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Understanding the urban ecosystem

interactions between plants, animals, and people

Jensen, Johan Kjellberg

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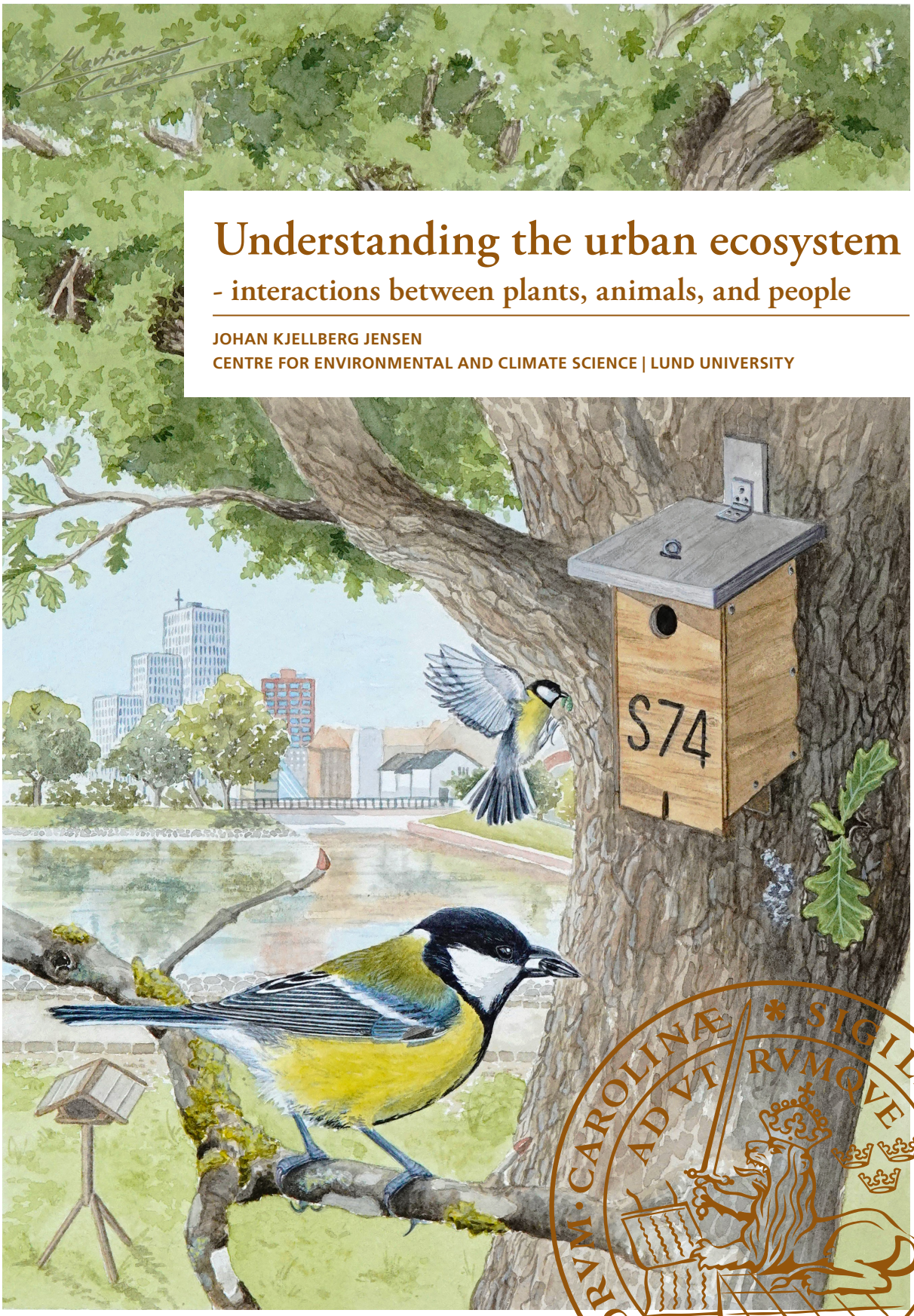

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CENTRE FOR ENVIRONMENTAL AND CLIMATE SCIENCE | LUND UNIVERSITY

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- interactions between plants, animals, and people

Understanding the urban ecosystem

- interactions between plants, animals, and people

Johan Kjellberg Jensen

LUND
UNIVERSITY

DOCTORAL DISSERTATION

Doctoral dissertation for the degree of Doctor of Philosophy (PhD) at the Faculty of Science, Lund University. To be publicly defended on the 15th of September 2023 at 09.30 a.m. in Blå Hallen, Department of Biology, Ecology building, Sölvegatan 37, Lund.

