = 0.35$ (NS)	-0.186 ± 0.020	-0.053 ± 0.055
	400	1.19	$F_{1,51.4} = 1.71$	$P = 0.20$ (NS)	-0.179 ± 0.020	-0.075 ± 0.055
	800	0.89	$F_{1,43.5} = 1.98$	$P = 0.17$ (NS)	-0.176 ± 0.021	-0.084 ± 0.058
	1600	0.00	$F_{1,32.2} = 2.83$	$P = 0.10$ (NS)	-0.168 ± 0.022	-0.113 ± 0.066
	3200	0.22	$F_{1,26.8} = 2.67$	$P = 0.11$ (NS)	-0.160 ± 0.027	-0.148 ± 0.089
	50	7.95	$F_{1,69.6} = 5.07$	$P = 0.028$ (*)	4.993 ± 0.113	-0.027 ± 0.012
	100	0.00	$F_{1,60.0} = 13.82$	$P = 0.0004$ (***)	5.116 ± 0.116	-0.036 ± 0.010
	200	2.81	$F_{1,71.6} = 9.83$	$P = 0.0025$ (**)	5.127 ± 0.122	-0.029 ± 0.009
	400	5.30	$F_{1,72.5} = 6.92$	$P = 0.010$ (*)	5.113 ± 0.127	-0.024 ± 0.009
	800	5.40	$F_{1,46.3} = 6.86$	$P = 0.012$ (*)	5.123 ± 0.130	-0.025 ± 0.009
	1600	6.80	$F_{1,31.2} = 5.57$	$P = 0.025$ (*)	5.110 ± 0.134	-0.023 ± 0.010
	3200	7.23	$F_{1,26.9} = 5.34$	$P = 0.029$ (*)	5.124 ± 0.139	-0.029 ± 0.013
	50	7.17	$F_{1,75.2} = 2.02$	$P = 0.16$ (NS)	8.646 ± 0.276	-0.047 ± 0.032
	100	3.66	$F_{1,64.4} = 5.57$	$P = 0.021$ (*)	8.894 ± 0.294	-0.069 ± 0.029
	200	1.79	$F_{1,76.5} = 7.39$	$P = 0.0081$ (**)	9.045 ± 0.310	-0.071 ± 0.025
	400	1.58	$F_{1,65.8} = 7.44$	$P = 0.0082$ (**)	9.080 ± 0.319	-0.066 ± 0.023
	800	0.00	$F_{1,41.4} = 9.19$	$P = 0.0042$ (**)	9.152 ± 0.318	-0.071 ± 0.023
	1600	1.39	$F_{1,29.7} = 7.94$	$P = 0.0085$ (**)	9.124 ± 0.326	-0.068 ± 0.024
	3200	5.51	$F_{1,26.7} = 3.70$	$P = 0.065$ ($^{\circ}$)	8.976 ± 0.360	-0.063 ± 0.033
	50	4.20	$F_{1,55.7} = 2.02$	$P = 0.16$ (NS)	4.170 ± 0.178	-0.024 ± 0.017
	100	0.00	$F_{1,48.1} = 6.59$	$P = 0.013$ (*)	4.323 ± 0.190	-0.037 ± 0.014
	200	2.21	$F_{1,56.5} = 3.92$	$P = 0.053$ ($^{\circ}$)	4.309 ± 0.200	-0.028 ± 0.014
	400	2.37	$F_{1,66.0} = 3.71$	$P = 0.059$ ($^{\circ}$)	4.330 ± 0.210	-0.027 ± 0.013
	800	3.65	$F_{1,50.8} = 2.51$	$P = 0.12$ (NS)	4.308 ± 0.223	-0.024 ± 0.014
	1600	5.20	$F_{1,32.2} = 0.99$	$P = 0.33$ (NS)	4.230 ± 0.236	-0.017 ± 0.016
	3200	5.68	$F_{1,26.5} = 0.51$	$P = 0.48$ (NS)	4.193 ± 0.251	-0.016 ± 0.022
	50	0.00	$F_{1,70.7} = 12.37$	$P = 0.0008$ (***)	-0.164 ± 0.037	-0.010 ± 0.003
	100	0.32	$F_{1,76.9} = 12.72$	$P = 0.0006$ (***)	-0.141 ± 0.042	-0.009 ± 0.003
	200	4.48	$F_{1,73.6} = 8.74$	$P = 0.0042$ (**)	-0.156 ± 0.044	-0.007 ± 0.002
	400	5.35	$F_{1,63.8} = 7.82$	$P = 0.0068$ (**)	-0.160 ± 0.044	-0.007 ± 0.002
	800	8.69	$F_{1,45.1} = 3.67$	$P = 0.062$ ($^{\circ}$)	-0.186 ± 0.044	-0.005 ± 0.003
	1600	10.37	$F_{1,31.1} = 1.68$	$P = 0.20$ (NS)	-0.204 ± 0.044	-0.004 ± 0.003
	3200	10.73	$F_{1,26.6} = 1.19$	$P = 0.29$ (NS)	-0.204 ± 0.048	-0.005 ± 0.004

Extended Data Table 4

Model output of abundance and diversity measures in relation to urbanisation.

Output of linear mixed models testing the relationship between abundance (N) and two diversity measures (species richness (S), Shannon index (H)) and percentage built-up (%BU) at the spatial scale providing the best-fitting models, with t-symbols indicating that log(x+1)-transformations improved residual fits. P-value symbols indicate significance levels ($^{\circ}P < 0.1$ / $^*P < 0.05$ / $^{**}P < 0.01$ / $^{***}P < 0.001$). Modelled (back-transformed) percentage change across a 0%BU to 25%BU gradient is given.

