Effects of urbanization on arthropods' biodiversity at various levels of biological organization (Project ID: NKFI K131459)
Final report

1. Background

The worldwide increase in anthropogenic activities is causing significant changes to the environment and is creating patchworks of modified land-cover types that exhibit considerably similar patterns throughout the world (Forman, 2008). A major component of this process is urbanization, which includes spatial expansion, as well as population growth in urban settlements. Today's 4.6 billion urban people will increase to 6.7 billion by 2050 (United Nations, 2022). Urbanization radically alters native environments and forms new, artificial habitats (Marzluff et al., 2001). From rural areas to urban centers the naturalness is generally decreasing, the number and density of human inhabitants increases, along with road density, the area covered by artificial surfaces, as well as air and soil pollution (Carreiro and Tripler, 2005). With urban development, habitats that support biodiversity becomes increasingly fragmented (Collins et al., 2000), and is also lost to managed areas (residential, commercial, and other regularly maintained green spaces), ruderal spaces (empty lots, abandoned farmland, and other cleared but not managed green spaces) and remnant patches of native habitats are invaded by non-native organisms (Deutschewitz et al., 2003; López-Bedoya et al., 2021; Ludányi et al., 2022). One of the main consequence of fragmentation is species loss. There are, however, many factors that can affect the rate and consistency of species loss vs. gain along the gradient, so empirical studies are crucial in measuring urban impacts (López-Bedoya et al., 2024; Magura et al., 2021a; McKinney, 2008).
The field of urban ecology, relatively recent but fast developing, shows some asymmetries and consequent knowledge gaps: there are many more studies on vertebrates than invertebrates (Gaston, 2010). Biodiversity is much higher in the latter group, and they have key roles in ecological functioning, which underlines the importance of studying invertebrates in urban areas (Niemelä et al., 2000). The majority of existing studies tackles changes in ecological structures (biodiversity, genetic diversity, turnover, density, etc.) and fewer studies focus on ecological functioning (see Inger et al., 2016; Swan et al., 2017). It is both of scientific and practical interest that these gaps are narrowed and inequalities lessened. A novel element in our project is the concurrent study of various levels of biological organization, from infra-individual (but with an ecological focus, i.e. the role of gut symbionts) to the supra-individual one.

2. Aims

Urbanization often has a detrimental effect on biodiversity and ecological functioning. On one hand, given the gross dependence of humankind on ecological processes and services provided also in cities, it is important to test and develop more sensitive methods that can provide early signals of ecological malfunctioning or damage. On the other hand, by importing and concentrating resources, urbanization has created a unique opportunity for humans to flourish. Do the urban conditions also provide evolutionary opportunities for other species, and if so, how do arthropods, the most successful group on Earth, react to these challenges and opportunities? Knowledge of these responses can help to design adaptive strategies for more diverse, healthy, and liveable cities for humans where biodiversity can also flourish. Therefore, our project covered the most important impacts of urbanization on arthropod diversity at various level of biological organization. For detailed analyses we organised three workpackages (WPs).

WP1 Impacts of urbanization at the individual level: fecundity, energy reserves, gut microbial symbionts and behaviour

(i) What is the effect of urbanization on the fecundity and energy reserves of arthropods?

(ii) What is the effect of urbanization on the diversity of microbial symbionts living in arthropod guts?

(iii) Do urban conditions select for specific behavioural attributes?

WP2 Effects of urbanization at the community level: functional traits and phylogenetic relatedness

(i) What an effect has the urbanization on community organization? Is there any difference in community assembly processes along urbanization gradients?

WP3 Influence of urbanization at the ecosystem level: on predation by natural enemies and decomposition as representative ecosystem services

To study the most important impacts of urbanization on arthropod diversity at various levels of biological organization, study sites were selected based on the intensity of urbanization (the extent of buildings, roads and asphalt-covered surfaces vs. those covered with natural vegetation) using aerial photographs. We classified non-urbanised sites where within a 1000-metre radius, the built-up area was 0%, while in the urbanized sites, the proportion of built-up surfaces was approximately 60%. Furthermore, urbanized sites were characterised by environmental changes associated with urbanization, expressed in higher soil and soil surface temperature, higher soil pH values, lower amount of decaying wood and higher concentration of calcium and zinc in the soil.

3. Results

3.1. WP1 Impacts of urbanization at the individual level: fecundity, energy reserves, gut microbial symbionts and behaviour

(i) What is the effect of urbanization on the fecundity and energy reserves of arthropods?