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Abstract:

Cities are the pinnacle of human change to the environment, creating unique types of ecosystems which present many challenges to local organisms: habitat fragmentation, introduced species, and various pollutants. Being crucibles of anthropogenic effects, urban ecosystems offer opportunities to understand how humans impact nature. Moreover, since a majority of the world's population resides in cities today, urban nature has become the most frequently encountered type of nature in everyday life. Studying urban ecology therefore has the potential to shed light on both sides of the interaction between people and nature. In this thesis, I used an interdisciplinary approach to explore the effects of urbanization on vegetation, arthropods, birds, and people. Studying several taxa, and using methods from Ecology, Physiology, Sociology, and Aerosol technology, I aimed to develop a holistic and multifaceted understanding of the urban ecosystem. Specifically, I investigated urban trophic interactions, how air pollution and nutrition may affect animal physiology, and how local wildlife influences children's well-being and perception of nature. I outline three key findings from the six papers forming the basis of my thesis: (1) plant origin is a strong determinant for urban arthropod abundance and breeding success of birds. Namely, non-native trees show a negative effect, with a magnitude and consistency over years, which indicates that vegetation composition is a key driver limiting animal populations in cities. (2) urban birds are constrained by food quality (specific nutrients) during breeding, likely due to low abundances of certain arthropods in cities. Moreover, high quantities of low-quality food (e.g., from human sources) do not compensate for the urban birds' dietary deficiency and may instead lead to reduced capacity to mount physiological responses to deal with air pollutants or infections. (3) children's relation to nature (attitude and knowledge) is not impacted by urbanization but predicted instead by socioeconomic factors and the quality of nature close to their homes. These local differences call for more detailed approaches when studying cities since both social and environmental variation within urban areas can be more consequential than general divides. In this thesis, I demonstrate the importance of native vegetation in cities and food quality for urban animals. Local wildlife influences people and by better understanding the urban ecosystem, we are one step closer to building cities that will allow future generations to learn about species and enjoy nature near their homes.

Key words: air pollution; avian physiology; fatty acids; human-nature interactions; nature connection; non-native plants; nutrition; trophic interactions; urban ecology; urbanization

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Table of contents

Abstract

Cities are the pinnacle of human change to the environment, creating unique types of ecosystems which present many challenges to local organisms: habitat fragmentation, introduced species, and various pollutants. Being crucibles of anthropogenic effects, urban ecosystems offer opportunities to understand how humans impact nature. Moreover, since a majority of the world's population resides in cities today, urban nature has become the most frequently encountered type of nature in everyday life. Studying urban ecology therefore has the potential to shed light on both sides of the interaction between people and nature. In this thesis, I used an interdisciplinary approach to explore the effects of urbanization on vegetation, arthropods, birds, and people. Studying several taxa, and using methods from Ecology, Physiology, Sociology, and Aerosol technology, I aimed to develop a holistic and multifaceted understanding of the urban ecosystem. Specifically, I investigated urban trophic interactions, how air pollution and nutrition may affect animal physiology, and how local wildlife influences children's well-being and perception of nature. I outline three key findings from the six papers forming the basis of my thesis: (1) plant origin is a strong determinant for urban arthropod abundance and breeding success of birds. Namely, non-native trees show a negative effect, with a magnitude and consistency over years, which indicates that vegetation composition is a key driver limiting animal populations in cities. (2) urban birds are constrained by food quality (specific nutrients) during breeding, likely due to low abundances of certain arthropods in cities. Moreover, high quantities of low-quality food (e.g., from human sources) do not compensate for the urban birds' dietary deficiency and may instead lead to reduced capacity to mount physiological responses to deal with air pollutants or infections. (3) children's relation to nature (attitude and knowledge) is not impacted by urbanization but predicted instead by socioeconomic factors and the quality of nature close to their homes. These local differences call for more detailed approaches when studying cities since both social and environmental variation within urban areas can be more consequential than general divides. In this thesis, I demonstrate the importance of native vegetation in cities and food quality for urban animals. Local wildlife influences people and by better understanding the urban ecosystem, we are one step closer to building cities that will allow future generations to learn about species and enjoy nature near their homes.