	Taxon	N/S/H	Scale	F-test	P-value	% change 0-25%BU
	Orthopterans	tN	200	$F_{1,66.2} = 20.58$	$P < 0.0001$ (***)	-82.9
		S	400	$F_{1,78.5} = 16.24$	$P = 0.0001$ (***)	-34.5
		H	400	$F_{1,63.0} = 0.68$	$P = 0.41$ (NS)	-8.4
	Macro-moths	tN	3200	$F_{1,4.0} = 52.6$	$P = 0.0019$ (**)	-89.2
		tS	3200	$F_{1,4.0} = 108.1$	$P = 0.0005$ (***)	-82.7
		H	800	$F_{1,5.2} = 55.8$	$P = 0.0006$ (***)	-43.5
	Rotifers	tN	400	$F_{1,67.1} = 2.1$	$P = 0.15$ (NS)	+108.1
		tS	400	$F_{1,67.9} = 0.4$	$P = 0.53$ (NS)	+15.6
		H	3200	$F_{1,37.9} = 1.2$	$P = 0.28$ (NS)	+38.8
	Butterflies	tN	200	$F_{1,71.4} = 42.1$	$P < 0.0001$ (***)	-85.3
		S	200	$F_{1,69.7} = 54.2$	$P < 0.0001$ (***)	-59.1
		H	200	$F_{1,75.8} = 7.3$	$P = 0.0085$ (**)	-22.5
	Web-spiders	tN	200	$F_{1,54.1} = 7.9$	$P = 0.0069$ (**)	-18.3
		tS	200	$F_{1,53.8} = 15.1$	$P = 0.0003$ (***)	-29.2
		tH	200	$F_{1,54.0} = 12.3$	$P = 0.0009$ (***)	-21.1
	Ostracods	tN	50	$F_{1,71.1} = 3.6$	$P = 0.06$ ($^{\circ}$)	-69.2
		tS	50	$F_{1,71.3} = 2.1$	$P = 0.15$ (NS)	-38.6
		H	1600	$F_{1,35.1} = 2.2$	$P = 0.15$ (NS)	-41.2
	Ground-spiders	N	100	$F_{1,65.1} = 5.7$	$P = 0.020$ (*)	-43.6
		S	800	$F_{1,43.3} = 2.3$	$P = 0.14$ (NS)	-13.4
		H	3200	$F_{1,26.6} = 12.3$	$P = 0.0016$ (**)	-20.3
	Ground-beetles	tN	800	$F_{1,47.2} = 5.8$	$P = 0.020$ (*)	-50.7
		tS	800	$F_{1,44.3} = 11.9$	$P = 0.0013$ (**)	-39.9
		tH	200	$F_{1,76.9} = 11.5$	$P = 0.0011$ (**)	-21.9
	Weevils	tN	100	$F_{1,56.9} = 12.0$	$P = 0.0010$ (**)	+547.9
		tS	100	$F_{1,56.8} = 4.5$	$P = 0.038$ (*)	+99.2
		tH	400	$F_{1,63.9} = 0.7$	$P = 0.40$ (NS)	+25.0
	Cladocerans	tN	3200	$F_{1,27.2} = 1.2$	$P = 0.29$ (NS)	-68.5
		S	200	$F_{1,62.8} = 1.1$	$P = 0.29$ (NS)	+12.7
		H	3200	$F_{1,26.2} = 0.2$	$P = 0.65$ (NS)	-11.4

Extended Data Table 5

Taxon-specific overview of species present at non-urban sites (<5%BU) that are absent at urban sites, separately for (left columns) sensitive species absent at sites >10%BU (i.e. urbanised sites) and (right columns) less-sensitive species that only disappeared at sites >20%BU (i.e. highly urbanised sites). Species-specific functional profiles are provided, using the following abbreviations: H (herbivory), Po (pollination), Pr (prey), Pc (predation/pest control), D (detritivory), A (algal grazer), Pf (pollen-feeding), Ff (filter-feeding).

