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**Urbanization drives community shifts towards thermophilic and dispersive species at local and landscape scales**

**Running head:** urbanization drives community shifts

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## Original Research

### Abstract

The increasing conversion of agricultural and natural areas to human-dominated urban landscapes is predicted to lead to a major decline in biodiversity worldwide. Two conditions that typically differ between urban environments and the surrounding landscape are increased temperature, and high patch isolation and habitat turnover rates. However, the extent and spatial scale at which these altered conditions shape biotic communities through selection and/or filtering on species traits are currently poorly understood. We sampled carabid beetles at 81 sites in Belgium using a hierarchically nested sampling design wherein three local-scale (200 x 200 m) urbanization levels were repeatedly sampled across three landscape-scale (3 x 3 km) urbanization levels. First, we showed that communities sampled in the most urbanized locations and landscapes displayed a distinct species composition at both local and landscape scale. Second, we related community means of species-specific thermal preferences and dispersal capacity (based on European distribution and wing morphology, respectively) to the urbanization gradients. We showed that urban communities consisted on average of species

with a preference for higher temperatures and with better dispersal capacities compared to rural communities. These shifts were caused by an increased number of species tolerating higher temperatures, a decreased richness of species with low thermal preference, and an almost complete depletion of species with very low dispersal capacity in the most urbanized localities. Effects of urbanization were most clearly detected at the local scale, although more subtle effects could also be found at the scale of entire landscapes. Our results demonstrate that urbanization may fundamentally and consistently alter species composition by exerting a strong filtering effect on species dispersal characteristics and favouring replacement by warm-dwelling species.

## INTRODUCTION

The increasing human population has an overwhelming impact on natural communities worldwide and has led to marked changes in species composition and a strong reduction in biodiversity (MEA, 2005). Globally, the increased conversion of (semi-)natural lands to urban environments, together with increased land-use change around growing urban environments, is recognized as one of the core factors responsible for these changes (Sala *et al.*, 2000, Grimm *et al.*, 2006). The area affected by urbanization is expected to increase even further and estimated to triple from 2000 until 2030 (Seto *et al.*, 2012).

The high human population density and intensive industrial and transport activities in urban areas (McDonnell *et al.*, 1997) result in profound changes in both environmental conditions and landscape structure (Parris, 2016). These altered environmental conditions of urban areas are expected to differentially affect species within the original communities by either favouring species that are well adapted to urban environments and/or disfavouring less adapted species (McKinney, 2008). Such a selection process may either cause species loss or

species replacement. It is likely to act on particular functional traits, which can be morphological or physiological attributes measured at the individual level (Violle *et al.*, 2007; Webb *et al.*, 2010), as well as aspects of the realized niche of the species (Bowler *et al.*, 2015). Urban communities are therefore expected to show community-wide shifts in average values of traits compared to communities outside urban areas (Croci *et al.*, 2008).

Exploring shifts in the average value of traits in a community could substantially improve our insight into species-disturbance relationships (McGill *et al.*, 2006). Compared to metrics based only on species composition, additional advantages of the trait-based approach are its general applicability to a wide range of systems because it is less taxon-dependent, and its functional interpretation of changes in community composition (Webb *et al.*, 2010). Demonstrating if particular traits are strongly affected by urbanization can deepen our understanding of the processes underlying the recently reported homogenization of urban communities (Knop, 2016).

Two key environmental drivers shaping urban environments are (i) increased temperature and (ii) changes in landscape structure and turnover rates of habitat patches (Parris, 2016). An increase in ambient temperature in urban environments mainly stems from the release of solar energy absorbed in built-up zones (Oke, 1982; Arnfield, 2003). Although this Urban Heat Island (UHI) effect has been shown to severely affect single species dynamics in urban environments (Chown & Duffy, 2015; Kaiser *et al.*, 2016), the extent to which it may alter the composition of entire communities has hardly been addressed (but see Clavero *et al.*, 2011; Menke *et al.*, 2011). Given that species differ in thermal preference, we predict for urban environments a shift towards species with preferences for higher temperatures. Second, suitable habitat patches in urban environments are typically isolated, small, and dynamic, resulting in high turnover rates of local habitat characteristics (Parris, 2016). Hence, habitat patches whose conditions become suitable for particular species are more likely to be

colonized by good rather than poor dispersers, in particular when isolated from other suitable patches (MacArthur & Wilson, 1967). This process may ultimately result in a strong decrease of low dispersing species, even at a more regional scale, in dynamic landscapes (Henle *et al.*, 2004; Hendrickx *et al.*, 2009, 2013). While such a decrease in low dispersive species due to agricultural intensification has been clearly demonstrated (Hendrickx *et al.*, 2009), information on selection against poor dispersers in urban landscapes remains scant (but see Concepción *et al.*, 2015).

