Evolutionary changes in urban environments

How evolutionary mechanisms contribute to biodiversity in cities.

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Colophon

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Abstract

Urbanisation has dramatically increased over the last decades. More and more is known about the impact of urbanisation on local and global biodiversity. The majority of studies indicate that urbanisation leads to a reduction in biodiversity. However, beneficial effects of urbanisation on biodiversity often remain unclear. This report theoretically investigates the functioning of random and adaptive evolutionary mechanisms in relation to urbanisation based on literature study. It is also examined whether these mechanisms lead to speciation. This report shows that there are many examples in which random and adaptive evolutionary mechanisms influence organisms that occur in the city, in one case even speciation. Nevertheless, the decline in biodiversity is currently still higher than the increase. It is important that we limit the loss of biodiversity and ensure that the increase can continue. Based on this study is suggested that the urban environment form relatively new ecosystems which have the potential for species to occur and adapt. Small adjustments to our cities may ensure contribution to biodiversity, making it more suitable living environments.

Layman's summary

Urbanisation has dramatically increased over the last decades. In 40 years, the total land covered by cities has doubled and its population has more than doubled, from 1.5 billion people living in cities in 1975 to 3.5 billion in 2015. At the same time, urbanisation possibly also threatens future life. The majority of studies indicate that urbanisation leads to a reduction in biodiversity. However, beneficial effects of urbanisation on biodiversity often remain unclear.

This study investigates the impact of evolutionary mechanisms on urban species. Four evolutionary processes were subject during this literature study: genetic drift, gene flow, re-application and natural selection. Natural selection is the only adaptive mechanisms, which means that species adapt to their environment. The other processes are random, which means no adaptation occurs. The study shows that there are many examples in which random and adaptive evolutionary mechanisms influence organisms that occur in the city. In one case even a new species emerged.

In summary, evolution does occur because of urbanisation and there are species that benefit from urban environments. Nevertheless, the decline in biodiversity is higher than the increase. That is why it remains important to preserve and facilitate biodiversity in cities as much as possible and ensure that increase can continue. Based on this study is suggested that the urban environment is a relatively new ecosystem which has the potential for species to occur and adapt. Small adjustments to our cities may ensure contribution to biodiversity, making it more suitable living environments.

Introduction

Urbanisation has dramatically increased over the last decades. In 40 years, the total land covered by cities has doubled and its population has more than doubled, from 1.5 billion people living in cities in 1975 to 3.5 billion in 2015 [1–3]. In the meantime, the world passed a crucial milestone in 2007. For the first time in history, more people lived in cities than outside [4]. Future prospective estimate that by 2030 10% of the total land will be occupied by cities, with much of the remainder covered by man-made agriculture, stockbreeding or forestry [5]. In other words, we cannot deny that the urban environment has become a major part of everyday life.
At the same time, urbanisation possibly also threatens future life. Recent studies showed that urbanisation leads to a decrease in environmental health and therefore long-term potential implications on biodiversity [6–9] (BOX I). In addition, the vegetation that is made available by humans in cities is very limited. First of all, the available area for plants and animals in cities is extremely reduced, compared to rural areas. Over 80% of most central cities are covered with pavement and building, resulting in 20% or less vegetation area [10]. Secondly, this vegetation area is fragmentated which amplifies the decrease of biodiversity according to the theory of Island Biogeography[i] [11]. And lastly, the existing vegetation areas are highly simplified and therefore not always a suitable habitat for organisms [12]. The limited supply of biodiversity has also extensive effects on human health [13,14]. The quantity and quality of vegetation in urban areas is therefore a major problem.

These insights are a source of motivation for organisations within real estate to make the transition towards more green and sustainable building designs. After centuries of using mainly bricks and concrete, the use of natural building materials in addition to the reuse of unsustainable materials is becoming more prominent. Moreover, many architects and engineers aim to attract flora and fauna towards cities in order to restore the lost local biodiversity, for examples by placing bee hotels, bat boxes and green envelopes[ii] [15,16]. Others are willing to take a step future, biomimicry architects strive to integrate buildings into their local ecosystem and therefore harmonise human construction within nature [17]. Both methods contribute to biodiverse and sustainable building techniques. However, both approaches assume that there is a distinction between what is natural and what is built by humans. We have seen the major impact of urbanisation on our planet in the last decades. And yet, we act like 'actual' nature should be untouched by humans.
The following historical events might implicate that past human influence and ancient urbanisation were not considered unnatural. The first example is domestication, which dates back to the Pleistocene [18,19]. It is one of the best-known forms of cooperation between humans and another organisms. Domestication is a mutualistic relation in which animals or plants were kept and tamed at human homes. During the process, an increasing mutual dependence occurred between humans and domesticated animals. According to science, the oldest form of domestication is between humans and dogs and reaches back to around 14.000 BC [18]. This symbiosis probably arose in order to reinforce each other during hunting and indicates that the arrival and habits of humans made positive contributions to the pre-existence of dogs. Later, other animals were domesticated for alternative purposes as well, such as milk, wool, motion power, warfare, sport and prestige [20]. The origin of livestock production began with the domestication of sheep and later also goats, horses, cattle, chicken and other poultry. This symbiosis also benefited both parties. While animal received regularly food and protection from humans, humans benefited from easier access to the animal and its valuable meet, bones and skins without the need for hunting [19]. The maintenance of livestock increased widespread and large grazers were grouped and fenced for consumption purposes. One can argue that this form of human influence

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[i] The theory of Island Biogeography indicates a species-area relationship in which the number of species on an island depends on the size of that island and the distance to the mainland. Both an increase of size and decrease of distance result in a higher number of species. In urban areas, fragmented vegetation can be considered as islands of habitat.
[ii] Green envelopes concern both green facades and roofs.

contributed to the existence of several predator species such as wolves and foxes. However, there is no scientific evidence to support this thesis. But later as well, in the 14th century, human influences contributed to the existence of certain species. At this time, people had set up their first major settlements. This contributed to several plague pandemics that occurred at that time. The most famous one was caused by the bacteria *Yersinia pestis*. The plague was transmitted by fleas from rats that were infected with these bacteria. Since humans and rats lived together in high density, the bacteria were able to infect humans as well. Although this is not a memorable event in human history, it shows that the first human settlements were suitable environments for large rat populations and perhaps other organisms too.

