Body–size shifts in aquatic and terrestrial urban communities

Thomas Merckx\textsuperscript{1,8}, Caroline Souffreau\textsuperscript{2}, Aurélien Kaiser\textsuperscript{1}, Lisa F. Baardsen\textsuperscript{3}, Thierry Backeljau\textsuperscript{1,4}, Dries Bonte\textsuperscript{5}, Kristien I. Brans\textsuperscript{2}, Marie Cours\textsuperscript{6}, Maxime Dahirel\textsuperscript{5,7}, Nicolas Debortoli\textsuperscript{8}, Katrien De Wolf\textsuperscript{9}, Jessie M. T. Engelen\textsuperscript{2}, Diego Fontaneto\textsuperscript{9}, Andros T. Gianuca\textsuperscript{2,10,11}, Lynn Govaert\textsuperscript{2}, Frederik Hendrickx\textsuperscript{4,5}, Janet Higuti\textsuperscript{12}, Luc Lens\textsuperscript{5}, Koen Martens\textsuperscript{8,13}, Hans Mathiessens\textsuperscript{3}, Elena Piano\textsuperscript{4,14}, Rose Sablon\textsuperscript{4}, Isa Schön\textsuperscript{6,15}, Karine Van Doninck\textsuperscript{8}, Luc De Meester\textsuperscript{2,16} & Hans Van Dyck\textsuperscript{1,16}

Body size is intrinsically linked to metabolic rate and life-history traits, and is a crucial determinant of food webs and community dynamics\textsuperscript{1,2}. The increased temperatures associated with the urban–heat-island effect result in increased metabolic costs and are expected to drive shifts to smaller body sizes\textsuperscript{3}. Urban environments are, however, also characterized by substantial habitat fragmentation\textsuperscript{4,7}, which favours 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. In addition, although 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 urbanization gradients. Our results show that the general trend towards smaller-sized species is overruled by filtering for larger species when there is positive covariation between size and dispersal, a process that can mitigate the low connectivity of ecological resources in urban settings\textsuperscript{2}. We thus demonstrate that the urban–heat-island effect and urban habitat fragmentation are associated with contrasting community–level shifts in body size that critically depend on the association between body size and dispersal. Because body size determines the structure and dynamics of ecological networks\textsuperscript{5}, such shifts may affect urban ecosystem function.

Body size is a fundamental species trait relating to space use and key life-history features such as longevity and fecundity\textsuperscript{6}. It also drives interspecific relationships, thus affecting ecological network dynamics\textsuperscript{1,2}. Size-biased species loss has profound effects on ecosystem function\textsuperscript{2,8}. Ectotherms rely on ambient conditions to achieve operational body temperatures\textsuperscript{9}. Because higher ambient temperature increases metabolic rates and the associated costs for a given body size\textsuperscript{10}, global climatic warming is expected to drive shifts to communities consisting of smaller species\textsuperscript{3,11}.

Our planet is urbanizing quickly\textsuperscript{10}, which is a primary example of human-induced rapid environmental change. Cities are urban heat islands characterized by increased temperatures that are decades ahead of global averages\textsuperscript{11}. Not only are cities warmer than surrounding areas, but they also experience extensive fragmentation of (semi-)natural habitats, and both of these effects increase with percentage built-up cover (BUC; a proxy for urbanization)\textsuperscript{12,13}. This provides an opportunity to study the opposing 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 urbanization causes shifts in community-level body size, and that these shifts are dictated by the community-specific association between body size and dispersal. We generally expect the urban–heat-island effect to drive shifts to species with smaller body sizes in communities of ectothermic species, in line with Atkinson’s temperature–size rule\textsuperscript{14}. 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\textsuperscript{5,13}. Filtering for increased mobility has been demonstrated for urban ground beetle and plant communities\textsuperscript{16,17}. Hence, for taxa characterized by a positive body-size–dispersal link, we predict that the general community-level pattern of smaller species with increasing urbanization may be neutralized or even reversed.

To test our hypothesis, we engaged in an analysis of community-level shifts in body size across a broad range of both terrestrial and aquatic taxa along the same systematically sampled urbanization gradients. We studied the direction of change of community-level body size in ten taxa using a replicated, highly standardized and nested sampling design that covers urbanization gradients at seven spatial scales (50–3,200 m radii; Fig. 1). We sampled each taxon at up to 81 sites, sampling 95,001 individuals from 702 species, with species-specific body size varying by a factor of 400 (0.2–80 mm; Extended Data Table 1). Three of the ten groups are characterized by a positive association between body size and dispersal capacity (see Extended Data Table 1).