A prerequisite for clearly assessing community trait responses along environmental gradients is the accurate assessment of trait values for each species in the community. Carabid beetles are one of the most diverse groups of beetles for which relevant trait data are available to address these questions (Koivula, 2011; Kotze *et al.*, 2011). Due to their high diversity, community responses are less biased towards single species dynamics. Because species-specific distributions of all west European species are well documented, it is possible to accurately reconstruct their thermal preference based on distribution maps. According to Bowler *et al.* (2015), species thermal preference is a key parameter in explaining population trends of carabid beetles, confirming their role as model organisms to assess the impact of climatic change. Also, long-distance dispersal capacity varies considerably between individual species and is largely determined by their possession of functional wings and flight muscles (Desender, 1989; den Boer, 1990; Kotze & O'Hara, 2003; Zalewski & Ulrich, 2006; Hendrickx *et al.*, 2009; Kotze *et al.* 2011). Although carabids may cross substantial distances by walking, species with reduced wings or lacking functional flight musculature are unable to disperse over longer distances, in particular if this requires the crossing of unsuitable matrix (reviewed in Kotze *et al.*, 2011). By contrast, species with fully developed wings may readily cross several hundreds to thousands of meters of unsuitable habitats by flight (Chapman *et al.*, 2005). Many species are dimorphic, with individuals possessing either reduced or fully

developed wings, a trait that evolved to counteract fluctuations in local population sizes within heterogeneous landscapes (Hendrickx *et al.*, 2013). As winged individuals of these species are able to colonize vacant habitat patches, they are generally considered to be good dispersers unless the frequency of winged individuals is very low (Hendrickx *et al.*, 2009; 2013).

Urbanization gradients are indirect and complex since they include different types of disturbance at different spatial scales (McDonnell *et al.*, 1997; Parris, 2016). The extent to which local populations, communities and ecosystems react to environmental change may critically depend on the interaction between local and landscape responses (Urban *et al.*, 2011). For instance, studies across a wide range of organisms demonstrated that adverse effects of land use modification are not necessarily confined to the local scale but can be more severe at larger spatial scales (Hendrickx *et al.*, 2007; Vergnes *et al.*, 2014). Concerning urban environments, Shochat *et al.* (2006; 2010) proposed that the patterns of community changes associated with urbanization gradients could result from several mechanisms, at both local (e.g. changes in patch quality and stability) and landscape (e.g. the alteration of the habitat structure and connectivity) scales. As suggested in Turrini & Knop (2015), interactions between local and landscape levels of analysis should also be taken into account since not only local urbanization, but also urbanization at the landscape level may affect community composition. Since spatial heterogeneity plays a key role in ecological and evolutionary responses to environmental change, generalizing the effects of urbanization calls for a hierarchical approach, which takes into consideration the nested nature of ecological systems by simultaneously addressing different spatial scales (McDonnell & Hahs, 2008).

We here take advantage of a highly replicated and nested design wherein a local urbanization gradient was repeatedly sampled within landscapes that also differed in the extent of urbanization. Based on this hierarchical design, we investigate at both the local and landscape

scale (i) to what extent urban areas are characterised by a consistent shift in species community composition; (ii) whether these shifts are driven by selection of species based on their thermal preference and dispersal capacity, and (iii) whether this selection process encompasses a mere filtering process that depletes maladaptive species from urban environments or additionally favours species with traits that make them pre-adapted to urbanization.

## MATERIALS AND METHODS

### *Study area and sampling design*

The study area is located in Belgium, which is one of the most strongly urbanized countries in northwest Europe with an average human population density of more than 300 inhabitants/km<sup>2</sup> (Dumortier *et al.*, 2007). Sampling was conducted in a polygon of approximately 5000 km<sup>2</sup>, encompassing the city centres of Brussels, Antwerp and Ghent (Fig. 1). This region is densely populated, and the landscape consists of urban areas embedded within an agricultural or semi-natural matrix.

Given our interest in testing the effect of spatial scale, we applied a hierarchically nested sampling design wherein three local-scale levels of urbanization were repeatedly sampled across three landscape-scale levels of urbanization. As a proxy for the amount of urbanization, we used the % built-up area since this information was readily available from digital maps. Hence, only the area covered by buildings was taken into account for (sub)plot selection while roads, pavements, parking places, etc.... were excluded. As a result, even a built-up area of 5% was retained already quite substantial and a built-up area higher than 10% refers to highly urbanised areas. At the landscape scale, we sampled nine plots (3 x 3 km)

with low, nine plots with intermediate, and nine plots with a high built-up area (i.e. 0-3%, 5-10%, >15% built-up area, respectively). Within each plot, the effect of local-scale urbanization was investigated by sampling three 200 x 200 m subplots, which were selected based on exactly the same built-up ratio levels. This resulted in a total of 81 subplots (Fig. 1).