Yet, modern urbanisation is happening on a greater scale and has a greater impact than is ever seen before in the history of human construction [21]. One could argue that the effects of modern urbanisation are therefore not comparable with that of ancient urbanisation. Nonetheless, several studies confirm the increase of local biodiversity in modern urbanisation. Ecological transects from rural to urban areas show that biodiversity decrease towards urban environments is not so strong as expected. In fact, there is an enrichment of diversity for plants and insects towards urban areas [22]. Research of Chytrý *et al.* showed that urban and industrial land use had a positive effect on the proportion of both archaeophytes (non-native plants that arrived before 1500 BC) and neophytes (non-native plants that arrived after that time). And also a meta-analysis of McKinney, in which 105 studies were investigated on the effects of urbanisation on species richness, showed that 65% of all plants studies, 30% of all invertebrate studies and 12% of all non-avian vertebrate studies indicate increasing species richness with moderate urbanisation [12].

This implies that certain organisms can establish in urban areas and that nature may adapt to these new ecosystems. If this is the case, this could be explained by evolutionary mechanisms underlying the introduction, adaptation or formation of species in urban environments. Which leads to the main question of this literature review:

What is the impact of evolutionary mechanisms on urban species?

This question will be answered based on the following sub-questions:

- What is the impact of random evolutionary mechanisms on urban species?
- What is the impact of adaptive evolutionary mechanisms on urban species?
- Do new species emerge in urban areas?

The report will focus on examples of species diversity of eukaryotic organisms. The first chapter will discuss the impact of random and adaptive mechanisms on urban species. Thereafter will be discussed if new species emerge in urban. And finally, an overview of all findings will be discussed in the discussion.

BOX I

Biodiversity is defined as the biological variety and variability among organisms and their environment; this includes diversity within species, between species and of ecosystems [80]. The three main types of biodiversity are ecological diversity, genetic diversity, and species diversity. In addition, diversity can be considered on different scales; within an ecosystem (Alpha diversity), between ecosystems (Beta diversity), or overall diversity within a large region (Gamma diversity). A rich biodiversity on all these levels is not only of importance for environmental health, but for human health as well. Both environmental and human health benefits from maintaining ecosystems and its services [81,82]. These include provisioning services such as food and water; regulating services such as flood and disease control; cultural services such as spiritual, recreational, and cultural benefits; and supporting services such as nutrient cycling that maintain the conditions for life on Earth.

Evolutionary mechanisms

Changes within populations, including urban areas, occur because of changes in allele frequencies[iii] as a result of evolution. There are four fundamental evolutionary mechanisms: mutations, genetic drift, gene flow and natural selection. Each mechanism can be characterised by its effects on fitness, adaptation, and the genetic diversity of the population. The four mechanisms can be divided into two groups: evolution by random processes and evolution by adaptation. In the following paragraphs multiple examples of urban species will be discussed and the corresponding evolutionary mechanisms.

Evolution by random processes

In evolution through random processes, selection does not occur. Therefore, genes do not necessarily have any advantage over other genes. Yet changes in the composition of genes in a population do occur. This can be caused by mechanisms such as mutations, genetic drift and gene flow [11].
Mutations are random changes in DNA sequences over generations and are therefore a major source of genetic variation within a population. Mutations can have negative, neutral or positive consequences for the fitness of organisms. In response to this, natural selection may react to this variety by selecting beneficial mutations which will increase in a population over time. Undoubtedly, mutations also occur in urban environments, yet examples of this will not be addressed specifically in this report. The reason for this is that eventual changes in the gene pool of urban population is only initiated by mutations, natural selection in particular ensures a visible result (see chapter *Evolution by adaptation – Natural selection*). [11]
The other two evolutionary mechanisms by random processes, genetic drift and gene flow, will be discussed and is explained below in more detail. In addition to these evolutionary mechanisms, another phenomenon can be noticed in urban environments. Some introduced species seem to be very well adapted to urbanisation. However, these cases are not a result of selection, but of the random process of re-application. Re-application and associated examples are further explained at the end of this chapter.

Genetic drift

Genetic drift concerns fluctuations of allele frequencies within a population which may cause the proportion of alleles to increase or decrease. The process happens by chance and therefore mainly neutral alleles are subject to it. Genetic drift occurs in any population of non-infinite size, but has the strongest effects in small populations. **The bottleneck effect** is an extreme example of genetic drift that happens when the population size is reduced. It is caused by events like natural disasters that leave a small and random assortment of survivors. **The founder effect** is another extreme example of genetic drift that occurs when a small group of individuals breaks off from the original population to establish a colony in a new location. Because this is a random event as well, the colony may not represent the diversity of the original population. In both the bottleneck and founder effect small populations are formed from a larger population. The bottleneck effect is mainly caused by disaster, while the founder effect is rather caused by colonisation. Because of their small size, these samples may experience a strong effect of genetic drift. [11,23,24]

The rise of globalisation contributes to genetic drift, especially the founder effect. The spread of human individuals and cultures began with the introduction of transportation, which allowed humans to travel longer distances [25]. The technological development of transportation caused this exchange to grow massively. Not only is the human gene pool scattered all over the world, other organisms were able to spread along with us. This was caused mainly due to trade of organic matter or attachment of organisms on transportation vehicles [26]. Transported organisms can vary from microbes (e.g. fungi,

[iii] An allele is a variant of a gene which codes for a hereditary trait. One gene is made up of two alleles.

bacteria and viruses), to plants, to small (e.g. arthropods, nematodes) and large animals (e.g. mammals, reptiles, amphibians and fish) [27]. However, not all introduced species will persist and reproduce successfully. This depends, among other things, on the availability of resources, the local climate and land size [28].