We show that the local temperature of pond, grassland and woodland habitats significantly increases with urbanization (linear mixed regression models, $P<0.002$; Extended Data Table 2). The intensity of these urban–heat-island effects is consistently larger during night and summer, in accordance with slower night-time city cooling and higher irradiation levels in summer\textsuperscript{18} (Fig. 2, Extended Data Fig. 1, Extended Data Table 2). We also show that increased urbanization is linked to significant declines in habitat amount and the patch size of terrestrial habitats, and significant increases in distances among patches for both terrestrial and aquatic habitats (Pearson’s $r$ correlations, $P<0.020$; Extended Data Fig. 2).

Confirming our metabolism-based prediction that interspecific mean body size decreases with increasing temperature, urban communities for four out of the seven taxa (ground spiders, ground beetles, weevils and cladocerans) that did not have a positive size–dispersal link display reduced community-weighted mean body size (CWMBS). For ostracods, bdelloid rotifers and water spiders, no relationship with urbanization is found. By contrast, all three taxa with positive size–dispersal links display increased CWMBS in response to urbanization.

\textsuperscript{1}Behavioural Ecology and Conservation Group, Biodiversity Research Centre, Earth and Life Institute, Université catholique de Louvain, Louvain-la-Neuve, Belgium. \textsuperscript{2}Laboratory of Aquatic Ecology, Evolution and Conservation, K.U. Leuven, Leuven, Belgium. \textsuperscript{3}Evolutionary Ecology Group, University of Antwerp, Antwerp, Belgium. \textsuperscript{4}Directorate Taxonomy and Phylogeny, Royal Belgian Institute of Natural Sciences, Brussels, Belgium. \textsuperscript{5}ECCOBIO (Ecosystèmes, biodiversité, évolution), CNRS, Université de Rennes, Rennes, France. \textsuperscript{6}Laboratory of Evolutionary Genetics and Ecology, URBE, NAXYS, University of Maringá, Maringá, Brazil. \textsuperscript{7}Limnology Research Unit, Biology Department, Ghent University, Ghent, Belgium. \textsuperscript{8}Department of Life Sciences and Systems Biology, University of Turin, Turin, Italy. \textsuperscript{9}Zoology Research Group, University of Hasselt, Hasselt, Belgium. © 2018 Macmillan Publishers Limited, part of Springer Nature. All rights reserved.
study-wide level. Comparing the percentage changes in body size between taxa with a positive size–dispersal link (13.6% ± 8.3% body size increase) versus the other taxa (15.6% ± 5.3% body size decrease) (weighted two-sided analysis of variance (ANOVA): F_{1,8} = 12.38; P = 0.0079). These community-level shifts in body size occur independently of shifts in species abundance and diversity along the urbanization gradients. For example, reduced diversity is apparent for taxa that display positive and negative size shifts, as well as for web spiders that lack a size shift. By contrast, cladocerans show size reduction without diversity change (Extended Data Table 4). For butterflies, macro-moths and orthopterans (that is, species than in terrestrial species as a result of the greater oxygen limitation in water). However, the size reduction for the ostracods is much smaller (13%) and non-significant (linear mixed regression model, P = 0.10), and 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. The absence of a size shift for web spiders may be explained by behavioural flexibility in their extended phenotype, as modified web designs help web-spider communities to adapt to urbanization-induced lower average body size of aerial dipteran prey.

Our multi-scale approach allows the pinpointing of the spatial scales at which urbanization best explains the observed effects. During winter, the urban-heat-island effect fades with increasing spatial scale during the day but not at night, whereas during summer both diurnal and nocturnal urban-heat-island effects are more pronounced at small scales (Fig. 2, Extended Data Fig. 1, Extended Data Table 2). The spatial scale at which most of the variation in CWBMS is explained varied considerably among taxa, with effects for smaller-sized taxa prevailing at small spatial scales (Figs. 3, 4, Extended Data Table 3).

Urbanization induces biodiversity loss and biotic homogenization (see also Extended Data Table 4). Here, we demonstrate that urbanization also leads to community-wide shifts in body size for the majority of studied species groups. The size reductions within aquatic and terrestrial taxa follow metabolic rules in line with the urban-heat-island effect, especially as our data on various pollutants suggest no correlation with percentage BUC (data not shown).
contrast, the increased fragmentation that is a result of urbanization appears to cause size increases for taxa with positive size–dispersal links. Hence, our multi-taxa study provides evidence of bi-directional shifts in community body size. In addition to the interspecific patterns reported here, shifts in body size can also occur at the intraspecific level, through phenotypic plasticity and genotypic change. Our results should enable mechanistic studies that elucidate the cause of the variation in the observed shifts in body size along urban gradients and quantify their functional effects in urban ecosystems. A better insight into the mechanisms behind shifts in body size will allow prediction of the intertwined effects of climate change and urbanization on the body-size distribution of communities.