Within each subplot, carabid beetles were captured using two pitfall traps (25-50 m apart), which were consistently placed in grassy-herbaceous vegetation (e.g. road verges, park grasslands and semi-natural grasslands), in an area of at least 100 m<sup>2</sup> around the pitfall, to reduce confounding effects of differences in habitat type between plots with varying levels of urbanization. Traps were emptied every two weeks for a total of six sampling sessions between April and June 2013. Within each subplot, carabid beetles were captured using two pitfall traps (25-50 m apart), resulting in 18 samples per local/regional urbanization level combination, which were consistently placed in grassy-herbaceous vegetation (e.g. road verges, park grasslands and semi-natural grasslands) that covered an area of at least 100 m<sup>2</sup> around the pitfall, to reduce confounding effects of differences in habitat type between plots with varying levels of urbanization. Traps were emptied every two weeks for a total of six sampling sessions between April and June 2013. This sampling period encompasses the activity period of the majority of carabid beetles in Western Europe (Turin, 2000). That few additional species would have been captured by extending our sampling period was verified by a species accumulation curve, which revealed that only few additional species were captured after the fourth sampling session (Fig. S1). The complete sampling campaign resulted in a total of 972 processed samples (2 traps/site x 81 sites \* 6 sampling sessions).

#### *Community composition and species richness*

Collected samples were sorted and all carabid specimens were counted and identified to species level using the identification keys of Boeken *et al.* (2002) and Luff (2007).

Nomenclature of the species is according to Turin (2000). For each subplot, species composition and species richness were obtained after pooling specimens from both pitfalls and from the different sampling dates.

#### *Community thermal preference*

To test if urbanization alters community composition by selecting species with preferences for higher temperatures, we first estimated the optimal thermal preference for all captured species following Bowler *et al.* (2015). We overlaid the distribution map of each species in Europe (Turin, 2000) with the E-obs gridded climatic data layer of average annual temperature from 1961 to 1990 (Haylock *et al.*, 2008) projected onto a 25 km equal area grid. The intersection of the temperature raster and the distribution map was then used to calculate the mean temperature across the range (mean temperature of the occupied cells), maximum temperature (grid cell with the warmest average temperature value) and minimum temperature (grid cell with the coolest average temperature value) over the distributional range by means of the Zonal Statistic plugin in Quantum Gis Desktop v 2.1.1 (Quantum Gis Development Team, 2015).

For each subplot we calculated the Community Temperature Index by averaging the mean (CTI-mean), maximum (CTI-max) and minimum (CTI-min) temperatures of the species distribution across the community (Table S1). As species abundance from pitfall data is generally strongly biased by species activities, we opted for calculating the average across species rather than weighted by species abundance.

To test if urbanization results in a decrease of species with low thermal preference and/or an increase of species with high thermal preference, species were assigned to one of three equally sized classes of thermal preference, i.e. species preferring lower temperatures (low-T° species), species preferring average temperatures (medium-T° species) and species preferring

higher temperatures (high-T° species). This classification was applied for CTI-mean, CTI-max and CTI-min (Fig. S2). Thresholds were chosen in order to have a balanced number of species in the three classes.

#### *Community dispersal capacity*

Each species was assigned to one of four dispersal classes according to criteria described in Hendrickx *et al.* (2009), based on the extent of wing development, flight muscles and flight observations reported in literature: (Disp-1) species lacking flight capacity and brachypterous species as well as dimorphic and macropterous species with insufficiently developed wings or absence of functional flight musculature; (Disp-2) wing-dimorphic and polymorphic species for which a minority (<10%) of the investigated individuals exhibit functional wings and/or functional flight musculature; (Disp-3) dimorphic and polymorphic species for which flight records based on visual observations and window trap captures have been reported; (Disp-4) constantly macropterous species with functional flight musculature and for which flight records are frequently reported (Table S1).

Average dispersal capacity of the community was obtained by averaging the dispersal class values across species for each sample. In line with the calculation of the CTI values, average dispersal capacity was not weighted by species abundance to avoid potential biases due to species activities.