Under this topic we selected a forest-living ground beetle as model organism. Adults of our model organism (*Carabus convexus*) were collected from rural vs. urban populations in three consecutive breeding seasons. We found no significant differences in body length or body mass between the rural and urban beetles from the overwintered cohort in their first breeding season (Magura et al., 2021b). Pronotum volume corrected for body size (as a proxy for muscle mass) showed no significant differences between urban and rural individuals. The size of the tibia and femur of the front, mid, and hind legs corrected for body size (as a proxy for leg muscle mass) differed significantly between the sexes, males having significantly larger tibia and femur than females. Furthermore, urban males had significantly larger hind tibia (and marginally significantly larger hind femur) than rural ones. Larger tibia of urban males can be a successful adaptation to a larger home range, ensuring that males successfully find mating partners even in the low-density urban populations. Body condition, assessed by fat reserve scores, was similarly poor in both habitats, indicating that beetles were not able to accumulate substantial fat reserves in either habitat. Females with ripe eggs in their ovaries were first captured at the same time in both areas. The number of ripe eggs, however, was significantly higher in females of the low-density urban population than in those of the high-density rural population, indicating density-dependent fecundity (Magura et al., 2021b).

(ii) What is the effect of urbanization on the diversity of microbial symbionts living in arthropod guts?

The substantial role of microbial symbionts in arthropods on nutrition, immunity and fitness are increasingly recognised. To test whether urbanization has an impact on such bacterial symbionts, we studied adult *Carabus convexus* by next generation high-throughput sequencing of the bacterial 16S rRNA gene. This is an expensive procedure, so our sample size is necessarily limited. Processing gut samples of 31 rural (15 females, 16 males) vs. 17 urban (8 females, 9 males) adult beetles, we identified 1163 bacterial operational taxonomic units (OTUs), and 3839 bacterial amplicon sequence variants (ASVs; Magura et al., 2024a, 2024b, 2024c). Many of these represent undescribed entities. Based on bacterial OTUs, the composition of the *C. convexus* gut bacterial microbiome was significantly different between rural and urban individuals (Magura et al., 2024c), while it was not significantly different using ASVs (Magura et al., 2024b). The microbiome taxonomic diversity (evaluated by the Rényi diversity function and Hill numbers) was significantly higher in rural than urban adults, irrespective of the characteristics used (either OTUs or ASVs; Magura et al., 2024a, 2024b). Smaller differences were found in microbiome functional diversity, assessed by the Rao's quadratic entropy which was marginally significantly higher in urban than rural beetles (Magura et al., 2024c).

(iii) Do urban conditions select for specific behavioural attributes?

In the urbanized and non-urbanized sites we live-trapped more than 3000 adult arthropod individuals, on which we performed ca. 15000 behavioural tests. To evaluate these data, we developed a purpose-built activity-tracking software (Málik-Roffa et al., 2023). Analysing the exploratory and risk-taking behaviour of seven ground beetle species, we documented habitat-specific differences. Both sexes of urban adult *C. convexus* showed more risk-taking behaviour than rural females (153 tested beetles; Magura et al., 2021b). Furthermore, we demonstrated the existence of sex-specific differences. Rural males of *Calathus fuscipes* showed more risk-taking behaviour than rural females (51 tested beetles). Rural females of *Platyderus rufus*, and urban females of *C. convexus* were significantly more exploratory than their respective males (88 and 153 tested beetles, respectively). In contrast, rural males of both *Pseudoophonus rufipes* and *Pterostichus melas* were significantly more exploratory than females (37 and 69 tested beetles, respectively). In two other species, *Pt. niger* and *Pt. strenuus*, no sex-specific differences in exploratory and risk-taking behaviour were found (31 and 126 tested individuals, respectively).

Testing the exploratory and risk-taking behaviour of 223 rural and urban individuals of three forest-associated rove beetle species (*Abemus chloropterus*, *Ocypus nitens*, *Platydracus fulvipes*) we found a higher exploratory behaviour in males than females in *O. nitens*, but no urbanization-related differences (Magura et al., 2022).

Analysing the exploratory and risk-taking behaviour of two wolf spider species we detected both habitat-, sex-, and season-specific differences. Urban females of *Trochosa terricola* from autumn were significantly more exploratory than rural ones (215 tested individuals). *Trochosa terricola* females also showed seasonal differences: autumn-collected urban individuals were significantly more exploratory than those collected in spring. In spring, both rural and urban males of *Pardosa alacris* were significantly more exploratory than females (253 tested individuals).

The isopod *Armadillidium vulgare* (789 tested individuals) showed habitat- and season-specific differences in both the exploratory and risk-taking behaviour, and also sex-specific differences in exploratory behaviour. Rural isopods were significantly more exploratory, but less risk-taking than urban ones. Isopods sampled in summer were significantly more exploratory, but less risk-taking than individuals from spring or autumn. Furthermore, females were significantly more exploratory than males.

We tested an additional ~800 individuals of other arthropod species but these did not occur in sufficient numbers in all studied sites or in all studied seasons to allow the statistical analysis of their behaviour.