Taxon	Absent at 10%BU	Functional profile	Absent at 20%BU	Functional profile
Orthopterans	<i>Conocephalus dorsalis</i>	H grasses in wet biotopes; Pr		
	<i>Metrioptera roeselii</i>	H grasses; Pr		
Macro-moths	<i>Abrostola triplasia</i>	H grasses/herbs; Po; Pr	<i>Agrotis clavis</i>	H grasses/herbs; Po; Pr
	<i>Achlya flavicornis</i>	H shrubs/trees; Po; Pr	<i>Agrotis exclamationis</i>	H grasses/herbs; Po; Pr
	<i>Acronicta leporina</i>	H shrubs/trees; Po; Pr	<i>Aplocera efformata</i>	H grasses/herbs; Pr
	<i>Acronicta megacephala</i>	H shrubs/trees; Po; Pr	<i>Bryophila domestica</i>	H shrubs/trees; Po; Pr
	<i>Acronicta psi</i>	H shrubs/trees; Po; Pr	<i>Clostera curtula</i>	H shrubs/trees; Pr
	<i>Acronicta rumicis</i>	H grasses/herbs; Po; Pr	<i>Colostygia pectinataria</i>	H grasses/herbs; Pr
	<i>Aglia tau</i>	H shrubs/trees; Pr	<i>Conistra vaccinii</i>	H shrubs/trees; Po; Pr
	<i>Agriopsis marginaria</i>	H shrubs/trees; Po; Pr	<i>Craniophora ligustri</i>	H shrubs/trees; Po; Pr
	<i>Agrotis ipsilon</i>	H grasses/herbs; Po; Pr	<i>Cyclophora punctaria</i>	H shrubs/trees; Po; Pr
	<i>Alcis repandata</i>	H shrubs/trees; Po; Pr	<i>Deltote pygarga</i>	H grasses/herbs; Po; Pr
	<i>Alsophila aescularia</i>	H shrubs/trees; Pr	<i>Diarsia rubi</i>	H grasses/herbs; Po; Pr
	<i>Angerona prunaria</i>	H shrubs/trees; Pr	<i>Eilema griseola</i>	H lichens; Po; Pr
	<i>Anorthoa munda</i>	H shrubs/trees; Po; Pr	<i>Epirrhoe alternata</i>	H grasses/herbs; Po; Pr
	<i>Anticollix sparsata</i>	H grasses/herbs; Pr	<i>Eupithecia valerianata</i>	H grasses/herbs; Pr
	<i>Arctia caja</i>	H grasses/herbs; Pr	<i>Euthrix potatoria</i>	H grasses/herbs; Pr
	<i>Arenostola phragmitidis</i>	H grasses/herbs; Pr	<i>Hemithea aestivaria</i>	H shrubs/trees; Po; Pr
	<i>Axylla putris</i>	H grasses/herbs; Po; Pr	<i>Herminia tarsicrinalis</i>	H shrubs/trees; Po; Pr
	<i>Biston betularia</i>	H shrubs/trees; Pr	<i>Hoplodrina ambigua</i>	H grasses/herbs; Po; Pr
	<i>Biston strataria</i>	H shrubs/trees; Pr	<i>Hydraecia micacea</i>	H grasses/herbs; Po; Pr
	<i>Cabera pusaria</i>	H shrubs/trees; Pr	<i>Hydriomena furcata</i>	H shrubs/trees; Pr
	<i>Callimorpha dominula</i>	H grasses/herbs; Po; Pr	<i>Hypena proboscidalis</i>	H grasses/herbs; Po; Pr
	<i>Caradrina morpheus</i>	H grasses/herbs; Po; Pr	<i>Idaea dimidiata</i>	H grasses/herbs; Po; Pr
	<i>Catocala nupta</i>	H shrubs/trees; Po; Pr	<i>Idaea fuscovenosa</i>	H grasses/herbs; Pr
	<i>Catocala sponsa</i>	H shrubs/trees; Po; Pr	<i>Lacanobia suasa</i>	H grasses/herbs; Po; Pr
	<i>Chloroclysta truncata</i>	H shrubs/trees; Po; Pr	<i>Laothoe populi</i>	H shrubs/trees; Pr
	<i>Cilix glaucata</i>	H shrubs/trees; Pr	<i>Lasiocampa quercus</i>	H shrubs/trees; Pr
	<i>Cryphia algae</i>	H lichens; Po; Pr	<i>Ligdia adustata</i>	H shrubs/trees; Pr
	<i>Cyclophora albipunctata</i>	H shrubs/trees; Po; Pr	<i>Lomaspilis marginata</i>	H shrubs/trees; Pr
	<i>Cyclophora linearia</i>	H shrubs/trees; Pr	<i>Lycia hirtaria</i>	H shrubs/trees; Pr
	<i>Cyclophora porata</i>	H shrubs/trees; Po; Pr	<i>Mamestra brassicae</i>	H grasses/herbs; Po; Pr
	<i>Deilephila elpenor</i>	H grasses/herbs; Po; Pr	<i>Mesoligia furuncula</i>	H grasses/herbs; Po; Pr
	<i>Diachrysia chrysis</i>	H grasses/herbs; Po; Pr	<i>Mythimna albipuncta</i>	H grasses/herbs; Po; Pr
	<i>Diaphora mendica</i>	H grasses/herbs; Pr	<i>Ochropleura plecta</i>	H grasses/herbs; Po; Pr
	<i>Diarsia mendica</i>	H shrubs/trees; Po; Pr	<i>Oligia strigilis</i>	H grasses/herbs; Po; Pr
	<i>Drepana curvatula</i>	H shrubs/trees; Pr	<i>Opisthograptis luteolata</i>	H shrubs/trees; Pr