#### *Statistical analyses*

We first visually inspected whether species composition differs among the three urbanization levels at landscape (plot) and local (subplot) scale by means of a non-metric multidimensional scaling (NMDS) using the Sørensen dissimilarity index, which ordinated the samples along three dimensions. We tested whether the observed differences in species

composition were significantly different from a random distribution across plot and subplot urbanization levels with a Permutational Multivariate Analysis of Variance (PERMANOVA) (Anderson, 2001). Statistical significance was tested via 9999 random permutations with the ID of each plot as stratum. Both analyses were conducted with the *vegan* package (Oksanen *et al.*, 2015) in R version 3.2.3 (R Development Core Team, 2015).

The effect of urbanization level at both the local (subplot) and landscape (plot) scale and their interaction on the (i) species richness, (ii) community-averaged thermal preference (CTI-mean, CTI-max and CTI-min), and (iii) community-averaged dispersal capacity was tested by means of general(ized) linear mixed models (GLMMs) (Hothorn *et al.*, 2008) performed with PROC MIXED and PROC GLIMMIX in SAS 9.4. Levels of urbanization (low, intermediate, high) at the subplot (U\_Splot) and plot (U\_Plot) scale and their interaction were used as fixed factors. In order to account for the spatial dependency of subplots within the same plot, a plot identifier (PlotID) was incorporated as a random factor, nested within U\_Plot. For species richness we assumed a Poisson error distribution, while for community-averaged thermal preference and dispersal capacity we assumed a normal error distribution. Potential deviations from the model assumptions were checked by visually inspecting the distribution of the residuals in the normal model and by assessing the degree of overdispersion in the Poisson model.

We further investigated if shifts in average community traits in response to urbanisation were the result of either species replacement or due to a decrease of species with particular trait values (i.e. representing nested subsets of trait values of the less urbanized communities). To test this, species were categorized according to their trait value (either temperature or dispersal capacity) and the increase or decrease in species richness in each category was then tested by means of the same Poisson model that was used to test for differences in species richness in response to urbanisation as described above. Compared to a standard nestedness

analysis (cfr. Lomolino, 1996), this approach explicitly test if species with particular trait values are over- or underrepresented in the urban communities and allows to account for the hierarchical sampling.

Species traits can covary significantly among species, resulting in correlated responses of community trait values along environmental gradients (Ribera *et al.*, 2001; Kotze & O'Hara, 2003; van Noordwijk *et al.*, 2015). To verify this, we tested by means of a one-way ANOVA whether species thermal preferences were significantly different between species assigned to the different dispersal classes.

## RESULTS

### *Community composition*

NMDS produced a three-dimensional outcome with final stress of 0.21, indicating a good representation of the variance of communities along the three dimensions. Visual inspection of the ordination depicts a clear difference in species composition in response to urbanization, in particular at the subplot scale (Fig. 2). This pattern was further confirmed by the PERMANOVA analysis, which revealed significant differences in species composition at both the plot and subplot scale (Table 1), indicating that communities from urban sites are distinct from those of less urbanized sites. The effect of urbanization levels at plot and subplot scale on species composition appeared to be additive as no significant interaction between these two factors was observed. The combined percentage of variance explained by these two factors was 13%.

### *Species richness*

Species richness showed significant differences among urbanization levels at the subplot scale ( $F_{2,28} = 7.07, P = 0.002$ ), but not at plot level ( $F_{2,28} = 1.96, P = 0.15$ ), with the averages varying from 17.93 species in low, 18.37 species in intermediate and 14.77 species in highly urbanized subplots. Significant differences were observed between low and highly urbanized subplots as well as between intermediate and highly urbanized subplots (Tukey's post-hoc,  $P < 0.007$ ). No significant differences were observed between the low and intermediate urbanized subplots (Fig. 3). The interaction between urbanization levels at plot and subplot scale was not significant ( $F_{4,28} = 0.90, P = 0.47$ ).

### *Community thermal preference*

Community-averaged thermal preference differed significantly among urbanization levels at the subplot scale, when based on CTI-mean as well as CTI-max, but not for CTI-min (Table 2). Post-hoc tests revealed that community-averaged thermal preference in low urbanized subplots is significantly lower compared to those sampled at intermediate and highly urbanized subplots for CTI-mean, with values ranging from 8.25 °C to 8.56 °C on average, and CTI-max, with values ranging from 17.10 °C to 17.46 °C on average, but not for CTI-min (Tukey's post-hoc,  $P < 0.0034$  and  $P < 0.003$  when based on average and maximum thermal preference, respectively) (Fig. 4). For CTI-max, urbanization at both spatial scales interacts significantly, which is primarily due to the much lower community-averaged thermal preference in low urbanized subplots located in low urbanized plots (Tukey's post-hoc,  $P < 0.03$ ).