Populärvetenskaplig sammanfattning

En stad är resultatet av otaliga mänskliga förändringar av miljön. Föroreningar, mindre grönska och ett varmare lokalt klimat är typisk för stadsmiljö, men på trots av detta finns det fortfarande natur här. Även om stadsnaturen överlag är väldigt förändrad kan det finnas höga naturvärden och biologisk mångfald i våra städer, särskilt i större parker. En av anledningarna till detta är att städer har byggts i områden som historiskt sett haft många naturresurser och därmed ofta också biologisk mångfald. Eftersom städer koncentrerar många miljöförändringar på en plats är staden en utmärkt arena för att studera hur människor påverkar natur och miljö. Dessutom bor en majoritet av jordens befolkning i städer, vilket betyder att stadsnatur idag är den vanligaste naturtypen att möta i vardagen. Det innebär att stadsnaturen har en viktig roll att spela i naturupplevelser, vilka både kan påverka vårt välmående och våra generella uppfattningar om djur och växter.

Att studera hur städer påverkar och formar lokal natur kallas urban ekologi, vilket refererar till samspelet mellan djur, växter och den fysiska miljö som urbanisering har skapat (t.ex. luftföroreningar och hårdgjorda ytor). I den här avhandlingen undersökte jag det urbana ekosystemet: hur djur och växter påverkas av städer, men även hur vi människor kan bli påverkade av den natur som skapats här. Avhandlingen syftar till att framställa en övergripande och sammanhängande bild av det urbana ekosystemet och hur det fungerar. Mina studier omfattade därför olika organismer och metoder från flera forskningsfält: ekologi, fysiologi, sociologi och aerosolteknologi. Gällande studieorganismer fokuserade jag främst på näringskedjan från träd till fåglar, vilken också inbegriper insekter och spindlar. Störst fokus låg dock hos fåglarna, som är en mycket välstuderad djurgrupp, inte minst i urban ekologi. Mer specifikt undersökte jag hur främmande trädarter, vilka är vanliga i stadsplanering, påverkade småfåglars häckning och mängden lokala insekter samt spindlar. Jag testade även vilket näringsämne som stadsfåglar kan tänkas ha brist på och hur effekten av både diet och vegetation kan påverkas av luftföroreningar. Här använde jag mig av fysiologiska markörer, det vill säga mätningar som gav insikt i fåglarnas fysiska tillstånd och hälsa, till exempel blodvärden. Därtill studerade jag också hur barns välmående och uppfattning av natur (kunskap och attityd) påverkas av interaktioner med vilda djur i och utanför städer.

Resultaten av de sex forskningsartiklarna som min avhandling bygger på, visar att inhemska växter (arter som har funnits i ekosystemet i över 700 år) är mycket viktiga för djur i staden. Främmande träd hyser påtagligt färre insekter och spindlar; småfåglar (blåmes och talgoxe) undviker att häcka i områden med många främmande träd och ungarna väger mindre om fåglarna trots allt bosätter sig där. Effekten av trädens ursprung var stor och ihållande över flera år, vilket tyder på att just växtsammansättning är en av huvudförklaringarna till varför många djur klarar sig sämre i städer. Jag kunde även visa att det är kvaliteten (näringsämnena) av fåglarnas föda som sannolikt gör att många fågelarters ungar är i sämre skick i städer: en särskild omega-3 fettsyra (DHA) visade sig vara viktigare för stadstalgoxars tillväxt än mängden mat. Den sannolika källan till fettsyran i naturen är spindlar. En stor mängd mat av lägre kvalitet, till exempel matrester eller vanlig fågelmat, verkar inte kunna kompensera för näringsbristen och kan istället minska fåglars kapacitet att klara av luftföroreningar. Att mata fåglar kan däremot vara ett sätt att skapa ett band till naturen för människor, ett band som forskare tidigare har resonerat kan ha nötts ut på grund av urbanisering. Mina resultat visar däremot att det inte är någon tydlig skillnad i barns kunskap eller uppfattning av natur beroende på om de bor i städer eller ej. Istället är det socioekonomiska faktorer, som inkomst och utbildningsnivå, tillsammans med kvaliteten på grönområdena närmast där barnen bor, som styr deras kunskap och attityd till natur. Sammantaget visar min avhandling vikten av inhemsk vegetation i städer och behovet av kunskap kring ekologiska samband för att bygga städer som gynnar både natur och människor, något som är avgörande för att framtida generationer ska kunna lära sig om arter och glädjas av natur nära deras hem.