<i>Drepana falcataria</i>	H shrubs/trees; Pr	<i>Orthosia incerta</i>	H shrubs/trees; Po; Pr
<i>Drymonia obliterata</i>	H shrubs/trees; Pr	<i>Phragmatobia fuliginosa</i>	H shrubs/trees; Pr
<i>Drymonia querna</i>	H shrubs/trees; Pr	<i>Selenia dentaria</i>	H shrubs/trees; Pr
<i>Drymonia ruficornis</i>	H shrubs/trees; Pr	<i>Thalpophila matura</i>	H grasses/herbs; Po; Pr
<i>Ecliptopera silaceata</i>	H grasses/herbs; Po; Pr	<i>Xanthorhoe fluctuata</i>	H grasses/herbs; Pr
<i>Eilema complana</i>	H lichens; Po; Pr	<i>Xylocampa areola</i>	H shrubs/trees; Po; Pr
<i>Eilema depressa</i>	H lichens; Pr	<i>Zanclognatha tarsipennalis</i>	H shrubs/trees; Po; Pr
<i>Ennomos autumnaria</i>	H shrubs/trees; Pr		
<i>Ennomos quercinaria</i>	H shrubs/trees; Pr		
<i>Epione repandaria</i>	H shrubs/trees; Pr		
<i>Epirrhoe rivata</i>	H grasses/herbs; Pr		
<i>Euchoeca nebulata</i>	H shrubs/trees; Pr		
<i>Eulithis prunata</i>	H shrubs/trees; Pr		
<i>Euphyia unangulata</i>	H grasses/herbs; Pr		
<i>Eupithecia abbreviata</i>	H shrubs/trees; Po; Pr		
<i>Eupithecia absinthiata</i>	H grasses/herbs; Pr		
<i>Eupithecia subfuscata</i>	H shrubs/trees; Pr		
<i>Eupithecia tripunctaria</i>	H grasses/herbs; Pr		
<i>Eupithecia virgaureata</i>	H grasses/herbs; Po; Pr		
<i>Euplexia lucipara</i>	H shrubs/trees; Po; Pr		
<i>Euproctis similis</i>	H shrubs/trees; Pr		
<i>Eupsilia transversa</i>	H shrubs/trees; Po; Pr		
<i>Geometra papilionaria</i>	H shrubs/trees; Pr		
<i>Herminia grisealis</i>	H shrubs/trees; Po; Pr		
<i>Heterogenea asella</i>	H shrubs/trees; Pr		
<i>Horisme tersata</i>	H shrubs/trees; Pr		
<i>Hylaea fasciaria</i>	H shrubs/trees; Pr		
<i>Hypomecis punctinalis</i>	H shrubs/trees; Pr		
<i>Hypomecis roboraria</i>	H shrubs/trees; Po; Pr		
<i>Idaea aversata</i>	H grasses/herbs; Po; Pr		
<i>Idaea subsericeata</i>	H grasses/herbs; Pr		
<i>Jodis lactearia</i>	H shrubs/trees; Pr		
<i>Lomographa temerata</i>	H shrubs/trees; Pr		
<i>Lymantria dispar</i>	H shrubs/trees; Pr		
<i>Lymantria monacha</i>	H shrubs/trees; Pr		
<i>Macaria alternata</i>	H shrubs/trees; Pr		
<i>Macaria liturata</i>	H shrubs/trees; Pr		
<i>Macaria notata</i>	H shrubs/trees; Pr		
<i>Meganola albula</i>	H shrubs/trees; Pr		
<i>Melanchra persicaria</i>	H shrubs/trees; Po; Pr		
<i>Mitochondria miniata</i>	H lichens; Po; Pr		
<i>Mythimna impura</i>	H grasses/herbs; Po; Pr		
<i>Mythimna pallens</i>	H grasses/herbs; Po; Pr		
<i>Noctua fimbriata</i>	H shrubs/trees; Po; Pr		
<i>Nonagria typhae</i>	H grasses/herbs; Pr		
<i>Notodonta dromedarius</i>	H shrubs/trees; Pr		

	<i>Ochropacha duplaris</i>	H shrubs/trees; Po; Pr		
	<i>Orgyia antiqua</i>	H shrubs/trees; Pr		
	<i>Orthosia cruda</i>	H shrubs/trees; Po; Pr		
	<i>Pelosia muscerda</i>	H lichens; Po; Pr		
	<i>Peridea anceps</i>	H shrubs/trees; Pr		
	<i>Perizoma alchemillata</i>	H grasses/herbs; Pr		
	<i>Phalera bucephala</i>	H shrubs/trees; Pr		
	<i>Pheosia gnoma</i>	H shrubs/trees; Pr		
	<i>Pheosia tremula</i>	H shrubs/trees; Pr		
	<i>Plagodis pulveraria</i>	H shrubs/trees; Pr		
	<i>Platyperigea kadenii</i>	H grasses/herbs; Pr		
	<i>Pseudoips prasinana</i>	H shrubs/trees; Pr		
	<i>Ptilodon capucina</i>	H shrubs/trees; Pr		
	<i>Ptilodon cucullina</i>	H shrubs/trees; Pr		
	<i>Scoliopteryx libatrix</i>	H shrubs/trees; Po; Pr		
	<i>Scopula imitaria</i>	H shrubs/trees; Pr		
	<i>Selenia tetralunaria</i>	H shrubs/trees; Pr		
	<i>Sphinx pinastri</i>	H shrubs/trees; Po; Pr		
	<i>Spilosoma lubricipeda</i>	H grasses/herbs; Pr		
	<i>Stauropus fagi</i>	H shrubs/trees; Pr		
	<i>Tethea ocularis</i>	H shrubs/trees; Po; Pr		
	<i>Tethea or</i>	H shrubs/trees; Po; Pr		
	<i>Tetheella fluctuosa</i>	H shrubs/trees; Po; Pr		
	<i>Thaumetopoea processionea</i>	H shrubs/trees; Pr		
	<i>Tholera decimalis</i>	H grasses/herbs; Po; Pr		
	<i>Thyatira batis</i>	H shrubs/trees; Po; Pr		
	<i>Trichopteryx carpinata</i>	H shrubs/trees; Po; Pr		
	<i>Trisateles emortualis</i>	H shrubs/trees; Pr		
	<i>Watsonalla binaria</i>	H shrubs/trees; Pr		
	<i>Watsonalla cultraria</i>	H shrubs/trees; Pr		
	<i>Xanthorhoe ferrugata</i>	H grasses/herbs; Pr		
	<i>Xanthorhoe quadrifasiata</i>	H grasses/herbs; Pr		
	<i>Xanthorhoe spadicearia</i>	H grasses/herbs; Pr		
	<i>Xestia sexstrigata</i>	H grasses/herbs; Po; Pr		
	<i>Xestia triangulum</i>	H shrubs/trees; Po; Pr		
Rotifers	<i>Mniobia obtusicalcar</i>	Ff; A; D; Pr	<i>Habrotrocha bidens</i>	Ff; A; D; Pr
	<i>Mniobia recurvicornis</i>	Ff; A; D; Pr	<i>Macrotrachela nana</i>	Ff; A; D; Pr
	<i>Philodina morigera</i>	Ff; A; D; Pr		
Butterflies	<i>Coenonympha pamphilus</i>	H mesotrophic grasses; Po; Pr	<i>Aphantopus hyperantus</i>	H shaded grasses; Po; Pr
	<i>Ochlodes sylvanus</i>	H grasses in wet biotopes; Po; Pr	<i>Araschnia levana</i>	H nettles; Po; Pr
	<i>Papilio machaon</i>	H Umbelliferae; Po; Pr	<i>Celastrina argiolus</i>	H shrubs; Po; Pr
	<i>Thymelicus silvestris</i>	H mesotrophic grasses; Po; Pr	<i>Polygonia c-album</i>	H nettles (but not only); Po; Pr
Web-spiders	<i>Tetragnatha nigrita</i>	Pc small flying insects; Pr	<i>Araneus marmoreus</i>	Pc small flying insects; Pr
			<i>Argiope bruennichi</i>	Pc orthopterans; Pr
			<i>Tetragnatha extensa</i>	Pc small flying insects; Pr
Ostracods	<i>Cyclocypris ovum</i>	D; A; Pr	<i>Candonopsis kingslei</i>	D; Pr