To investigate these shifts in community temperature indices in more detail, we tested if the number of species with high, intermediate and low thermal preferences increased or decreased in response to urbanization. For species with a low thermal preference, we found a

significant decline in the number of species in the subplots with the highest percentage of built-up area, irrespective if species were classified based on the mean (ranging from 7.44 in low urbanized subplots to 4.74 in highly urbanized subplots on average) maximum (ranging from 6.22 in low urbanized subplots to 3.56 in highly urbanized subplots on average) or minimum (ranging from 11.04 in low urbanized subplots to 8.78 in highly urbanized subplots on average) temperature across their distribution (Tukey's post-hoc,  $P < 0.029$ ) (Table 3, Fig. S3). When species were classified according to their maximum thermal preference, a significant decline in low thermal preference species in response to urbanization is also present at plot scale (ranging from 6 in low urbanized plots to 3.89 in highly urbanized plots on average) (Table 3, Fig. S3). For species with an intermediate thermal preference, a significant decline in species number in response to urbanization is only observed when species were classified according to their maximum thermal preference (ranging from 6.96 in low urbanized subplots to 4.93 in highly urbanized subplots on average). Finally, we observed a significant increase in species with a high thermal preference in the highly urbanized subplots compared to intermediate and low urbanized subplots (ranging from 4.89 in low urbanized subplots to 6.30 in highly urbanized subplots on average) (Tukey's post-hoc,  $P < 0.015$ ) (Table 3, Fig. S3). This effect was only observed when species were classified according to their maximum thermal preference.

#### *Community dispersal capacity*

Community-averaged dispersal capacity significantly differed in response to urbanization at subplot, but not at plot scale, and no significant interaction in degree of urbanization at both spatial scales was observed (Table 4). Differences in community-averaged dispersal capacity at the subplot scale are mainly due to a significantly higher dispersal capacity of communities, increasing from an average value of 2.55 in low urbanized subplots to an average value of 2.86 in highly urbanized subplots (Tukey post-hoc,  $P < 0.005$ ) (Fig. 5).

The number of species with the lowest dispersal capacity (Disp-1 and Disp-2) declined significantly in the most urbanized compared to the least urbanized subplots (Table 4) (Tukey post-hoc,  $P < 0.020$  and  $P < 0.023$  for Disp-1 and Disp-2 respectively). In the most urbanized subplots, there was an almost complete depletion of species lacking dispersal capacity (Disp-1), since their average number dropped from 2.33 in low urbanized subplots to 0.74 in high urbanized subplots (Table 4, Fig. S4). Also at the plot scale, the number of species belonging to this dispersal class decreased significantly in the most urbanized compared to the least urbanized plots, dropping from an average value of 2.22 to 0.85 (Tukey post-hoc,  $P = 0.007$ ) (Table 4, Fig. S4).

Thermal preference did not differ among species belonging to different dispersal classes (ANOVA:  $F_{3,124} = 0.856$ ,  $P = 0.47$ ), which shows an absence of covariation between the two traits.

## DISCUSSION

Our results first revealed that urban communities are clearly distinct from those sampled in less urbanized settings, especially at the local scale, which confirms earlier findings based on single gradients (Sadler *et al.*, 2006; Gaublomme *et al.*, 2008; Magura *et al.*, 2008). The highly replicated design used here allowed us to demonstrate that communities sampled at urbanized sites are not only distinct from those sampled at less-urbanised sites, but also that this shift is consistent along the replicated gradient. This indicates a repeatable response to urbanization. Analysis of species richness revealed that these subplots are also less species rich, which suggests that this shift is at least partly determined by a species filtering process, such that only a limited set of species — with particular trait combinations — can survive in the most urbanized settings (Niemelä & Kotze, 2009). The consistent selection of the same

species is also expected to strongly contribute to the recently reported homogenizing effect of urbanization (Knop, 2016).

To further scrutinize if urbanization consistently favours species that share particular traits, we tested if urban communities are shifted towards species that prefer higher temperatures and possess higher dispersal capacities. We showed a clear shift towards warmer-dwelling species in urban subplots. This pattern was much more pronounced when considering the maximum compared to the minimum thermal preferences and suggests that urban environments favour species able to tolerate high temperature extremes. A similar shift towards warm-dwelling species in urban areas was found by Clavero *et al.* (2011) and Menke *et al.* (2011) for ants and birds respectively. However, as land-use type differed profoundly between urban and non-urban sites in these studies (i.e. urban areas versus woodland, respectively), it remained less clear in these former studies to what extent their observed effects were caused by the higher temperatures in urban sites *per se* (cf. UHI-effect) or due to in thermal preference of species preferring different habitat types. Since we sampled the same habitat type (i.e. grasslands) in high versus low urbanized settings, our data strongly support the idea that the UHI-effect may alter community composition by shifting species composition towards thermophilous species. Moreover, UHI-effect seems also to select for species with a wider thermal niche, i.e. tolerating a wider range of temperature, since the CTI-max increased but not the CTI-min. Interestingly, this effect appears not only to be due to negative selection against cold-dwelling species, but also due to an increase in high temperature tolerant species, as shown by the significant absolute increase in species preferring higher temperatures in the most urbanized subplots. This shows that urbanization does not only filter cold-dwelling species, but that this species loss is at least partly compensated by positive selection of warm-dwelling species. This urbanization-driven replacement of species mirrors the effects of climatic change, whose impacts have been