One species that very successfully spread across the globe is the house crow (*Corvus splendens*) (Figure 1). This Indian bird was initially introduced at the end of the 18th century in Malaysia as a pest control in coffee plantations, where it fed on caterpillars. However, the bird seemed very successful in urban areas. Between the 1960s and early in the 21st century, their numbers have increased from a few hundred to many hundreds of thousands. The bird is dispersed both intentionally (as pest control agent) and unconsciously (via human transport). The species appears to be able to make efficient use of human resources, as there are no known populations that exist independently of humans. Study showed that roosting behaviour of the house crow mainly takes place in areas enclosed by tall buildings and of greater human activity [29]. The latter may be an explanation for another study that showed that house crows prefer urban over rural landscapes, and business over park areas [30]. Great human activity leads to a positive association with high levels of food waste. Which enabled extensional growth of the house crow population. Nowadays, the house crow is spread over almost all tropical areas, such as the Indian Ocean rim, Arabian Peninsula, some Indian Ocean Islands, additional sites in southern Asia and, in addition, eastern and south-eastern Africa, Europe and the United States [31,32].

Figure 1 - The House Crow (Corvus splendens).

Not only house crows benefit from human activity. Research has shown that red foxes (*Vulpes vulpes*), gray foxes (*Urocyon cinereoargenteus*) and kit foxes (*Vulpes macrotis mutica*) in urban regions have higher biomasses compared to their species in suburban or rural areas (Figure 2) [33–36]. For kit foxes was also shown that urban individuals have better blood circulation (more red blood cells, hemoglobin and hematocrit), while suburban individuals have higher blood urea nitrogen and lower cholesterol [36]. Moreover, urban juveniles were growing up at a more rapid rate than suburban juveniles. These contrasts are results of differences in food availability of the two populations. Food was scare for non-urban foxes, while anthropogenic food sources were plentiful for urban foxes. Also, urban raccoon populations (*Procyon lotor*) benefit from constant food sources provided by humans. Density of (sub)urban populations of raccoons are greater than for rural sites during all seasons [37]. However, this is not only caused by food availability. Multiple factors are responsible for high-density raccoon populations in urban areas, including increased survival, higher annual recruitment, and increased site fidelity. Urban raccoons experience the fewest mortality sources, whereas rural raccoons experience the most. Disease was the greatest mortality factor at the urban site, while vehicle-related mortalities dominated at the suburban and rural sites.

Figure 2 - The Kit Fox (Vulpes macrotis mutica).

Thus, genetic drift occurs in cities. These examples show that globalisation in particular leads to the introduction of many new species, by example of the founder effect. Because areas worldwide are more connected with each other than ever before, species can disperse to areas they would otherwise never been able to reach. Presumably there are also cases where the bottleneck effect was applicable. This would have been in the situation where a natural area was replaced with a city and local species would remain to occur. Cases such as these were not found and discussed in this study.

Gene flow is the movement of genes from one population into another. It is an important mechanism for the creation and maintenance of genetic variation. Gene flow is facilitated by migration, which enables genetic exchange on a greater scale through populations, groups or individuals. If selection is not operating, gene flow will cause genetic frequencies of two different population to converge over time. So in general, gene flow tends to unify gene frequencies among populations. [11,24,38]

The rise of globalisation contributes to gene flow as well. The high intensity of human transport enables exchange of genes between populations of the same species even after introduction into a new area. Populations that would have been separated without globalisation, now continue to exchange genes. A clear example of the impact of globalisation on gene flow is the black widow spider (*Latrodectus Hesperus*) (Figure 3). A study by Miles *et al.* (2018) examined the genetic diversity of these spiders in various urban and non-urban areas [39]. Although the populations of spiders in each area were segregated, the research showed a strong connectivity pattern between urban populations. Not only was genetic diversity in urban populations higher than in non-urban populations, but genetic differentiation in urban populations was lower than in non-urban populations. The authors confirmed that many non-urban populations only found each other through intermediate urban populations. This indicates that the connectivity between urban areas is higher than between non-urban areas and thus a high level of gene flow between urban areas. Therefore, species differentiation does occur on a relatively low level in urban areas, while on a higher level in non-urban areas. Miles argues that exchange between populations occurs mainly through human transport. Beforehand, black widow spider were not able to spread across larger areas, while the arrival of transport within cities enables them to do so.

Figure 3 - The Black widow spider (Latrodectus Hesperus).

Not only globalisation, but urbanisation itself also supports gene flow. A study by Beninde (2018) showed that urban populations of the common wall lizard (*Podarcis muralis)* had numerous clusters of hybrid swarms (Figure 4) [40]. These swarms held vast genetic diversity and showed recent admixture with other hybrid swarms. It appears that the introduction of non-native lizards in cities is common. The unique structure of cities provides individuals to disperse into new areas and therefore enables hybridisation to occur. The study showed that one of the urban aspects that facilitate gene flow are railway tracks, while water bodies are strong barriers to gene flow.

Figure 4 - The common wall lizard (Podarcis muralis).

However, the same aspects could benefit another species. For example, the dispersal of false brome (*Brachypodium sylvaticum*) in urban areas is improved by water bodies, especially rivers [41]. For false brome, rivers form corridors for gene flow. These examples highlight the major role which humans, urbanisation and globalisation play in providing the distribution of organisms in the cities.