List of papers

Chapter I

Jensen, J. K., Jayousi, S., von Post, M., Isaksson, C., & Persson, A. S. (2022). Contrasting effects of tree origin and urbanization on invertebrate abundance and tree phenology. *Ecological Applications*, *32*(2), e2491.

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Chapter IV

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Chapter V

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Chapter VI

Jensen, J. K., Olsson, J. A., von Post, M., & Isaksson, C. Children's relation to nature and response to wildlife interaction depend on factors other than urbanization. *Manuscript*.

*Shared first authorship

Author contributions

Chapter I

All authors contributed to the design of the study. SJ and **JKJ** carried out the fieldwork and processed the data. **JKJ** analyzed the data with input from ASP, MvP, and CI. **JKJ** drafted the manuscript. All authors contributed critically to the writing of the paper.

Chapter II

The study design was conceptualized by **JKJ**, JE, and CI. HW, PS, CI, and **JKJ** carried out the fieldwork. PO performed the initial GIS work. **JKJ** analyzed the data together with JE and input from all the authors. **JKJ** drafted the manuscript. All the authors contributed critically to the writing of the paper.

Chapter III

The study was conceptualized and designed by **JKJ** and CI, with input from MNA and GCB. **JKJ**, EC, and CI performed the field experiment. CI performed the sampling of adults. ZT and MNA carried out the lab work. **JKJ** analyzed the data and drafted the manuscript. All authors contributed critically to the writing of the paper.

Chapter IV

The study design was conceptualized by **JKJ**, AKZ, JÅN, and CI. AKZ and **JKJ** carried out the fieldwork. **JKJ** mapped the territories. AKZ, CIX, and JR performed the initial data management of the $PM_{2.5}$ data. **JKJ** carried out the laboratory analysis with help from LJG, SGD, and AKZ. **JKJ** analyzed the data and drafted the manuscript with input from AKZ and CI. All authors contributed critically to the writing of the paper.

Chapter V

AKZ, **JKJ**, JR, AG, JÅN, and CI designed the experiment. AKZ and **JKJ** conducted the experiment. AKZ, **JKJ,** and LJG did the laboratory work. AKZ performed the statistical analysis. AKZ wrote the first draft of the manuscript. AKZ, **JKJ**, JÅN, and CI edited and revised the manuscript. All authors contributed critically to the writing of the paper.

Chapter VI

The study design was conceptualized by CI and **JKJ**, with input from MvP and JAO. Field visits were performed by **JKJ**, with help from MvP. **JKJ** analyzed the data and drafted the manuscript with input from all authors.

Authors

Martin N. Andersson (MNA), Graham C. Burdge (GCB), Eugenio Carlon (EC), Susana Garcia Domínguez (SGD), Johan Ekroos (JE), Anders Gudmundsson (AG), Caroline Isaksson (CI), Christina Isaxon (CIX), Sherin Jayousi (SJ), Lucía Jiménez-Gallardo (LJG), Johan Kjellberg Jensen (JKJ), Jan-Åke Nilsson (JÅN), Peter Olsson (PO), Johanna Alkan Olsson (JAO), Anna S. Persson (ASP), Jenny Rissler (JR), Pablo Salmón (PS), Zsófia Tóth (ZT), Maria von Post (MvP), Hannah Watson (HW), Ann-Kathrin Ziegler (AKZ)

Abbreviations

CO	carbon monoxide
DHA	docosahexaenoic acid
EPA	eicosapentaenoic acid
FAs	fatty acids
FRAP	ferric reducing antioxidant power
GSH	glutathione
GSSG	glutathione disulfide (oxidized glutathione)
HOCl	hypochlorous acid
LPS	lipopolysaccharide
MDA	malondialdehyde
NO_2	nitrogen dioxide
NO_X	nitrogen oxides
O_3	ozone
PC	principal component
PCA	principal component analysis
PM	particulate matter
PUFAs	polyunsaturated fatty acids
ROMs	reactive oxygen metabolites
SO_2	sulfur dioxide
UHI	urban heat island
VOCs	volatile organic compounds