Overall, these tests demonstrated the widespread existence of personalities in arthropods. Urbanization seems to select for bolder, more exploratory individuals, but this leads to population-level differences only in species with lower dispersal power.

3.2. WP2 Effects of urbanization at the community level: functional traits and phylogenetic relatedness

(i) What an effect has the urbanization on community organization? Is there any difference in community assembly processes along urbanization gradients?

The urban heat island (UHI) effect represents one of the most consistent human-induced environmental change in urbanized areas. The UHI effect has a very considerable impact on community organization, as it causes community-wide shifts towards species with smaller body sizes in urban communities of ectotherms due to increased metabolic costs (Gardner et al., 2011; Magura and Lövei, 2021; Merckx et al., 2018). Using geographically distant species-level abundance data of ground beetles from spatially replicated, clearly defined, similarly vegetated rural and urban habitats, we highlighted that body-size shifts in urban communities are strongly trait-dependent. We detected no general trend towards a reduced community-level body size in urbanized forest fragments for either the total community or the non-specialist sub-assemblage, but the sub-assemblages of forest specialist species consistently displayed a shift towards smaller size in urban habitats with respect to the original, forest-inhabiting sub-assemblages (Lövei and Magura, 2022; Magura et al., 2020).

Dispersal among habitat patches is a key feature in community organization. However, not only the size, the spatial configuration, and the connectivity of habitat fragments determine the success of dispersal events, but also the permeability of the habitat patches. Evaluating the trait-based edge response of ground beetles in various forest edges, we showed that structural and environmental changes at edges sustained by repeated urbanization-related impacts significantly influences the permeability of urban habitat patches (Magura et al., 2019; Magura and Lövei, 2020a, 2020b, 2024).

Community assembly processes along urbanization gradients were further examined by analysing the published literature. A literature search on Web of Science for the period 1975-2021 yielded 107 publications. Of these, 11 studies fulfilled the selection criteria, (the study had to contain species-level abundance data of ground beetles from at least three spatially replicated, clearly defined, similarly vegetated rural and urban habitats), providing data on 207 ground beetle species. We identified the community assembly mechanism by calculating the functional-phylogenetic distances using the functional traits of body size, wing morphology, overwintering type, daily activity, diet, habitat affinity, and humidity preference. Distances between species based on functional traits (FDist) were calculated by Gower's distance metric, while phylogenetic (evolutionary) distance (PDist) was characterized by the distance between species based on the branch length to the common ancestor using Beutel et al.'s (2008) phylogenetic tree (Cadotte et al., 2013). Contrary to our hypothesis, in some urban habitats the co-occurring species were functionally and phylogenetically different from the null model, indicating that urban assemblages are not uniformly randomly structured. Based on this result, our next hypothesis to be tested is that the composition of the landscape matrix surrounding urban habitat fragments fundamentally determines the assembly processes of communities living in these habitat islands.

In an international co-operation, using a dataset encompassing six terrestrial faunal taxa (amphibians, bats, bees, birds, ground beetles and reptiles) across 379 cities on 6 continents, our results showed that urbanization produces taxon-specific changes in trait composition, with traits related to reproductive strategy showing the strongest response. Our findings suggested that urbanization results in four trait syndromes (mobile generalists, site specialists, central place foragers, and mobile specialists),with resources associated with reproduction and diet likely driving patterns in traits associated with mobility and body size (Hahs et al., 2023).

3.3. WP3 Influence of urbanization at the ecosystem level: on predation by natural enemies and decomposition as representative ecosystem services

(i) What is the effect of urbanization on the important ecosystem processes of predation pressure and decomposition?

These questions were studied by the sentinel approach. Testing predation pressure in rural and urban habitats, dummy caterpillars (made from green plasticine and glued to pieces of bark) were exposed to predators for 24h in each month (from April to October). Marks of chewing insects, birds and small mammals on the exposed dummy caterpillars were identified. Studying riparian forest habitats along a riverside urbanization gradient, we found a generally decreasing predation pressure from rural to urban habitats as predicted by the increasing disturbance hypothesis (higher predator abundances in rural than in urban habitats). The only predators that reacted differently to urbanization were ground active arthropods, where results did support the intermediate disturbance hypothesis (highest in the moderately disturbed suburban habitats). We did not find any evidence that communities exposed to extreme flood events were preadapted to the effects of urbanization (Eötvös et al., 2020). Contrarily, in flood-free lowland forest stands the overall predation pressure was significantly higher in urban than rural habitats. This trend, however, showed a marked seasonal pattern: no significant difference in spring (April and May), significantly higher in rural areas during summer (June, July and August) and marginally different in autumn (September and October).