	<i>Fabaeformiscandona breuili</i>	D; Pr	<i>Limnocythere inopinata</i>	D; Pr
	<i>Potamocypris unicaudata</i>	D; A; Pr	<i>Notodromas monacha</i>	Pf; Pr
	<i>Pseudocandona hartwigi</i>	D; Pr		
	<i>Trajancypris serrata</i>	D; Pr		
Ground-spiders	<i>Agyneta cauta</i>	Pc; Pr	<i>Amaurobius ferox</i>	Pc; Pr
	<i>Alopecosa cuneata</i>	Pc; Pr	<i>Araeoncus humilis</i>	Pc; Pr
	<i>Antistea elegans</i>	Pc; Pr	<i>Bathypantes approximatus</i>	Pc; Pr
	<i>Bianor aurocinctus</i>	Pc; Pr	<i>Ceratinella brevipes</i>	Pc; Pr
	<i>Centromerus prudens</i>	Pc; Pr	<i>Cnephalocotes obscurus</i>	Pc; Pr
	<i>Ceratinella scabrosa</i>	Pc; Pr	<i>Dicymbium nigrum</i>	Pc; Pr
	<i>Cercidia prominens</i>	Pc; Pr	<i>Diplocentria bidentata</i>	Pc; Pr
	<i>Clubiona corticalis</i>	Pc; Pr	<i>Diplocephalus cristatus</i>	Pc; Pr
	<i>Clubiona diversa</i>	Pc; Pr	<i>Diplocephalus latifrons</i>	Pc; Pr
	<i>Clubiona pallidula</i>	Pc; Pr	<i>Dismodicus bifrons</i>	Pc; Pr
	<i>Clubiona phragmitis</i>	Pc; Pr	<i>Drassodes lapidosus</i>	Pc; Pr
	<i>Clubiona stagnatilis</i>	Pc; Pr	<i>Enoplognatha ovata</i>	Pc; Pr
	<i>Clubiona terrestris</i>	Pc; Pr	<i>Episinus angulatus</i>	Pc; Pr
	<i>Coelotes inermis</i>	Pc; Pr	<i>Euryopis flavomaculata</i>	Pc; Pr
	<i>Coelotes terrestris</i>	Pc; Pr	<i>Gongyliellum vivum</i>	Pc; Pr
	<i>Dictyna latens</i>	Pc; Pr	<i>Haplodrassus silvestris</i>	Pc; Pr
	<i>Diplocephalus permixtus</i>	Pc; Pr	<i>Meioneta rurestris</i>	Pc; Pr
	<i>Drassodes cupreus</i>	Pc; Pr	<i>Milleriana inerrans</i>	Pc; Pr
	<i>Drassodes pubescens</i>	Pc; Pr	<i>Oedothorax apicatus</i>	Pc; Pr
	<i>Drepanotylus uncatus</i>	Pc; Pr	<i>Ozyptila simplex</i>	Pc; Pr
	<i>Enoplognatha latimana</i>	Pc; Pr	<i>Ozyptila trux</i>	Pc; Pr
	<i>Enoplognatha tecta</i>	Pc; Pr	<i>Pardosa hortensis</i>	Pc; Pr
	<i>Erigone promiscua</i>	Pc; Pr	<i>Pelecopsis parallela</i>	Pc; Pr
	<i>Gnathonarium dentatum</i>	Pc; Pr	<i>Pirata piraticus</i>	Pc; Pr
	<i>Gonatium rubens</i>	Pc; Pr	<i>Pisaura mirabilis</i>	Pc; Pr
	<i>Gongyliellum latebricola</i>	Pc; Pr	<i>Porrhoma egeria</i>	Pc; Pr
	<i>Haplodrassus signifer</i>	Pc; Pr	<i>Robertus lividus</i>	Pc; Pr
	<i>Histopona torpida</i>	Pc; Pr	<i>Steatoda phalerata</i>	Pc; Pr
	<i>Lepthyphantes flavipes</i>	Pc; Pr	<i>Tegenaria atrica</i>	Pc; Pr
	<i>Lophomma punctatum</i>	Pc; Pr	<i>Theridion bimaculatum</i>	Pc; Pr
	<i>Macrargus rufus</i>	Pc; Pr	<i>Walckenaeria acuminata</i>	Pc; Pr
	<i>Mangora acalypha</i>	Pc; Pr	<i>Zora spinimana</i>	Pc; Pr
	<i>Marpissa muscosa</i>	Pc; Pr		
	<i>Meioneta mollis</i>	Pc; Pr		
	<i>Microlinyphia pusilla</i>	Pc; Pr		
	<i>Nerienne montana</i>	Pc; Pr		
	<i>Oedothorax agrestis</i>	Pc; Pr		
	<i>Oedothorax gibbosus</i>	Pc; Pr		
	<i>Ozyptila atomaria</i>	Pc; Pr		
	<i>Pocadicnemis pumila</i>	Pc; Pr		
	<i>Pseudeuophrys erratica</i>	Pc; Pr		
	<i>Saarietia abnormis</i>	Pc; Pr		