The size-biased species loss reported here is expected to strongly affect ecosystem function. If taxa in urban areas are represented by smaller or larger species, ecosystem structure and function will be affected in several ways. Metabolic theory and a recent artificial-selection experiment predict that shifted size distributions affect whole-ecosystem properties such as primary productivity, carbon cycling and
decomposition. Shifts in body size also translate into altered life histories, demographic rates and interspecific relationships. For example, consumer–resource dynamics have recently been modelled for warming-related intraspecific size shifts mediated by phenotypic plasticity. A clear-cut effect of shifts in body size on ecosystem function can be predicted for cladoceran zooplankton. Smaller-sized cladoceran communities are typified by reduced densities of large Daphnia species (highly efficient filter feeders that consume phytoplankton), and are thus less able to maintain top-down control on algal blooms than larger-sized communities. Also, the observed shifts in macro-moth body-size distributions may be functionally linked to flowering plant diversity through pollination.

The shifts in body size that we observe across a range of animal taxa will be directly relevant to future efforts to understand, predict and mediate population resilience, trophic interactions, and ecosystem function in urban ecosystems. Such insights will be essential to design the biodiverse towns and cities of the future. For example, urban planners could mitigate the micro–climatic effects and habitat fragmentation that result from urbanization with measures implemented at multiple spatial scales. Such interventions could involve the creation and/or modification of urban ponds and urban green infrastructure to increase the amount and quality of habitats. Doing so would reduce the urban-heat island effect and favour dispersal, and hence gene flow, in urban animal populations. Our results indicate that such impacts would maintain variation in the body-size distributions of urban communities and potentially mitigate the effect that shifts in body size may have on ecosystem function.

Online content
Any Methods, including any statements of data availability and Nature Research reporting summaries, along with any additional references and Source Data files, are available in the online version of the paper at https://doi.org/10.1038/s41586-018-0140-0.

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METHODS

Sampling design. Sampling was performed according to a nested design in which a local urbanization gradient (three classes: non-urban, semi-urban and urban) was repeatedly sampled within landscapes distributed along a landscape-scale urbanization gradient (three classes: non-urban, semi-urban and urban). For each of ten taxa a total of up to 81 local-scale subplots (200 × 200 m2) were sampled within 27 landscape-scale plots (3 × 3 km2) situated in an 8,140 km2 study area in northern Belgium (Fig. 1, Extended Data Table 1). The average human population density of this highly urbanized area amounts to 693 individuals per km2, with cities and urban sprawl embedded within an agricultural and semi-natural matrix. As a proxy for urbanization we used percentage BUC, which was assessed in a geographic information system (GIS) using an object-oriented reference map of Flanders with the precise contours of all buildings, excluding roads and parking infrastructures, as a vectorial layer. Given that only buildings are considered, 15% BUC can be considered highly urbanized. Within each of the nine urban (BUC > 15%), nine semi-urban (5% < BUC < 10%) and nine non-urban (BUC < 5%) plots, one urban, one semi-urban and one non-urban subplot was chosen using identical BUC cut-off values, for a total of 81 subplots. Within each subplot, and for each of the ten taxa, a single grassland, woodland or pond habitat patch was targeted for sampling during the most appropriate season for each taxon (Extended Data Table 1). As each taxon was sampled in only one of three habitat types (that is, grassland, woodland or ponds), it was often impossible to sample all taxa within the same 200 × 200 m2 subplot. As such, independent subplots containing the corresponding habitats were sometimes selected among taxa, but these subplots were always of the same urbanization level and located within the same 3 × 3 km2 plot.

The classification of urban, semi-urban and rural (inhabitants only) subplots on the basis of BUC cut-off values was used to establish the nested sampling design, which allowed samples to display a wide range of urbanization values at both local (subplot) and landscape (plot) scales. To increase precision in the data analysis, however, we moved away from having BUC as a class variable with three levels, and instead quantified BUC as a continuous variable, at seven spatial scales around the sampling site (50, 100, 200, 400, 800, 1,600 and 3,200 m radii). Owing to our nested design, BUC values at small scales were not correlated with values at large scales, hence allowing the pinpointing of the scales at which the effects of urbanization are most pronounced.

Using this highly replicated, nested sampling design, our sampling effort involved counting and assigning 95,001 individuals to 702 species in 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 (that is, grasshoppers and bush crickets), macro-moths, ground beetles, weevils, web spiders and ground spiders sampled in grassland and woodland habitats (Extended Data Table 1). No statistical methods were used to predetermined sample size and the investigators were not blinded to allocation during experiments and long-term observation.

Urban-heat-island effect. The urban-heat-island effect was quantified using hourly temperature readings that were collected automatically across 104 sampling sites for the three habitat types in which the ten taxa were sampled: ponds, grasslands and woodlands. Aquatic probes (Hobo, Tidbit v2 UTB-001; HOBOware ONSET; resolution: 0.02 °C) were attached to a floating device to log temperatures at 15 cm depth for 18 ponds (27 November 2014–29 November 2015). Terrestrial probes (iButton, Thermochron DS1923, Maxim Integrated; resolution: 0.06 °C) logged air temperature at 20 cm height near 59 pitfall sites (that is, grassland habitat; 8 May 2014–20 September 2015; 59 and 49 sites during summer and winter, respectively) and 27 macro-moth sampling sites (that is, woodland habitat; 1 April 2015–20 March 2016; 26 sites each during summer and winter). For each day, temperature averages of twelve diurnal (07:00–18:00) and twelve nocturnal (19:00–06:00) readings were calculated, which were labelled as summer from 21 March–20 September, and as winter from 21 September–20 March.