Introduction

Cities are both hotspots for human changes to the environment and junctures between people and nature. In terms of changes, urbanization alters local habitats for plants and wildlife through numerous processes, including habitat fragmentation, introduction of non-native species, and increased temperature and levels of pollutants. It is clear that human-mediated changes impact the local ecosystem as a whole, but the individual effects caused by specific factors and their relative importance are still not well-understood. Cities are however projected to grow both in size and numbers, and the impact of urbanization on nature is therefore bound to increase. Today, a majority of the world's population already resides in cities, which means most people also meet urban nature daily and rely on it for ecosystem services. From this, we can identify three core subjects in urban ecology: first, we may view urban areas as laboratories of anthropogenic changes. High concentrations of widespread pollutants, e.g., air pollutants and artificial light at night, make cities excellent arenas to study the impacts of environmental pollution on physiological responses, species-interactions, and evolutionary processes. Second, urbanization is an ongoing land-use change and threat to biodiversity, which is further amplified by the trend of cities being settled in areas with high species richness. Urban ecology therefore has a role in conservation efforts and in creating applicable management advice. Finally, cities serve as meeting points between people and nature, making it highly relevant to understand how the urban ecosystem might influence human perceptions of, interactions with, and benefits derived from nature.

Thesis aims

In this thesis, I used an interdisciplinary approach to explore the effects of urbanization on vegetation, arthropods, birds, and people. I aimed to identify specific environmental factors that impact urban arthropods and birds and to study trophic interactions in cities. More precisely, I set out to shed light on the consequences of altered vegetation in urban areas and how such an effect might carry across the ecosystem through diminished food resources to birds (*Chapters I-III*).

Additionally, I studied how other factors, mainly air pollutants, may interact with urban vegetation in their effects on birds, or interact with certain nutrients associated with humans through food waste and bird feeding (*Chapters IV-V*). To this end, I used physiological measures in birds, aiming to create a detailed and mechanistic understanding of the urban ecosystem and its processes. Since cities are built by humans and for humans, I also investigated the relationship between people and nature, aiming to better understand the forces that shape urban nature. More specifically, I studied urban and rural children's attitudes to and knowledge of birds, which factors modulate this, and how bird feeding potentially can benefit people (*Chapter VI*). In general, I tried to identify and use the variation of environmental factors within cities, to generate applicable and general knowledge of urban ecosystems. By using multiple methods and studies of different taxa, my overarching goal was to create an encompassing picture of the urban ecosystem.

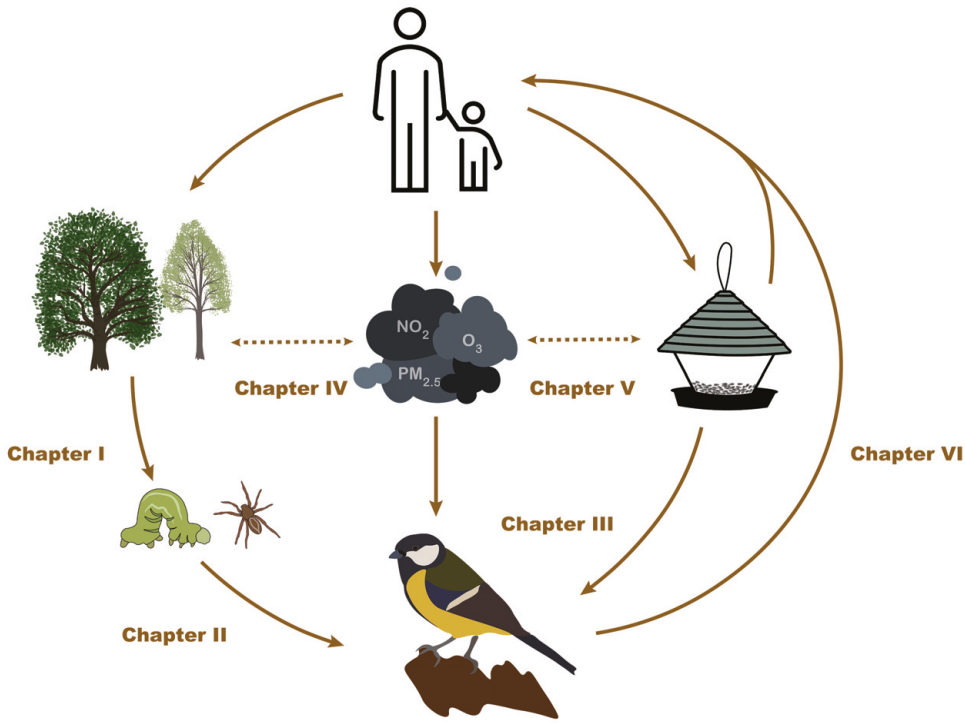

Figure 1. A schematic overview of the connection between thesis chapters and themes.