reported for many taxonomic groups (Parmesan & Yohe, 2003; Hickling *et al.*, 2006; Chen *et al.*, 2011).

Second, we predicted that the highly dynamic nature and isolation of suitable habitat patches in urban settings would select against species with low dispersal capacity. We found a highly significant increase in the community-averaged dispersal capacity for the highly urbanized subplots. A more in-depth analysis of the change in species richness within each dispersal class revealed that this pattern was primarily driven by a significant decrease in the absolute number of low-dispersal species. As these species are less likely to colonize vacant patches in the landscape, they are generally found in more stable, late-successional habitats (den Boer, 1970; Roff, 1994). Hence, the observed decline in low-dispersal species is in strong accordance with the dynamic nature of urban environments, where human activities result in high turnover rates of suitable habitat patches (Parris 2016). This dynamic environment selects against species that cannot easily disperse to spatially disconnected favourable sites (Ribera *et al.*, 2001; Sadler *et al.*, 2006). The increase in patch extinction rates in urbanized habitats may additionally be caused, or even strengthened, by isolation of suitable patches. However, as disturbance and fragmentation are strongly correlated and often act synergistically along urbanization gradients, both resulting in similar demographic consequences, it is difficult to distinguish between the two factors.

An important challenge in the interpretation of effects of urbanization on traits might be the covariation with other species traits (Bowler *et al.*, 2015). Also for ground beetles, traits can be highly correlated (Ribera *et al.*, 2001; Kotze & O'Hara, 2003; van Noordwijk *et al.*, 2015). Since differences in thermal preference were not statistically different between the dispersal classes, we conclude that urban habitats select independently against both species preferring low temperatures and species with low dispersal capacity.

Our results emphasize how the trait-based approach can help in unravelling apparently contradictory patterns of biodiversity in urban areas. Indeed, we disentangled the additive effect of two mechanisms, which may act with varying intensities depending on the considered trait. When considering dispersal capacity, species loss represents the dominant mechanism, since non-adapted species are filtered out, that is also demonstrated by a reduction in species richness. On the other hand, species replacement also plays a role, as warmer-dwelling species, which may be disadvantaged in rural areas, are favoured in urban environment due to the UHI-effect.

Changes in the carabid assemblages and their community traits were most clearly detected at the local scale, although changes in species composition and the decline of low dispersive species were also present at the landscape scale. Furthermore, the decrease in thermal community preference (based on CTI-max) in response to decreasing local urbanization levels was significantly stronger in the least urbanized landscapes. Translating these observations as stronger local versus landscape effects of urbanization should be interpreted with caution. Although an equal number of sites were sampled to investigate landscape versus local urbanization effects, our nested sampling design could potentially lead to higher statistical power to detect local versus landscape effects. This is because the effect of urbanization at subplot (local) level could be tested within each landscape and therefore accounts for the potential heterogeneity among landscapes. Based on the standard errors of the random plot effect variance, random variation in community traits between landscapes was generally not larger than zero, which indicates an only marginal statistical dependence of subplots within a landscape. Thus, urbanization likely exerted a stronger effect at the local compared to the landscape level, albeit more subtle changes were clearly present at the scale of entire landscapes. These stronger local effects could be partly due to the “organism-scaled” environmental perception, since poor mobile species with a narrow thermal niche are

potentially more affected by environmental changes occurring at a local scale than at a landscape scale (Concepción *et al.*, 2015). Local rises in average temperature could ultimately lead to an increase in temperature at the level of entire landscapes if the percentage of non-urbanized area becomes increasingly small (Parris, 2016). In line with this, the decrease in community temperature preference among subplots was significantly stronger in the least urbanized landscapes.

Overall, the results show that urbanization has large-scale negative impact on community composition by selecting on particular trait combinations. Most carabids are predators that can exert a significant top-down control on invertebrate communities (Kotze *et al.*, 2011). Changes in their trait values may have strong repercussions on lower trophic levels, potentially impacting the resilience of urban ecosystems to disturbance (Chapin *et al.*, 2000). The development and implementation of measures targeted at preserving the functionality of biotic communities in urban settings could help to preserve the ecosystem goods and services.