On the other hand, urbanisation can also lead to low levels of gene flow. In this case, human construction form barriers that disable organisms to drift between areas. Mosquito populations in the London Underground system are a result of differentiation processes. Here, differentiation could happen because of the low levels of gene flow between this Underground mosquito, *Culex molestus*, and its close relative the common house mosquito (*Culex pipiens*) (Figure 5). Despite being closely related, there are several major differences between both groups. Not only is there a difference their occurrence, but also between the mating methods, host preference, egg production and life cycle. *C. pipiens* occurs above ground, they mate in large numbers, they have winter diapauses, their reproduction requires blood meals, and they feed on bird blood. Unlike *C. molestus,* which occurs underground, they do simple one-to-one mating, they do not have winter diapauses, their reproduction is not dependent on blood meals, and they feed on mammalian (particularly humans) blood. Besides these behavioural differences, a study of Byrne *et al.* (1999) showed genetic differentiation that support the division of these populations [42]. Genetic differentiation could occur here because the mosquito populations were physically separated, in which the Underground and its tunnel system acted as barriers.

Figure 5 - Mosquito in London Underground (Culex molestus).

The examples above showed that gene flow can occur on both high and low levels. However, it is not the case that gene flow is simply 'on' or 'off'. It can occur in varying degrees or occur on different scales. An example of varying levels of gene flow on different scales is given by another spider, the long-bodied cellar spider (*Pholcus phalangioides*) (Figure 6). This spider occurs regularly in human-made constructions. Urbanisation causes populations of the long-bodied cellar spider to spread and seclude at the same time. Research by Schäfer (2001) showed that spiders within the same building shared similar gene pools, but those gene pools differed significantly with gene pools of other buildings [43]. This can be explained by the ability of spiders to spread between different rooms and floors within a building. However, the distance between buildings forms a blockage for the spiders to travel. Even between adjacent constructions gene flow is minimal, resulting in isolated spider populations per building (at least for a few generations). The authors argue that the effect of genetic drift is present on larger scale. In which each building forms a separate island with its own population of spiders, similar to Darwin's finches on the Galápagos islands [44]. Schäfer shows that the gene pool of any population forms significant, but also unpredictable patterns of genetic differentiation. Thus, in this case gene flow does occur on relatively small scale, but not on a larger scale.

Figure 6 - The long-bodied cellar spider (Pholcus phalangioides).

In a similar way, urban gardens can form vegetative islands throughout the city. Almost every garden has a completely different palette of flora and fauna. First of all, this naturally affects the gene flow of plant species. Smith's research shows that urban gardens are dominated by non-native species [45]. This indicates that urban gardens provide a suitable habitat for non-native plant species and that there is gene flow with other vegetations. In addition, several studies show that urban gardens, despite their small size, play a vital role in supporting urban insect biodiversity [46–48]. Depending on the physiology of the species, the species can spread easily or with difficulty from garden to garden. Research by Beninde (2015) showed that patch areas and vegetative corridors have strong positive effects on biodiversity [49].

On the one hand, these types of islands can ensure that species such as the long-bodied cellar spider are isolated. However, the formation of these islands can also be an important contribution to connectivity of populations and therefore an important aspect for gene flow. Without the connectivity, genes cannot be exchanged and there will be no gene flow.

As with genetic drift, globalisation also plays an important role in gene flow. In particular transport between cities or towards cities appear to be an important factor for the exchange of genes between different populations. In addition, human constructions can contribute to gene flow in some case. While in other cases human constructions block gene flow. It has become clear that populations can be formed on completely different scales. Gene flow can take place between populations in different cities, or within a city between buildings. When no gene flow occurs, and populations become separated from each other, then those populations can start to differ greatly from each other.

Re-application

In some cases it may seem that species have adapted to their new environment because they function so well in it. However, it is not an adaptive process. In this report, the term re-application is introduced. **Re-application** is the mechanism in which genes or traits as a result of evolution suit well within an environment that is not their original biotope [iv]. Elements from their natural biotope correspond to the new biotope, so that they happen to be well adapted to the new environment. Re-application is related to the terms exaptation, or pre-adaptation, and co-optation. All include the proposition that genes or traits in an evolutionary ancestor may serve another function later in time. An example of exaptation are feathers, which arose initially as an insulation layer for warm-blooded animals. Later turned out that *Reptilia* with feathers also had a beneficial effect on flying. However, exaptation and co-optation are not used in this report, because they specifically concern a new function. The examples that will be mentioned here will make use of a new biotope, the urban environment, in which species happen to be well adapted. The emergence of new functions does not apply here. In addition, terms as pre-adaptation carry misconceptions that lead to suspicion of theological interpretations. Adaptation did not proceed to serve a future function or serve in a future biotope. So instead, the term re-application is used. [24]

Figure 7 - The house sparrow (Passer domesticus).

When looking to biodiversity, cities seem to mainly contain bird species, and that is not surprising. Earlier was explained what the importance is of genes and species movement for a successful existence. Due to the long distances that birds can travel independently, they are more likely to occur in urban environments. But of all these types, a few stand out that seem explicitly suitable for the city. The first example is that of the house sparrow (*Passer domesticus*) (Figure 7). Their natural habitat contains a lot of undergrowth, thorny trees and shrubs where they roost and nest [50]. As a result of this habitat with messy and random structures, the house sparrows have developed short wings that enable them to make quick turns. This is very similar to the new biotope they have found in cities. House sparrows can be found in cities between messy constructions such as bicycle sheds. The variety of spokes, handlebars and saddles on bicycles mimic the crisscross structure of their natural habitat. The physical adaptations to their natural biotope are also very useful here. Research has confirmed that physical traits of urban and rural individuals do not differ for house sparrows, however differences have been found between behaviour [51]. For example, urban populations of the sparrow seem to be less afraid of new objects, take more risks and are more active.