Habitat fragmentation. Correlations between urbanization (BUC) and three habitat fragmentation variables (that is, habitat coverage, mean size of habitat patches, and mean nearest-neighbour distance among habitat patches) were quantified using Pearson’s coefficients (Extended Data Fig. 2). This was done at a 3 × 3 km2 plot scale, on the basis of detailed land-use data from all 27 sampling plots (Fig. 1), and separately for terrestrial (that is, all types of semi-natural habitat) and aquatic habitat (that is, all pond types).

Eutrrophic, mono-specific intensive grasslands as well as orchards, plantations and conifer woodlands were not retained for analyses.

Statistical analyses. Temperature averages were analysed in relation to site-specific urbanization (BUC) values and habitat type (grassland, woodland and pond) using linear mixed regression models (R package lme4). We ran separate models for both bi-seasons (summer and winter) and for both day and night conditions (diurnal and nocturnal). Site ID and date (nested within year) were included as random factors. We used a multi-scale approach, running separate models with BUC values quantified at seven spatial scales (50–3,200 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 for which the AICc values did not differ substantially from the value of the best-fitting model, using ∆AICc ≤ 2 as a criterion.

CWMBS was calculated as an index of the relative composition of large versus small species in local communities, and we use it here to quantify community response to urbanization. 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 CWMBS is appropriate to look into the relative effects of urbanization.

CWMBS was analysed for each taxon in relation to site-specific urbanization (BUC) values using linear mixed regression models with restricted maximum-likelihood estimation (R package lme4). Percentage BUC was used as a random variable to account for potential spatial autocorrelation of variables among sites belonging to the same landscape-scale plot. CWMBS values were log10-transformed for cladocerans and ostracods. For ostracods, we also transformed BUC values by taking the arcsine of square-rooted BUC 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 each displayed one outlying data point, and the residual plot for weevils displayed two such points. Because these five data points are legitimate (that is, they are not due to measurement, data or sampling errors) we assessed their effect on the consistency of the regressions in the model output. Filtering these data points out of 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 effect on the output, we opted to retain them in the analyses. We used a multi-scale approach, running separate models with BUC values quantified at seven spatial scales (50–3,200 m radii). For each taxon, we then selected the model (and hence the spatial scale) that fitted the data best using maximum-likelihood-based AICc values (R package AICcmodavg). We also retained a confidence set of the models for which the AICc values did not differ substantially from the value of the best model using ∆AICc ≤ 2 as a criterion.

For each taxon, and at the spatial scale of the best-fitting model, we calculated the percentage change (with 95% confidence interval) in CWMBS over a 0–25% BUC gradient, on the basis of the modelled intercept and slope, or of back-transformed values for ostracods and cladocerans (Fig. 3). These values were then contrasted for taxa with a positive size–dispersal link to determine whether they are significantly different from those of all other taxa.

All statistical analyses were performed using R v.3.2.3. Reporting summary. Further information on experimental design is available in the Nature Research Reporting Summary linked to this paper.

Data availability. The datasets generated and analysed during the current study are available from the corresponding author upon reasonable request.

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Extended Data Fig. 1 | Micro-climatic urban-heat-island effect strengths. a, b, Slopes of the urban-heat-island effects (measured as the increase in temperature (°C) per 1% increase in percentage BUC) as a function of spatial scale (the radius at which urbanization was quantified) with 95% confidence intervals (CI). Separate measurements are shown for summer (red) and winter (blue) using merged readings for pond, grassland and woodland habitats (n = 104 sites). a, Diurnal measurements. b, Nocturnal measurements. Data points are offset from one another horizontally to improve clarity.
Extended Data Fig. 2 | Correlations between urbanization and habitat fragmentation. Correlations between urbanization (measured as the percentage BUC) and three habitat fragmentation variables: habitat coverage (a, b), mean size of habitat patches (c, d), and mean nearest-neighbour distance among habitat patches (e, f). Separate plots are shown for terrestrial (that is, all types of (semi-)natural habitat, a, c, e) and aquatic (that is, all pond types, b, d, f) habitats (n = 27 landscape-scale sampling plots). Pearson’s r coefficients and P values are indicated; not significant (NS), P > 0.1; *P < 0.05; ***P < 0.001.
### Extended Data Table 1 | Taxon-specific details of sampling procedures, body-size data and size–dispersal links