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## Supplementary Information

Table S1: List of the collected species, with relative dispersal class, average, maximum and minimum species thermal preference.

Figure S1: Accumulation curve depicting the contribution of each sampling session to the total richness of area.

Figure S2: Histograms of the species thermal preference values of all species in the dataset when based on the mean, maximum and minimum temperature across their range.

Figure S3: Boxplots depicting the difference in richness of species with low, intermediate or high thermal preference in response to urbanization at plot and subplot level.

Figure S4: Boxplots depicting the number of species in each dispersal class in response to the three urbanization categories at plot and subplot levels.

Table 1. Results of the test for differences in species composition between urbanization at the landscape (plot) and local (subplot) level as inferred from PERMANOVA analysis (SS = Sum of Squares, MS = Mean Squares). Significant values are highlighted in bold.

	SS	MS	F	R <sup>2</sup>	P
U_Plot	0.8746	0.43732	1.44110	0.03491	<b>0.0015</b>
U_Splot	1.4472	0.72362	2.38454	0.05776	<b>0.0001</b>
U_Plot:U_Splot	0.8836	0.22090	0.72793	0.03527	0.9
Residuals	21.8494	0.30346		0.87206	

Table 2. Results of the test for the response in the community thermal preference (CTI) towards urbanization at plot (U\_Plot) and subplot (U\_Splot) level when based on the mean (CTI-mean), maximum (CTI-max) and minimum (CTI-min) temperature across the range of the species. Significant values are highlighted in bold.

<b>Fixed effects</b>	<b>CTI-mean</b>		<b>CTI-max</b>		<b>CTI-min</b>		
	<i>Factor</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
U_Plot	$F_{2,28} = 1.53$	0.24	$F_{2,28} = 0.96$	0.4	$F_{2,28} = 0.96$	0.4	
U_Splot	$F_{2,28} = 12.72$	<b>&lt;0.0001</b>	$F_{2,28} = 13.91$	<b>&lt;0.0001</b>	$F_{2,28} = 2.58$	0.09	
U_Plot:U_Splot	$F_{2,28} = 2.44$	0.06	$F_{2,28} = 3.03$	<b>0.03</b>	$F_{2,28} = 0.86$	0.49	
<b>Random effects</b>							
	<i>Factor</i>	<i>Estimate</i>	<i>SE</i>	<i>Estimate</i>	<i>SE</i>	<i>Estimate</i>	<i>SE</i>
PlotID	0.0144	0.009		0.009774	0.010	0.01593	0.024

Table 3. Results of the test for the response in the number of species preferring low, intermediate or high thermal preferences in response to urbanization at plot (U\_Plot) and subplot (U\_Splot) level. Classification of species into low, intermediate or high thermal preference species was based on the mean (MEAN), maximum (MAX) and minimum (MIN) temperature across their range. Significant values are highlighted in bold.

Factor	MEAN		MAX		MIN	
	F	P	F	P	F	P
<b>Species preferring low temperatures</b>						
<b>Fixed effects</b>						
U_Plot	$F_{2,28} = 3.09$	0.055	$F_{2,28} = 3.31$	<b>0.045</b>	$F_{2,28} = 2.20$	0.12
U_Splot	$F_{2,28} = 7.69$	<b>0.001</b>	$F_{2,28} = 9.48$	<b>0.0003</b>	$F_{2,28} = 4.66$	<b>0.014</b>
U_Plot:U_Splot	$F_{2,28} = 0.13$	0.97	$F_{2,28} = 0.70$	0.60	$F_{2,28} = 0.47$	0.76
<b>Random effects</b>	<i>Estimate</i> <i>SE</i>		<i>Estimate</i> <i>SE</i>		<i>Estimate</i> <i>SE</i>	
PlotID	0.075	0.04	0.07	0.04	0.057	0.027
<b>Species preferring medium temperatures</b>						
<b>Fixed effects</b>						
U_Plot	$F_{2,28} = 0.61$	0.25	$F_{2,28} = 0.91$	0.41	$F_{2,28} = 0.88$	0.42
U_Splot	$F_{2,28} = 2.01$	0.14	$F_{2,28} = 4.68$	<b>0.014</b>	$F_{2,28} = 1.88$	0.16
U_Plot:U_Splot	$F_{2,28} = 1.41$	0.55	$F_{2,28} = 0.20$	0.94	$F_{2,28} = 1.09$	0.37
<b>Random effects</b>	<i>Estimate</i> <i>SE</i>		<i>Estimate</i> <i>SE</i>		<i>Estimate</i> <i>SE</i>	
PlotID	0.035	0.026	0.01	0.02	0.02	0.02
<b>Species preferring high temperatures</b>						