Another bird species that seems well adapted to the urban environment is the feral pigeon (*Columba livia forma domestica*), descendants of the rock pigeon (*Columba livia*) (Figure 8). Previously, the

[iv] A biotope is an area of uniform environmental conditions providing living space for plants and animals.

presence of these pigeons was mainly linked to food availability by humans [52,53]. However, more recent research shows that the physiology of the environment has also played an important role in the occurrence of this species [54]. Rock pigeons get their name from their natural habitat, in which they often use cliffs and ledges of rocks for roosting and nesting behaviour. When humans started building tall buildings, pigeons also moved towards the cities, accepting buildings as artificial cliffs. Their natural biotope is very similar to high-rise cities in many aspects, they seemed perfectly adapted to it. In addition, research shows that they mainly nest on old buildings.


Figure 8 - The rock pigeon (Columba livia).

Besides birds, also a lot of different insect species also demonstrate re-application. The long-bodied cellar spider, a species that has been discussed before, and the bed bug (*Cimex lectularius*) both have a long-shared history with humans. Their natural biotope consists of caves and overhanging rocks. During prehistoric times, this biotope was very similar to that of humans. Therefore, these anthropods often shared caves with humans. But even nowadays they are often found in our homes. Research has shown that the cavities in cities and houses are very similar to the original habitat of the long-bodied cellar spider and are therefore very suitable for them [55]. In the case of bed bugs, they are nowadays found in and around the bed. This environment is comparable to their original biotope in which they nested in the fury environments, for example bat fur [55,56]. Therefore, long-bodied cellar spiders and bed bugs do not occur in the urban environment because they have adapted to it, but because their natural biotope is very similar to the aspects of the city. That makes this new, urban, environment a very suitable habitat.

Not all forms of re-application are beneficial to the organisms in question. Mayflies (*Ephemeroptera*), for example, normally lay their eggs on still water surfaces (Figure 9). Water surfaces provide very suitable environments for the eggs to develop. But since the rise of urbanisation, there have been more and more cases of mayflies laying their eggs on heated asphalt. Research by Kriska *et al.* (1998) has shown that asphalt roads deceive and attract mayflies because of the strongly horizontally polarised light reflected from the surface [57]. The darker and smoother the asphalt, the higher the degree of polarisation of reflected light and the more attractive is the road to mayflies. But the asphalt, unlike water surfaces, offers no chance of survival for the eggs. And not only do they attract mayflies, but numerous water insects are being deceived by glass panes, car roofs or wet asphalts streets [58,59].


Figure 9 - Mayflies (Ephemeroptera).

These examples show that some species appear to be well adapted to the urban environment, but not because of adaptation. When aspects of the urban environment are similar to the natural habitat of an organisms, then species may also thrive in the city. While in some cases, re-application disadvantage species.

Evolution by adaptation

The counterpart of evolution by random processes is evolution by adaptation. In evolution by adaption, selection does occur. No selection occurs in evolution through random processes. Therefore, genes do not necessarily have any advantage over other genes, yet changes in the composition of genes in a population do occur. This can be caused by mechanisms such as mutations, genetic drift and gene flow [11]. Mutations are random changes in DNA sequences over generations and are a major source of genetic variation within a population. Mutations can have negative, neutral or positive consequences for the fitness of organisms. In response to this, natural selection may react to this variety by selecting beneficial mutations. Those mutation will increase in a population over time. Undoubtedly, mutations also occur in urban environments, yet examples of this will not be addressed specifically in this report. The reason for this is that eventual changes in the gene pool of urban population is only initiated by mutations, natural selection in particular ensures a visible result (see chapter *Evolution by adaptation – Natural selection*). [11]
The other two evolutionary mechanisms by random processes will be discussed in detail and is explained below in more detail.

In addition to these evolutionary mechanisms, another phenomenon can be noticed in urban environments. Some introduced species seem to be very well adapted into urbanisation. However, these cases are not a result of selection, but of the random process of re-application. Re-application and associated examples are further explained at the end of this chapter.

Natural selection

Natural selection is the process that explains how species can become better adapted to their environment. Depending on environmental conditions, organisms with certain traits causes them to have a higher or lower fitness than others. By having a higher fitness, an individual or species has a higher survival rate than others and can have more fertile offspring. If advantageous traits are heritable, then those genes will be more common in next generations. Besides heredity, variation and differential fitness are necessary for natural selection to occur [11]. Natural selection can lead to speciation, where one species gives rise to a new and distinctly different species. As a result, populations can change and adapt. Natural selection is thus an adaptive or non-random mechanism. [23,24]

Figure 10 - Peppered moth (Biston betularia).

One of the best-known examples of selection as a result of urbanisation is the peppered moth (*Biston betularia*) (Figure 10). The moth is native to wooded areas. Birch trees and lichens in particular offer good protection against predators, because the moth is barely noticeable against these surfaces with its white body with black spots. The black variant of this moth was rare at the time, because it stood out relatively strongly compared to its white fellow species. When the coal industry in England emerged between 1770 and 1850, soot emissions also increased enormously. As a result, in many natural areas vegetation was covered with a layer of soot and lichens largely disappeared. The white variant of the peppered moth suddenly stood out against the black background. What used to be good camouflage was suddenly very noticeable. In contrast, black-bodied mutations of this species had higher chances on survival [60–62]. The population of black-bodied moths has increased enormously in a relatively short period of time. Never was evolution as a result of urbanisation noticeable before, especially on such short term. In addition, this change turned out to be reversable. After British legislation on air pollution was tightened in the 1950s, the covers of soot disappeared, the air became cleaner and lichens returned. As a result, the black-winged variant once again stood out and was more vulnerable to predators. Between 1965 and 2005, the black peppered moth declined at about the same rate as they had increased a century earlier. Today, the dark form is again as rare as it was in early 1848.