To measure decomposition, at each site 20 (previously weighted and soaked to remove water soluble fraction) rooibos teabags were buried in the soil at 5 cm depth (Kotze and Setälä, 2022). Five tea bags per site were removed after 3, 6, 9 and 12 months. Decomposition rate was expressed as the percentage of missing dry mass. Decomposition rate was assessed in two consecutive years under quite different weather conditions. Precipitation in 2020 was average, while 2021 was a dry year. The decomposition rate was significantly higher in urban than rural habitats in both years. In 2020 (average precipitation) decomposition after 6 months was significantly higher in the urban than rural habitats. Later, however, the decomposition rate evened out. In the dry year of 2021, the decomposition rate was also significantly higher in urban than rural habitats, but the difference remained even after 9 months, and evened out only after 12 months.

4. Conclusions

4.1. WP1 Impacts of urbanization at the individual level: fecundity, energy reserves, gut microbial symbionts and behaviour

Contrary to our hypothesis, the number of ripe eggs produced by our model organism (*C. convexus*) was significantly higher in females of the low-density urban population than in those of the high-density rural population, indicating density-dependent fecundity. It seems that females invested more into reproduction and produced more eggs in urbanized habitats, possibly to compensate the higher mortality rate of eggs and larvae in urbanized habitats under more stressful environmental conditions.

Similarly, body length, body mass, and body condition were not significantly different between the rural and urban arthropods. Although urbanized habitats may have lower food availability (Gaston, 2010), or lower food quality (”junk food”, McKinney, 2002), urban arthropods were able to consume enough food to reach the body size and condition of their rural counterparts. Urban arthropods were probably able to do this by extending their home range to access as much food as possible.

As we hypothesised, the composition of the *C. convexus* gut bacterial microbiome was different between rural and urban individuals, and the microbiome taxonomic diversity was significantly higher in rural than urban-living adults. These results suggest that the soil bacterial assemblages (potential sources of the gut microbiome) were impoverished in urbanized habitats, significantly affecting the composition and diversity of the gut bacterial microbiome. This, however, did not seem to translate to differences in the functional diversity of the microbiome.

Our hypothesis that urban arthropods are more exploratory and risk-taking than their conspecifics living in non-urbanized habitats was only partially confirmed, as the majority of tested arthropod species showed no consistent urbanization-related differences. However, both sexes of urban adult *C. convexus* showed more risk-taking behaviour than rural females, and rural isopods were significantly more exploratory, but less risk-taking than urban ones. This discrepancy may result from individual responses and different sensitivity of species to urbanization, suggesting the importance of individualistic and functional approach in future urban studies.

4.2. WP2 Effects of urbanization at the community level: functional traits and phylogenetic relatedness

We assumed that urbanization-related environmental changes have considerable impact on community organization, therefore due to the unpredictable, random species flow from surrounding matrix communities in urbanized habitats are stochastically structured, co-occurring species are not different, either functionally or phylogenetically, from random assemblages. Urbanization indeed caused community-wide shifts towards species with traits adapted to urban conditions (e.g. flexible reproduction strategy, generalist diet, good dispersal ability, and small body size). However, the co-occurring species were functionally and phylogenetically different from the null model in several of the studied sites, indicating that urban assemblages are often not randomly structured. We argue that the composition of the landscape matrix surrounding urban habitat fragments fundamentally determines the assembly processes of communities living in these habitat islands.

4.3. WP3 Influence of urbanization at the ecosystem level: on predation by natural enemies and decomposition as representative ecosystem services

We found that the predation pressure was not always higher in non-urbanized than in urbanized habitats. The overall predation pressure decreased from rural to urban habitats in riparian forested habitats along a riverside urbanization gradient (Eötvös et al., 2020), while it was significantly higher in urban than in rural habitats in a flood-free lowland forest. This inconsistency highlights that the composition and configuration of the landscape matrix surrounding urban habitat patches may also have fundamental impact on ecosystem functions and services in the urban fragments.

The decomposition of organic materials by soil organisms was significantly faster in urban than rural habitats and this difference was intensified by drought. This result also suggests that ecosystem services are influenced by urbanization and that this effect may be intensified by extreme climatic events.

4.4. Recommendations to urban management

Based on our results, changes in environmental conditions and habitat characteristics accompanying urbanization have significant effect at all levels of biological organisation: the individual, community and ecosystem levels. As urbanization is advancing world-wide, it is essential to effectively mitigate the negative impacts of the pronounced changes in environmental and habitat characteristics caused by this process. Urban management that seeks to minimize the modification of habitat characteristics and tries to maintain natural processes has a chance to successfully conserve diverse communities, thus contributing to the maintenance of well-functioning biotic communities that would allow a better quality of urban living for humans (Magura et al., 2020).

5. References

Papers emerging from our project are marked with asterisk

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