<b>Fixed effects</b>							
U_Plot	$F_{2,28} = 0.48$	0.62	$F_{2,28} = 0.11$	0.90	$F_{2,28} = 0.98$	0.38	
U_Splot	$F_{2,28} = 2.80$	0.07	$F_{2,28} = 4.39$	<b>0.018</b>	$F_{2,28} = 0.07$	0.93	
U_Plot:U_Splot	$F_{2,28} = 1.67$	0.17	$F_{2,28} = 2.52$	0.053	$F_{2,28} = 0.74$	0.57	
<b>Random effects</b>		<i>Estimate</i>	<i>SE</i>	<i>Estimate</i>	<i>SE</i>	<i>Estimate</i>	<i>SE</i>
PlotID	0.009	0.023	0.03	0.03	0.19	0.24	

Table 4. Results of the test for differences in community-averaged dispersal capacity and number of species in each dispersal class in response to urbanization at the plot (U\_Plot) and subplot (U\_Splot) level. Significant values are highlighted in bold.

<b>Fixed effects</b>	<b>Community-averaged dispersal capacity</b>	Disp-1		Disp-2		Disp-3		Disp-4	
		<i>Factor</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>
U_Plot	$F_{2,48} = 0.3$ 1.25	$F_{2,48} = 0.0$ 4.22	<b>2</b>	0.98	$F_{2,48} = 0.38$	0.48	0.	0.	$F_{2,48} = 0.$ 0.33
U_Splot	$F_{2,48} = \mathbf{0.000}$ 10.63	$F_{2,48} = \mathbf{0.0}$ <b>2</b>	<b>01</b>	$F_{2,48} = 0.01$	4.82	0.8	0.	$F_{2,48} = 0.$ 2.09	7 1
U_Plot:U_Splot	$F_{2,48} = 0.79$ 0.42	$F_{2,48} = 0.5$ 0.81	3	$F_{2,48} = 0.18$ 1.62	0.18	0.18	1	$F_{2,48} = 0.$ 0.62	0. 7
Random									

effects						
Factor	Estimate SE	Estimate SE	Estimate SE	Estimate SE	S E	S E
PlotID	0.0504 0.05	0.1295 2	0.1 0.0833 48	0.0	0 . .	0 . .

### Figure captions

Figure 1: Map of the study area in the northern part of Belgium, showing the location of the 27 3 x 3 km plots. Colours refer to urbanization categories (green (medium grey in printed version) = low urbanization with < 3% of built-up area; yellow (light grey in printed version) = intermediate urbanization with 5-10% of built-up area; red (dark grey in printed version) = high urbanization with > 15% of built-up area). The plots are subdivided in 200 x 200 m subplots and assigned the same colour codes as for the plots. Subplots characterized by urbanization values intermediate between these three classes are indicated in light green and orange. For each plot, three subplots belonging to the low, intermediate and high urbanization categories were selected as sampling sites (details illustrated in the frames).

Figure 2: Ordination of the sampled carabid communities according to the first three NMDS ordination axes. Samples are coloured according to urbanization categories at plot (a and b) and subplot (c and d) level (green (medium grey in printed version) = low urbanization; yellow (light grey in printed version) = intermediate urbanization; red (dark grey in printed version) = high urbanization). Ellipses represent standard deviations around the centroids of the three groups.

Figure 3: Distribution of species richness as a function of urbanization at plot and subplot level. Labels at the x-axis represent the degree of urbanization at plot level. Colours of the

boxplots refer to urbanization levels at the subplot level (green (medium grey in printed version) = low urbanization; yellow (light grey in printed version) = intermediate urbanization; red (dark grey in printed version) = high urbanization).

Figure 4: Distribution of: average community temperature indices (a = CTI-mean; b = CTI-max; c = CTI-min) as functions of urbanization at plot and subplot level. Labels at the x-axis represent the degree of urbanization at plot level. Colours of the boxplots refer to urbanization levels at the subplot level (green (medium grey in printed version) = low urbanization; yellow (light grey in printed version) = intermediate urbanization; red (dark grey in printed version) = high urbanization).

Figure 5: Distribution of community-averaged dispersal capacity as a function of urbanization at plot and subplot level. Labels at the x-axis represent the degree of urbanization at plot level. Colours of the boxplots refer to urbanization levels at the subplot level (green (medium grey in printed version) = low urbanization; yellow (light grey in printed version) = intermediate urbanization; red (dark grey in printed version) = high urbanization).