Spatial differentiation can lead to selection as well. Earlier was explained how two groups of mosquitoes in London could arise through separation in occurrence. These populations differ not only between their occurrence, but also between their mating methods, host preference, egg production and life cycle. Due to the location where they occur, underground or above ground, this affects the survival chance of the other aspects. The mating method has changed from a type where the males form large clouds that females fly through to fertilise to a type with one-to-one mating. The reason for this is that there is a much smaller chance that mosquitoes will encounter each other in the limited available space of the metro system. Furthermore, the proteins in the antennae of the mosquitos also have changed in shape to such an extent that they pick up human scents instead of bird scents. This is because of obvious reasons that birds do not occur in these underground tunnels, but humans do. And lastly, their genes responsible for the biological clock have been altered or even switched off. This is advantageous because there are no extreme temperature changes underground and human blood is always present. All these changes underlie natural selection because these adaptations led to a higher chance of survival. Individuals without such adaptations have less chance of survival and are less likely to produce fertile offspring. According to Byrne: “these differentiations can be interpreted in a straightforward way as adaptations to subterranean life” [63]. The 'underground mosquito' is not only found in the London metro system, but in all sorts of human underground constructions such as water systems or basements, and similar enclosed environment such as caves and sewers. In addition, they are found in cities across the globe. For example, in metropolitan Tokyo and the subway of New York. This indicates that the differentiation is not the result of chance, but of natural selection.

Another example of differences in behaviour as result of natural selection is bird song in cities. Several studies have shown that birds in urban areas have a relatively high song rate compared to birds in rural areas [64–66]. This is explained by the fact that cities are relatively noisy areas with mainly low frequencies. Birds can distinguish themselves in urban noise with high-frequency songs. In addition, research showed that urban songs are shorter and sung faster than songs in forests [64]. By distinguishing themselves from ambient noise, birds have higher chances of finding mates and defending their territory, resulting in a higher fitness. To make sure that this change in behaviour is only due to urban noise, and not to other urban factors, Francis *et al.* (2011) investigated this same principle in a more controlled environment [67]. During the experiment, Francis observed the diversity of desert birds located near gas sources. He compared the diversity between quiet and noisy sources. The experiment showed that nearby noisy gas sources no birds occur that use low frequencies for calls and song, such as the mourning dove (*Zenaida macrooura*). Birds with higher voices did occur, such as the chipping sparrow (*Spizella passerina*) and black-chinned hummingbird (*Archilochus alexandri*). The black-chinned hummingbird even prefers to build its nests as close to the noise as possible. Presumably because its predator, the Woodhouse's scrub jay (*Aphelocoma woodhouseii*), avoids noisy areas. Ambient noise can therefore challenge communication between birds, but it can also provide protection. Adaptation of an organism's behaviour as a result of exposure to stimuli, such as changing vocal behaviour to urbanisation, is called behavioural plasticity.

Changing of diet is another example of behavioural plasticity. It has already been discussed that the house sparrow thrives well in the urban environment through re-application of certain morphological traits. However, their success along urbanisation is not solely due to these traits. Research by Ravinet *et al.* (2018) has shown that in urban populations of house sparrows, selection occurs for two genes that are involved in starchy diets [68]. The authors argue that changes in these genes have allow house sparrows to thrive on a starchy diet, which is provided by humans in urban environment, as opposed to their species outside the city. House sparrows aren't the only animals that changed their diet as result of urbanisation. Urban squirrels have been shown to alter their diet to exploit the exotic plants common in urban environment, and gray foxes in urban areas consumed less plant matter and more birds and mammals compared to their rural species [35,69,70]. Other midsize omnivores, such as coyotes (*Canis latrans*), urban red foxes, and urban raccoons appear to utilise human food and trash [37]. Research has shown that urbanised coyotes obtain 14 to 15% of their diet and urban foxes obtain more than 50% of their stomach of anthropogenic foods [71,72].

Apart from behavioural changes, urbanisation can also result in different external characteristics. For example, urban populations of the great tit (*Parus major*) show a decrease in size for all morphological features, and bone measurements show in striped field mouse (*Apodemus agrarius*) show that urban and rural populations have different skull and bone measurements [73,74]. Thus, there appear to be differences between urban and rural populations, but it is difficult to determine whether these differences in the urban environment are caused by natural selection or morphological plasticity.

Investigation in flower displays shows clearer results. Research by Irwin & Warren (2018) shows higher selection for larger floral displays in urban areas than in non-urban areas [75]. According to the authors, this can be explained by a greater limitation in the distribution of pollen in the city. Because there is relatively less vegetation than in rural areas, the chance of pollination or seed dispersal in the city is smaller. Therefore, larger floral displays are beneficial. Some flowering plant species will also flower at other times of the year in urban environment compared to rural environments. For example, urban populations of common ragweed (*Ambrosia artemisiifolia*) flower earlier than rural populations [22]. Although this difference affects fitness very strongly, it is unclear whether this is cased by natural selection or the effect of morphological plasticity. Researchers argue that germination occurs early in cities due to extreme temperature changes (e.g. caused by heat island effects) compared to rural areas. Another flowering plant, the white clover (*Trifolium repens*), shows is a clear example of a result of natural selection. White clovers use chemical defence against herbivores. Research of Johnson *et al.* (2018) shows that urban populations have lower frequencies HCN (which is used as chemical defence) along a gradient towards an urban centre [76]. The same result was found in many cities and therefore the researchers argue that this result is driven by parallel evolution explained by natural selection.

These examples of natural selection show that selection can occur based on morphological characteristics, behaviour or diet. This is because, certain traits in concern to these aspects cause higher fitness than others. Advantageous traits will remain to exist and gradually this trait will spread across the population. Natural selection can lead directly to speciation. In the next chapter will be discussed if speciation occurred in one of all examples.