| Taxon          | Sampling method                                                                 | Sites | N  | S  | Body (proxy) (mm) | Body size data                                                                 | Size-dispersal link |
|----------------|---------------------------------------------------------------------------------|-------|----|----|-------------------|--------------------------------------------------------------------------------|-------------------|
| Butterflies    | Visual counts in grassland 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 (simultaneous sampling by two researchers) | 81    | 4,413 | 23 | Forewing length   | Means\(^{39}\), also for sexually or seasonally dimorphic species | Positive\(^{40-42}\) |
| Macro-moths    | Full-night light-trapping with one Heath trap (6W) at woodland; 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 Hoplodrina and Mesapamea sp. | 12    | 3,067 | 202 | Wing span         | Means\(^{63}\) (+ www.lepidoptera.e u), also for sexually dimorphic species; but males only for three species with flightless females | Positive\(^{43,44}\) |
| Orthopterans   | Auditive counts in grassland 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 (simultaneous sampling by two researchers) | 81    | 10,302 | 8  | Body length       | Means (without wings nor appendages)\(^{46}\) | Positive\(^{47}\) (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    | 2,456 | 18 | Cephalothorax width | Means of all captured adult spiders; microscope-measured | Neutral (bell-shaped)\(^{48}\) |
| 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    | 27,763 | 184 | Body length       | Values of females\(^{51}\) (+ www.araneae.unib e.ch) | Neutral (bell-shaped)\(^{50}\) |
| Ground beetles | Identical to ground spider sampling                                              | 81    | 7,604 | 128 | Body length       | Means\(^{49}\) | Neutral\(^{52}\) |
| Weevils        | Identical to ground spider sampling                                             | 78    | 2,600 | 73  | Body length       | Means of minimum + maximum values\(^{53}\) | Neutral\(^{54}\) |
| Rotifers       | Community sampling of bdelloid rotifers recovered from dormancy four hours after hydration of one Xanthoria 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    | 4,936 | 21  | Body length       | Maximum recorded lengths in literature; mostly from original species descriptions and\(^{55}\) | Neutral\(^{51}\) |
| Ostracods      | Handnet sampling in one pond/subplot at up to nine ponds/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    | 3,111 | 17  | Body length       | Values of females\(^{52}\) | Negative or neutral\(^{53,54}\) |
| Ciliates       | Zooplankton sampling with tube sampler in one pond/subplot, collecting 5 l 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/sample (Daphnia longispina, D. galeata and D. hyalina were combined in the D. longispina complex); individual counts were volume-corrected for each sample; 15 random individuals/species occurring in each sample were measured (if less individuals present/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\(^{55,56}\) | 81    | 28,749 | 28  | Body length       | Means (eye top till tail spine base) of up to 15 individuals per species per sample, with Ceriodaphnia values combined into one category. Means from all ponds were averaged further | Negative or neutral\(^{53,54}\) |

\(N\), counted individuals; \(S\), cumulative species richness. Some of the sampling methods and data on body size and size–dispersal links are from previously published work\(^{39-56}\).
Extended Data Table 2 | Model output of average temperature in relation to urbanization and habitat type

| Scale       | ΔAICc | Fixed effect                  | $\chi^2$ test | $P$ value | Estimate ± s.e.m. |
|-------------|-------|-------------------------------|---------------|-----------|------------------|
| **Diurnal summer** | 50    | BUC x Habitat                | $\chi^2_2 = 4.05$ | $P = 0.13$ | 0.0655 ± 0.0172  |
|             |       | BUC                           | $\chi^2_1 = 13.96$ | $P = 0.0001$ |                  |
|             |       | Habitat                       | $\chi^2_2 = 39.67$ | $P < 0.0001$ |                  |
| **Nocturnal summer** | 50    | BUC x Habitat                | $\chi^2_2 = 2.73$ | $P = 0.25$  | 0.0706 ± 0.0163  |
|             |       | BUC                           | $\chi^2_1 = 17.66$ | $P < 0.0001$ |                  |
|             |       | Habitat                       | $\chi^2_2 = 82.37$ | $P < 0.0001$ |                  |
|             | 100   | BUC x Habitat                | $\chi^2_2 = 0.14$ | $P = 0.93$  | 0.0579 ± 0.0138  |
|             |       | BUC                           | $\chi^2_1 = 16.76$ | $P < 0.0001$ |                  |
|             |       | Habitat                       | $\chi^2_2 = 83.19$ | $P < 0.0001$ |                  |
| **Diurnal winter** | 200   | BUC x Habitat                | $\chi^2_2 = 0.21$ | $P = 0.89$  | 0.0221 ± 0.0069  |
|             |       | BUC                           | $\chi^2_1 = 10.15$ | $P = 0.001$ |                  |
|             |       | Habitat                       | $\chi^2_2 = 5.45$  | $P = 0.06$  |                  |
| **Nocturnal winter** | 400   | BUC x Habitat                | $\chi^2_2 = 0.21$ | $P = 0.89$  | 0.0227 ± 0.0068  |
|             |       | BUC                           | $\chi^2_1 = 10.94$ | $P = 0.0009$ |                  |
|             |       | Habitat                       | $\chi^2_2 = 76.57$ | $P < 0.0001$ |                  |
|             | 800   | BUC x Habitat                | $\chi^2_2 = 0.39$ | $P = 0.82$  | 0.0213 ± 0.0068  |
|             |       | BUC                           | $\chi^2_1 = 9.61$  | $P = 0.0019$ |                  |
|             |       | Habitat                       | $\chi^2_2 = 77.55$ | $P < 0.0001$ |                  |