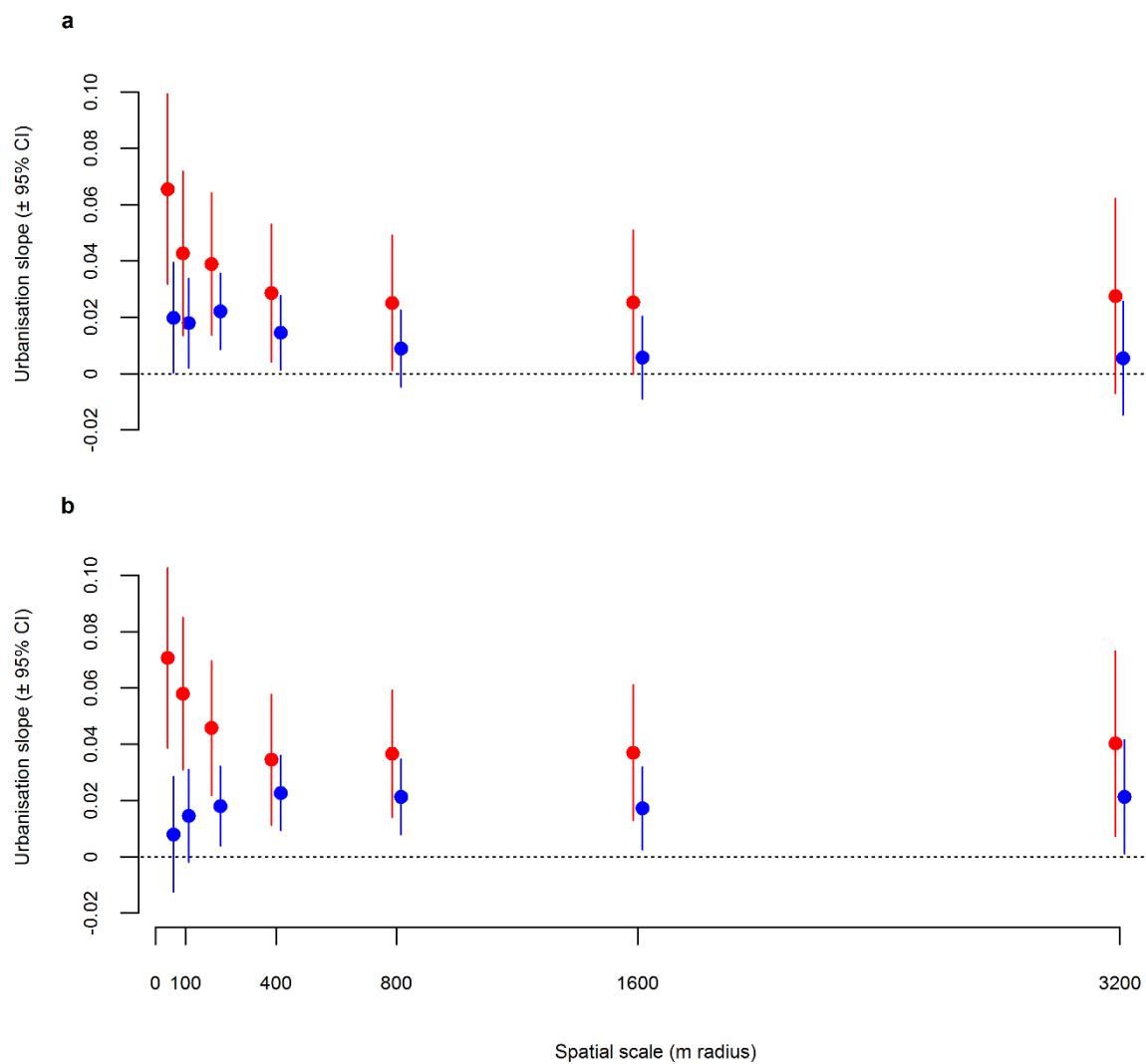
	<i>Savignya frontata</i>	Pc; Pr		
	<i>Sintula corniger</i>	Pc; Pr		
	<i>Steatoda triangulosa</i>	Pc; Pr		
	<i>Tallusia experta</i>	Pc; Pr		
	<i>Tegenaria duellica</i>	Pc; Pr		
	<i>Tegenaria picta</i>	Pc; Pr		
	<i>Trochosa spinipalpis</i>	Pc; Pr		
	<i>Walckenaeria cucullata</i>	Pc; Pr		
	<i>Walckenaeria cuspidata</i>	Pc; Pr		
	<i>Walckenaeria dysderoides</i>	Pc; Pr		
	<i>Walckenaeria furcillata</i>	Pc; Pr		
	<i>Walckenaeria mitrata</i>	Pc; Pr		
	<i>Walckenaeria monoceros</i>	Pc; Pr		
	<i>Walckenaeria nudipalpis</i>	Pc; Pr		
	<i>Walckenaeria unicornis</i>	Pc; Pr		
	<i>Xerolycosa miniata</i>	Pc; Pr		
	<i>Xerolycosa nemoralis</i>	Pc; Pr		
	<i>Zelotes petrensis</i>	Pc; Pr		
Ground-beetles	<i>Abax ater</i>	Pc; Pr	<i>Acupalpus flavicollis</i>	Pc; Pr
	<i>Abax parallelus</i>	Pc; Pr	<i>Agonum moestum</i>	Pc; Pr
	<i>Acupalpus dubius</i>	Pc; Pr	<i>Agonum viduum</i>	Pc; Pr
	<i>Agonum fuliginosum</i>	Pc; Pr	<i>Amara fulva</i>	Pc; Pr; H seeds
	<i>Agonum micans</i>	Pc; Pr	<i>Amara ovata</i>	Pc; Pr; H seeds
	<i>Agonum obscurum</i>	Pc; Pr	<i>Bembidion guttula</i>	Pc; Pr
	<i>Agonum sexpunctatum</i>	Pc; Pr	<i>Bembidion lunulatum</i>	Pc; Pr
	<i>Agonum viridicupreum</i>	Pc; Pr	<i>Bembidion quadrimaculatum</i>	Pc; Pr
	<i>Amara anthobia</i>	Pc; Pr; H seeds	<i>Bradycellus harpalinus</i>	Pc; Pr
	<i>Amara consularis</i>	Pc; Pr; H seeds	<i>Calathus fuscipes</i>	Pc; Pr
	<i>Badister sodalis</i>	Pc; Pr	<i>Carabus granulatus</i>	Pc; Pr
	<i>Calathus cinctus</i>	Pc; Pr	<i>Chlaenius nigricornis</i>	Pc; Pr
	<i>Carabus auronitens</i>	Pc; Pr	<i>Clivina fossor</i>	Pc; Pr
	<i>Carabus coriaceus</i>	Pc; Pr	<i>Dromius linearis</i>	Pc; Pr
	<i>Carabus nemoralis</i>	Pc; Pr	<i>Dyschirius globosus</i>	Pc; Pr
	<i>Carabus problematicus</i>	Pc; Pr	<i>Dyschirius politus</i>	Pc; Pr
	<i>Carabus violaceus</i>	Pc; Pr	<i>Nebria salina</i>	Pc; Pr
	<i>Dyschirius thoracicus</i>	Pc; Pr	<i>Notiophilus biguttatus</i>	Pc; Pr
	<i>Harpalus nitidulus</i>	Pc; Pr; H seeds	<i>Pterostichus anthracinus</i>	Pc; Pr
	<i>Harpalus rufipalpis</i>	Pc; Pr; H seeds	<i>Pterostichus diligens</i>	Pc; Pr
	<i>Lebia chlorocephala</i>	Pc; Pr	<i>Pterostichus melanarius</i>	Pc; Pr
	<i>Oodes helopioides</i>	Pc; Pr	<i>Pterostichus minor</i>	Pc; Pr
	<i>Pterostichus niger</i>	Pc; Pr	<i>Stenolophus teutonius</i>	Pc; Pr
	<i>Pterostichus oblongopunctatus</i>	Pc; Pr	<i>Stomis pumicatus</i>	Pc; Pr
	<i>Pterostichus rhaeticus</i>	Pc; Pr		
	<i>Stenolophus mixtus</i>	Pc; Pr		
	<i>Synuchus nivalis</i>	Pc; Pr		
	<i>Trechus quadristriatus</i>	Pc; Pr		