The emergence of new species

In previous chapters the impact of random and adaptive evolutionary mechanisms on urban species has been discussed, including several examples. However, do new species also emerge in urban areas? In this chapter is investigated if urbanisation impacts speciation, the evolutionary process by which a new species originates. The most classic definition of species is written by evolutionary biologist Ernst Mayr in 1924, as a group organisms that can reproduce with one another in nature and produce fertile offspring [77,78]. Here, each species is reproductively isolated from other groups, which means that one species is incapable of reproducing with other species. However, new definitions came to light since the discovery of DNA. Biologists Niles Eldredge and Joel Cracraft introduced phylogenetic species, in which genetic differences are used to determine separate species [79]. Both these definitions will be taken into account in this chapter.

But first, what is the impact of the evolutionary mechanisms that have been discussed? First of all, evolution by adaptation has clear impact on speciation. In adaptation, genes or behaviour of an organisms adapt to the environment. This happens because some traits have more advantage than others. Through natural selection, only the genetic information, individuals, and behaviour that are beneficial will persist in a population. If all traits in a population are equally valuable, then natural selection does not occur and variation in the population persists. Natural selection results in groups with certain traits becoming more distant from other groups without these traits. If that distance becomes so great, then species can develop separately from each other until they are no longer able to have fertile offspring. Therefore, natural selection can lead directly to species differentiation.
On the other hand, evolution by random processes can only indirectly lead to speciation. Genetic drift mainly results in composition changes of the population, and not necessarily in species differentiation. In particular, the bottleneck effect has little to no impact on speciation, because the environment and all its conditions remain the same. As a result, no new species will arise. The founder effect on the other hand can indirectly influence speciation because a random part of the population is brought to a new environment. If this new environment is different from the original environment, other traits may provide more chance of survival. Then natural selection will occur, and beneficial properties will be retained, which in this case is called peripatric speciation. For peripatric speciation, the founder effect is an important driving force.
Also, re-application does not directly lead to speciation, but, like genetic drift, it can lead directly to species differentiation. If populations thrive well in cities because of re-application, differences can arise between urban and non-urban populations. For example, the house sparrow seems to be well adapted to cities because of its short wings that are agile in the crowded and cluttered city aspects. Subsequently, changes have taken place in the diet of these urban populations, making them better adapted in the urban environment in terms of food as well. These kinds of small adjustments can eventually result in two separate groups with different habitats and specifications. And if the distance between those groups is large enough, speciation can occur. Re-application can therefore also be a driving force in the process to speciation.
Gene flow, on the other hand, counteracts the process of speciation. If genes continue to be exchanged between populations, this will help to maintain population variation. Suppose natural selection acts at the same time, then gene flow counteracts the effect of natural selection. If gene flow occurs minimally, so the effect of selection is greater, than speciation could occur. However, the more gene flow there is, the slower the process.

Of all the examples discussed in this report, there are many cases where urban and rural populations are distanced to varying degrees. The house sparrow, for example, has a different diet in the city than in rural areas. This probably creates a dichotomy between urban sparrows that are more adapted to cities and rural sparrows that maintain their original diet. But because the house sparrow can move relatively easily between these areas, the gene flow is very high. In contrast to the long-bodied cellar spiders, which form islands even within cities. Gene flow is low here, but so is the selection on certain traits. This is because their urban biotope largely corresponds to their original biotope. The only clear example of speciation discussed in this report is the underground mosquito. After constructions of the London Underground in 1863, mosquitoes in that area have split into two populations. Since then, there has been limited to no gene flow between these two groups. The environments of both groups are very different and require different traits for high fitness. As a result of natural selection, the two populations have shown different behaviours. One of these differences is reproductive behaviour. These differences prevent individuals from the above ground population from having offspring with individuals from underground populations. Difference in mating behaviour in particular means speciation in Mayr's definition. But Byrne's research has also shown that the populations differ genetically [42]. These two discoveries lead to the conclusion that the underground common mosquito, *Culex molestus*, is a new species that emerged as a result of urbanisation.

Even though this is the only example in the speciation report, presumably there will be more examples of speciation in the urban environment, discovered or yet to be discovered. This does indicate that there are relatively few cases of speciation in the urban environment.

Discussion & Conclusion

Urbanisation has dramatically increased over the last decades. In 40 years, the total land covered by cities has doubled and its population has more than doubled, from 1.5 billion people living in cities in 1975 to 3.5 billion in 2015 [1–3]. At the same time, urbanisation possibly also threatens future life. The majority of all studies indicate that urbanisation leads to a reduction in biodiversity. However, beneficial effects of urbanisation on biodiversity often remain unclear. This report investigates what the impact of evolutionary mechanisms are on urban species. This is done by investigation in both random and adaptive evolutionary mechanisms. It is also examined whether these mechanisms lead to speciation. An overview of all examples is showed in Table 1.

Table 1 - Overview of all examples mentioned and corresponding evolutionary mechanisms. Random evolutionary processes are marked with the following numbers: 1) genetic drift, 2) gene flow and 3) re-application. Also is marked if speciation applies.