Output of linear mixed regression models that test the relationship between average local ambient temperatures and the interaction between percentage BUC and habitat type (pond, grassland and woodland) ($n = 104$ sites). Only the output for the confidence set of models ($\Delta$AICc ≤ 2) is given, with scale referring to the associated radius scale (in metres) of percentage BUC. Model estimates (±s.e.m.) for percentage BUC regression coefficients are provided. Model output consistently shows clear temperature differences among habitats and a clear positive effect of urbanization on temperature, irrespective of habitat type (as shown by the non-significant interactions).
## Extended Data Table 3 | Model output of CWMBS in relation to urbanization

| Taxon          | Scale | ΔAICc | F test | P value | Intercept (± s.e.m.) | Slope (± s.e.m.) |
|----------------|-------|-------|--------|---------|---------------------|-----------------|
| **Orthoptera** | 50    | 9.24  | 0.14   | 0.71    | 21.458 ± 0.436      | 0.015 ± 0.040   |
|                | 100   | 8.48  | 0.48   | 0.49    | 9.370 ± 0.457       | 0.024 ± 0.035   |
|                | 200   | 6.83  | 2.49   | 0.12    | 21.104 ± 0.476      | 0.052 ± 0.033   |
|                | 400   | 8.29  | 1.01   | 0.32    | 21.203 ± 0.502      | 0.035 ± 0.034   |
|                | 800   | 7.85  | 1.43   | 0.24    | 21.084 ± 0.527      | 0.047 ± 0.038   |
| **Macromoths** | 1,600 | 5.67  | 3.64   | 0.065   | 20.752 ± 0.548      | 0.081 ± 0.042   |
|                | 3,200 | 5.00  | 10.46  | 0.002   | 20.122 ± 0.549      | 0.171 ± 0.053   |
| **Rotifers**   | 50    | 1.08  | 0.55   | 0.46    | 0.456 ± 0.021       | 0.002 ± 0.002   |
|                | 100   | 1.24  | 0.41   | 0.52    | 0.457 ± 0.022       | 0.001 ± 0.002   |
|                | 200   | 0.75  | 1.35   | 0.25    | 0.447 ± 0.022       | 0.002 ± 0.002   |
| **Butterflies**| 400   | 0.00  | 1.55   | 0.22    | 0.446 ± 0.022       | 0.002 ± 0.002   |
|                | 800   | 0.69  | 0.92   | 0.34    | 0.450 ± 0.023       | 0.002 ± 0.002   |
|                | 1,600 | 0.36  | 1.26   | 0.27    | 0.447 ± 0.024       | 0.002 ± 0.002   |
| **Web spiders**| 3,200 | 0.61  | 0.84   | 0.37    | 0.449 ± 0.025       | 0.002 ± 0.002   |
| **Ostracods**  | 50    | 0.14  | 0.96   | 0.33    | 3.133 ± 0.067       | -0.003 ± 0.003  |
|                | 100   | 0.83  | 0.32   | 0.58    | 3.128 ± 0.073       | -0.002 ± 0.004  |
|                | 200   | 0.83  | 0.31   | 0.58    | 3.131 ± 0.076       | -0.003 ± 0.005  |
| **Ground spiders** | 400 | 0.76  | 0.35   | 0.56    | 3.138 ± 0.081       | -0.003 ± 0.005  |
|                | 800   | 0.93  | 0.19   | 0.66    | 3.134 ± 0.087       | -0.002 ± 0.005  |
|                | 1,600 | 1.08  | 0.05   | 0.82    | 3.124 ± 0.093       | -0.002 ± 0.006  |
| **Ground beetles** | 3,200 | 0.00  | 1.06   | 0.31    | 3.190 ± 0.101       | -0.009 ± 0.008  |
| **Weevils**    | 50    | 3.17  | 1.64   | 0.001   | 0.000 ± 0.000       | -0.522 ± 0.016  |
|                | 100   | 2.72  | 0.27   | 0.60    | -0.194 ± 0.019      | -0.031 ± 0.058  |
| **Cladocera**  | 400   | 5.30  | 2.51   | 0.010   | 5.113 ± 0.127       | -0.024 ± 0.009  |
|                | 800   | 5.40  | 6.66   | 0.012   | 5.123 ± 0.127       | -0.025 ± 0.009  |
|                | 1,600 | 6.80  | 5.57   | 0.025   | 5.110 ± 0.134       | -0.023 ± 0.010  |
|                | 3,200 | 7.23  | 5.34   | 0.029   | 5.124 ± 0.139       | -0.029 ± 0.013  |
| **Weevils**    | 50    | 7.17  | 2.02   | 0.16    | 8.565 ± 0.276       | -0.047 ± 0.032  |
|                | 100   | 6.66  | 5.57   | 0.021   | 8.894 ± 0.294       | -0.069 ± 0.029  |
| **Cladocera**  | 200   | 1.79  | 7.39   | 0.0081  | 9.045 ± 0.310       | -0.071 ± 0.025  |
|                | 400   | 1.58  | 7.44   | 0.0082  | 9.080 ± 0.319       | -0.066 ± 0.023  |
|                | 800   | 0.00  | 9.19   | 0.0042  | 9.152 ± 0.318       | -0.071 ± 0.023  |
| **Weevils**    | 1,600 | 1.39  | 7.94   | 0.0085  | 9.124 ± 0.326       | -0.068 ± 0.024  |
|                | 3,200 | 5.51  | 3.70   | 0.065   | 8.976 ± 0.360       | -0.063 ± 0.033  |
| **Cladocera**  | 50    | 4.20  | 2.02   | 0.16    | 3.170 ± 0.178       | -0.024 ± 0.017  |
|                | 100   | 6.59  | 6.59   | 0.013   | 4.323 ± 0.190       | -0.037 ± 0.014  |
| **Weevils**    | 200   | 2.21  | 3.92   | 0.053   | 4.309 ± 0.200       | -0.028 ± 0.014  |
|                | 400   | 2.37  | 3.71   | 0.059   | 4.330 ± 0.210       | -0.027 ± 0.013  |
| **Weevils**    | 800   | 3.65  | 2.51   | 0.12    | 4.308 ± 0.223       | -0.024 ± 0.013  |
|                | 1,600 | 5.20  | 0.99   | 0.33    | 4.230 ± 0.236       | -0.017 ± 0.016  |
| **Weevils**    | 3,200 | 5.68  | 0.51   | 0.48    | 4.193 ± 0.251       | -0.016 ± 0.022  |