	<i>Trichocellus placidus</i>	Pc; Pr		
Weevils	<i>Acalles ptinoides</i>	H; Pr	<i>Brachysomus echinatus</i>	H; Pr
	<i>Alophus triguttatus</i>	H; Pr	<i>Chlorophanus viridis</i>	H; Pr
	<i>Amalus scortillum</i>	H; Pr	<i>Leiosoma deflexum</i>	H; Pr
	<i>Barynotus moerens</i>	H; Pr	<i>Microplontus campestris</i>	H; Pr
	<i>Brachypera zoilus</i>	H; Pr	<i>Notaris acridula</i>	H; Pr
	<i>Caenopsis fissirostris</i>	H; Pr	<i>Otiorhynchus porcatus</i>	H; Pr
	<i>Ceratapion onopordi</i>	H; Pr	<i>Phyllobius pyri</i>	H; Pr
	<i>Coelositona cambricus</i>	H; Pr	<i>Sitona lineatus</i>	H; Pr
	<i>Eutrichapion viciae</i>	H; Pr	<i>Strophosoma melanogrammum</i>	H; Pr
	<i>Glocianus distinctus</i>	H; Pr	<i>Tanymecus palliatus</i>	H; Pr
	<i>Glocianus punctiger</i>	H; Pr		
	<i>Grypus brunnirostris</i>	H; Pr		
	<i>Hypera arator</i>	H; Pr		
	<i>Hypera plantaginis</i>	H; Pr		
	<i>Hypera postica</i>	H; Pr		
	<i>Hypera suspiciosa</i>	H; Pr		
	<i>Ischnopterapion loti</i>	H; Pr		
	<i>Liophloeus tessulatus</i>	H; Pr		
	<i>Mecinus pascuorum</i>	H; Pr		
	<i>Mecinus pyraeter</i>	H; Pr		
	<i>Parethelcus pollinarius</i>	H; Pr		
	<i>Phyllobius pomaceus</i>	H; Pr		
	<i>Phyllobius subdentatus</i>	H; Pr		
	<i>Polydrusus tereticollis</i>	H; Pr		
	<i>Protapion fulvipes</i>	H; Pr		
	<i>Sitona cylindricollis</i>	H; Pr		
	<i>Sitona hispidulus</i>	H; Pr		
	<i>Sitona suturalis</i>	H; Pr		
	<i>Synapion ebeninum</i>	H; Pr		
	<i>Taeniapion urticarium</i>	H; Pr		
	<i>Trichosirocalus troglodytes</i>	H; Pr		
Cladocerans	<i>Alona quadrangularis</i>	A; D; Pr	<i>Daphnia magna</i>	A, D; Ff; Pr
	<i>Alonella exigua</i>	A; D; Pr	<i>Leydigia quadrangularis</i>	A; D; Pr
	<i>Alonella exisa</i>	A; D; Pr		
	<i>Eurycercus lamellatus</i>	A; D; Pr		
	<i>Pleuroxus trigonellus</i>	A; D; Pr		
	<i>Polyhemus pediculus</i>	Pc; Pr		
	<i>Scapholeberis kingi</i>	A; D; Ff; Pf; Pr		