	Random evolution	Adaptive evolution	Speciation
Plants			
False brome (*Brachypodium sylvaticum*)	2		
Common ragweed (*Ambrosia artemisiifolia*)		X	
White clover (*Trifolium repens*)		X	
Insects			
Black widow spider (*Latrodectus Hesperus*)	2		
Underground mosquito (*Culex molestus*)	2	X	X
Long-bodied cellar spider (*Pholcus phalangioides*)	2		
Bed bug (*Cimex lectularius*)	3		
Mayfly (*Ephemeroptera*)	3		
Peppered moth (*Biston betularia*)		X	
Reptiles			
Common wall lizard (*Podarcis muralis*)	2		
Birds			
House crow (*Corvus splendens*)	1	X	
House sparrow (*Passer domesticus*)	3		
Feral pigeon (*Columba livia forma domestica*)	3		
Woodhouse's scrub jay (*Aphelocoma woodhouseii*)		X	
Great tit (*Parus major*)		X	
Mammals			
Red fox (*Vulpes vulpes*)	1	X	
Gray fox (*Urocyon cinereoargenteus*)	1	X	
Kit fox (*Vulpes macrotis mutica*)	1		
Raccoon (*Procyon lotor*)	1	X	
Coyotes (*Canis latrans*)		X	
Striped field mouse (*Apodemus agrarius*)	4		

This study shows that evolutionary mechanisms do occur in and around cities. Some mechanisms even act simultaneously on an organism, but in different ways. For example, the house sparrow was subject of both re-application and natural selection. We discussed four evolutionary mechanisms. 1) Genetic drift has been shown to happen already a few centuries ago. Globalisation is an important aspect of genetic drift, and with the arrival of the first vehicles, it was possible for organisms to be introduced into places they could never reach otherwise. The majority of cases are based on the founder effect. However, presumably there are also cases where the bottleneck effect was applicable. This would have been in the situation where a natural area was replaced with a city and local species would remain to occur. This probably means that many local species have been lost, but not all species will have disappeared. There will probably have been cases that were able to survive or adapt in that new environment. Cases such as these were not found and discussed in this study. 2)The importance of globalisation also became clear in the process of gene flow, especially the transport between and to cities. However, human constructions can also contribute to gene flow, such as the case of the common wall lizard that can move effectively via railway tracks. Other constructions, on the other hand, can form barriers that hinder gene flow, just as the London metro system forms a barrier to gene flow between mosquito populations. In addition, it has also become clear that populations can be formed on completely different scales. Gene flow can take place between populations in different cities, or within a city between buildings. When no gene flow occurs, and populations become separated from each other, then those populations can start to differ greatly from each other. 3) The cases of re-application have shown that in some cases species happen to be well adapted to the urban environment, but not as a result of adaptation. This happens when the original biotope or certain aspects of the biotope corresponds to the urban biotope. Re-application can occur because morphological features or behaviour in the new biotope is successful. However, re-application can also be detrimental to the species in question. Like the mayflies that lay eggs on unsuitable surfaces. 4) Natural selection occurs when certain traits cause higher fitness than other traits. Advantageous traits will remain to exist and gradually this trait will spread across the population. The study identified examples in which selection is based on morphological characteristics, behaviour or diet. Factors that can determine whether a species can survive successfully in the city or not.
Evolutionary mechanisms therefore occur, but it is still unclear whether speciation is also involved in most cases. Both genetic drift and re-application can indirectly lead to speciation. Unlike gene flow, which counteracts the effect of species differentiation. Natural selection, on the other hand, is the only evolutionary mechanisms discussed that can directly lead to speciation. There are some indications that certain species are starting to differentiate, but these cases are still in contact with other populations and have not yet diverted to such an extent that they cannot have fertile offspring together or that their genetic code differs significantly. If these species are indeed differentiating, and populations originate that are specialised in urban areas or rural areas, this can lead to speciation.
The only clear example of speciation covered in this report is that of the underground mosquito. As a result of spatial differentiation, this mosquito has developed different behavioural aspects than its neatest relative, the common mosquito. Because of this difference in behaviour, the mosquitoes cannot have offspring. In addition, the appear to have different genetic codes. For these two reasons one can speak of speciation, according both Mayr's or Eldredge & Cracraft's definition of species.

The portfolio of examples mentioned in this report show that some groups are represented more often than others (Table 1). The report mentions many examples of insects, birds and mammals. An explanation for this could be that there are more generalists among these groups who can easily settle in new areas. For example, because they need fewer specific characteristics from their environment, or because they can move relatively easily to new areas. This would ultimately be beneficial for biodiversity in urban environments. Only if pioneer species are established in a new area, the foundation can be laid for a new natural ecosystem, which eventually also attracts specialists. Another explanation for the high representation of these groups is bias based selection of literature studies. It should be noted that the selection of species that is used as an example has been determined with a limited amount of time. In reality, there are many more organisms subject to urban evolution that remain uncovered in this report.

Another point of discussion is whether it is favourable to attract other organisms to cities. Initially, people often think of nuisance caused by stinging bees, gnawing mice or defecating birds. Increasing biodiversity in our immediate environment and therefore living hand in hand with other species comes with its challenges. However, biodiversity mainly has many advantages. Those mice that bother us are particularly a plague because they do not have their natural enemy nearby. More biodiversity also means more species regulation and therefore more balance. This will result in a decrease of plagues, such as mice. The bees that bother us, do first of all not sting. However, they bring enormous benefits. They are a major link in the services provided by the ecosystem, along with many other species. A good balance in biodiversity ensures, among other things, the purification of air, water and soil, it enriches soil which results in more crops, stores CO_2, and results in better human well-being. In addition, diversity in organisms ensures resistance of the ecosystem. The more variation there is in species and genes, the more resilient the ecosystem becomes and the more certainty we have that we can continue to receive ecosystem services. And lastly, humans have to adapt as well and enable other organism, such as those birds, to live along them. If cities are organised in such a way that waste becomes energy, humans cannot only create places where species coexist, but create a healthy living environment as well.

In conclusion to this study, evolution does occur through urbanisation and there are species that benefit from urban environments. Nevertheless, the decline in biodiversity is higher than the increase. That is why it remains important to preserve and facilitate biodiversity in the city as much as possible and ensure that the increase can continue. Based on this study is suggested that the urban environment is a relatively new ecosystem which has the potential for species to occur and adapt. Small adjustments to our cities may ensure contribution to biodiversity, making it more suitable living environments.

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