Output of linear mixed regression models testing the relationship between CWMBS and percentage BUC at multiple scales (radii in metres), for ten taxa (n=76, 12, 75, 80, 62, 60, 81, 81, 68 and 80 biologically independent communities, top to bottom). Confidence sets of models (ΔAICc ≤ 2) have grey shading and the best-fitting model output is given in bold. Modelled intercepts and slopes (± s.e.m.) are given.
## Extended Data Table 4 | Model output of abundance and diversity measures in relation to urbanization

| Taxon        | NIS/H | Scale | F test       | P value | % change 0–25% BUC |
|--------------|-------|-------|--------------|---------|-------------------|
| 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   | $F_{1,63.0} = 0.68$  | $P = 0.41$    | -8.4             |
| Macro-moths  | tN    | 3,200 | $F_{1,4.0} = 52.6$   | $P = 0.0019$  | -89.2            |
|              | tS    | 3,200 | $F_{1,4.0} = 108.1$  | $P = 0.0005$  | -82.7            |
|              | H     | 800   | $F_{1,5.2} = 55.8$   | $P = 0.0006$  | -43.5            |
| Rotifers     | tN    | 400   | $F_{1,67.1} = 2.1$   | $P = 0.15$    | +108.1           |
|              | tS    | 400   | $F_{1,67.9} = 0.4$   | $P = 0.53$    | +15.6            |
|              | H     | 3,200 | $F_{1,37.9} = 1.2$   | $P = 0.28$    | +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    | $F_{1,71.1} = 3.6$   | $P = 0.06$    | -69.2            |
|              | tS    | 50    | $F_{1,71.3} = 2.1$   | $P = 0.15$    | -38.6            |
|              | H     | 1,600 | $F_{1,35.1} = 2.2$   | $P = 0.15$    | -41.2            |
| Ground spiders | N | 100   | $F_{1,65.1} = 5.7$   | $P = 0.020$   | -43.6            |
|              | S     | 800   | $F_{1,43.3} = 2.3$   | $P = 0.14$    | -13.4            |
|              | H     | 3,200 | $F_{1,26.6} = 12.3$  | $P = 0.0016$  | -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   | $F_{1,63.9} = 0.7$   | $P = 0.40$    | +25.0            |
| Cladocerans  | tN    | 3,200 | $F_{1,27.2} = 1.2$   | $P = 0.29$    | -68.5            |
|              | S     | 200   | $F_{1,62.8} = 1.1$   | $P = 0.29$    | +12.7            |
|              | H     | 3,200 | $F_{1,26.2} = 0.2$   | $P = 0.65$    | -11.4            |

Output of linear mixed regression models for ten taxa ($n = 76, 12, 75, 80, 62, 60, 81, 81, 68$ and $80$ biologically independent communities, top to bottom), testing the relationship between abundance ($N$) and two diversity measures (species richness ($S$) and Shannon index ($H$)) and percentage BUC at the spatial scale (radius in metres) providing the best-fitting models. $t$ indicates that $\log(x + 1)$ transformations improved residual fits. Modelled (back-transformed) percentage change across a 0–25% BUC gradient is also given.
Experimental design

1. Sample size
   
   Describe how sample size was determined.