Extended Data Figure 1

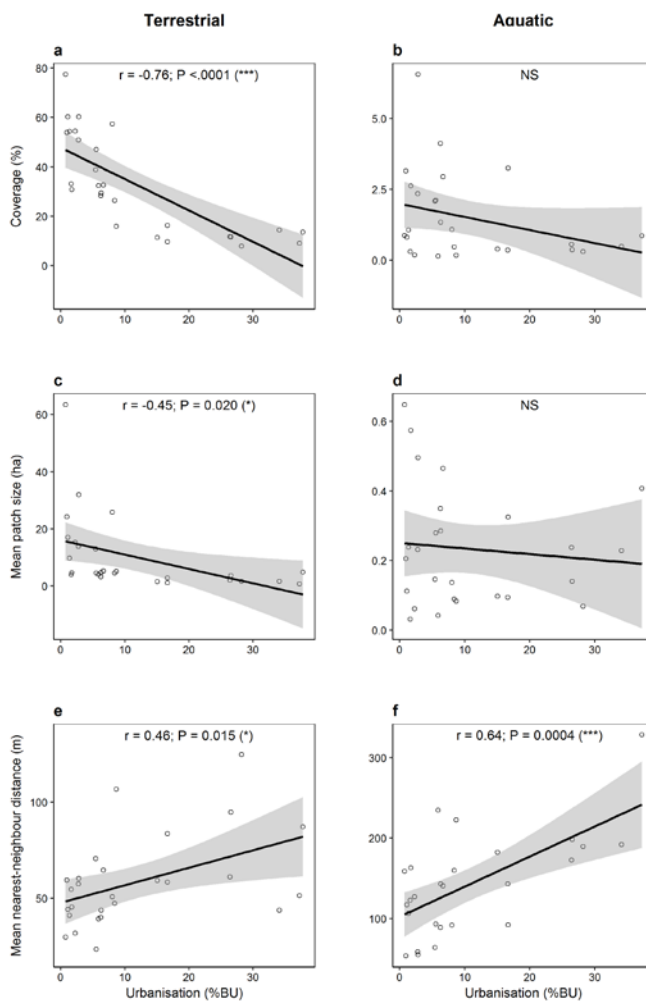
Micro-climatic urban-heat-island-effect strengths.

Slopes with 95% CI of the urban-heat-island-effects as the increase in temperature ($^{\circ}\text{C}$) per 1% increase in percentage built-up, separately for summer (red) and winter (blue), as a function of spatial scale (m radius at which urbanisation was quantified), lumped for pond, grassland and woodland habitats. a, diurnal. b, nocturnal. Data points are slightly jittered to improve clarity.



Extended Data Figure 2

Correlations between urbanisation (%BU) and three habitat fragmentation variables: (a-b) habitat coverage, (c-d) mean size of habitat patches, and (e-f) mean nearest-neighbour distance among habitat patches, separately for terrestrial (i.e. all types of (semi)natural habitat) and for aquatic habitat (i.e. all pond types) (left and right panels, respectively). Eutrophied, mono-specific intensive grasslands as well as orchards, plantations and conifer woodlands were not retained for analyses. Calculations are done at a 3 x 3 km plot scale, and are based on detailed land-use data (De Saeger *et al.* 2016; Packet *et al.* 2017) from all 27 sampling plots (Fig. 1). Pearson's r coefficients and P-values are provided, with symbols indicating significance levels (NS: $P > 0.1$ /* $P < 0.05$ /** $P < 0.001$).



References

- De Saeger, S. *et al.* Biologische Waarderingskaart en Natura 2000 Habitatkaart. Instituut voor Natuur- en Bosonderzoek, Brussels, Belgium (2016).
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