   Sample size was based on counts (visual or auditory) of sampled individuals, with sampling method adjusted according to taxon. The obtained species abundances allow to compute abundance-weighted mean body size of local communities, and allow to calculate reliable relative differences among sites as these were all sampled using equal methods.

2. Data exclusions
   
   Describe any data exclusions.

   No data were excluded.

3. Replication
   
   Describe whether the experimental findings were reliably reproduced.

   Our sampling design was highly replicated so that several communities were sampled at similar urbanisation levels; for each taxon, sampling sites were located within up to 81 subplots (200x200m) from 3 urbanisation categories: 27 urban, 27 semi-urban and 27 non-urban subplots, each located within a total of 9 urban, 9 semi-urban and 9 non-urban plots (3x3km).

4. Randomization
   
   Describe how samples/organisms/participants were allocated into experimental groups.

   Sampling plots (27 plots of each 3x3km) were chosen so that (i) all 27 plots were more or less evenly spread out within our study area, and (ii) 9 urban plots covered an area with a % built-up of more than 15% (%BU>15%), and similarly for 9 semi-urban (5%<%BU<10%) and 9 non-urban (%BU<3%) plots. Next, 1 urban, 1 semi-urban and 1 non-urban subplot were chosen within each of these 27 plots, following identical %BU cut-off values, for a total of 81 subplots.

5. Blinding
   
   Describe whether the investigators were blinded to group allocation during data collection and/or analysis.

   Blinding of investigators doing the species sampling of the various taxa was not relevant/necessary as at the time of sampling the focus was fully on recording abundance and species richness. No one was informed we would eventually look at species-specific sizes. As such, any such bias was avoided. Anyway, for those taxa where species identifications were carried out in the lab (as opposed to immediately at the sampling sites), sample containers were coded in such a way that urbanisation values were not known to the person scoring the individuals.

Note: all studies involving animals and/or human research participants must disclose whether blinding and randomization were used.
6. Statistical parameters

For all figures and tables that use statistical methods, confirm that the following items are present in relevant figure legends (or in the Methods section if additional space is needed).

- n/a
- Confirmed

- The exact sample size \((n)\) for each experimental group/condition, given as a discrete number and unit of measurement (animals, litters, cultures, etc.)
- A description of how samples were collected, noting whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
- A statement indicating how many times each experiment was replicated
- The statistical test(s) used and whether they are one- or two-sided (note: only common tests should be described solely by name; more complex techniques should be described in the Methods section)
- A description of any assumptions or corrections, such as an adjustment for multiple comparisons
- The test results (e.g. \(P\) values) given as exact values whenever possible and with confidence intervals noted
- A clear description of statistics including central tendency (e.g. median, mean) and variation (e.g. standard deviation, interquartile range)
- Clearly defined error bars

See the web collection on statistics for biologists for further resources and guidance.

7. Software

Policy information about availability of computer code

Describe the software used to analyze the data in this study.

All analyses were performed using the R-packages lme4 and AICcmodavg within R version 3.2.3; 34. R Development Core Team. R: A Language and Environment for Statistical Computing (R Foundation for Statistical Computing) (2015)

For manuscripts utilizing custom algorithms or software that are central to the paper but not yet described in the published literature, software must be made available to editors and reviewers upon request. We strongly encourage code deposition in a community repository (e.g. GitHub). Nature Methods guidance for providing algorithms and software for publication provides further information on this topic.

8. Materials availability

Policy information about availability of materials

Indicate whether there are restrictions on availability of unique materials or if these materials are only available for distribution by a for-profit company.

No unique materials were used

9. Antibodies

Describe the antibodies used and how they were validated for use in the system under study (i.e. assay and species).

No antibodies were used

10. Eukaryotic cell lines

- State the source of each eukaryotic cell line used.
- Describe the method of cell line authentication used.
- Report whether the cell lines were tested for mycoplasma contamination.
- If any of the cell lines used are listed in the database of commonly misidentified cell lines maintained by ICLAC, provide a scientific rationale for their use.

No eukaryotic cell lines were used

11. Animals and human research participants

Policy information about studies involving animals; when reporting animal research, follow the ARRIVE guidelines

Provide details on animals and/or animal-derived materials used in the study.

No animals were used
Policy information about studies involving human research participants

12. Description of human research participants

Describe the covariate-relevant population characteristics of the human research participants.

The study did not involve human research participants.