The chapters of my thesis cover the following individual research questions (Figure 1):

Chapter I: How does the altered tree composition of cities impact higher trophic levels, namely arthropods? What is the magnitude of this effect compared to other urban effects and is the phenology of non-native trees a potential cause?

Chapter II: Can local tree composition explain the lower reproductive success of passerine birds in cities? Which tree species are beneficial for urban birds in terms of nestling survival and growth?

Chapter III: Are urban bird populations food-limited and if so, is it the quantity or quality of food that is lacking? What specific nutrient might be deficient in the urban diet?

Chapter IV: How do we quantify the numerous factors that define the urban environment in a meaningful way? Which physical or biotic aspects of the urban environment impact nestling physiology and are there interactions between these factors?

Chapter V: Do nutrients interact with air pollution in their effect on avian health? Does the skewed diet of urban birds impact their response to ozone, and are there any interactions with the immune system?

Chapter VI: Is urbanization leading to an eroded connection between humans and nature? Can a simple wildlife interaction, such as bird feeding, strengthen nature connection in children? Which factors modulate the impact of wildlife interactions?

The urban habitat

"*The future of the world's population is urban.*" (United Nations, 2018).

The first cities are believed to have emerged over 8 000 years ago in Mesopotamia, with population numbers in the low thousands. Since then, urbanization has proceeded in waves resulting in historic cities such as Babylon and Rome, but it was not until the industrial revolution of the 18th century that the rise of cities began on the scale we know today (Chandler and Fox 1974, OECD 2015). Presently, the majority of the world's population (~56%) resides in urban settlements and the number and size of cities are projected to increase during the present century (Figure 2; United Nations 2018).

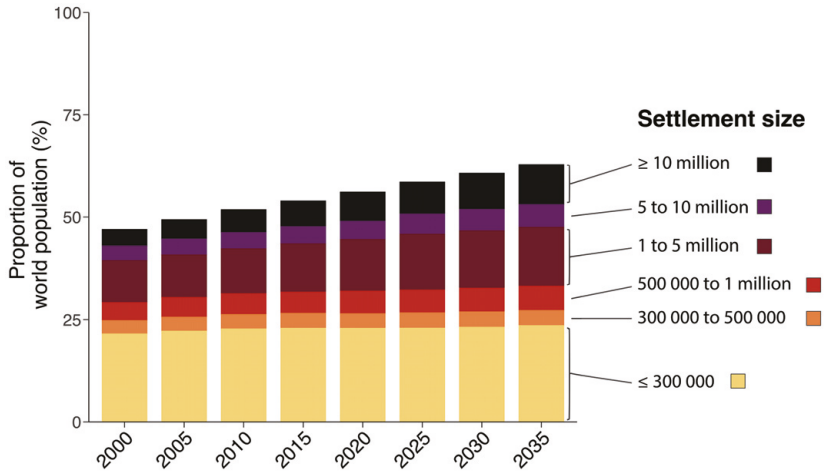

Figure 2. The world population in urban areas, divided by settlement size, based on population projections by the United Nations (data from United Nations 2018, 2022b).

The definition of a city may seem clear – built-up areas where large numbers of people reside – but a general and international definition of what constitutes an urban area has long been lacking (United Nations 2018). A contributing factor to this is that while a city generally is defined as a settlement with over 50 000 inhabitants, what constitutes the population threshold for towns, and thus urban areas in general, vary greatly on a country basis (United Nations 2022a). The United Nations has recently presented 'Degree of Urbanization' as an international definition of urban areas, with 5 000 residents being the cut-off point between urban and rural settlements (United Nations 2022a), but it is important to note several nations have other definitions (e.g., Sweden with ≥ 200 inhabitants being considered urban; SCB 2020). Moreover, the United Nations (2022a) argue urbanization should

be considered a continuum, something which ecological studies long have practiced, with the concept of urbanization gradients (McDonnell and Pickett 1990).

Ecological gradients rest on the idea that biologically relevant landscape characteristics will vary in intensity spatially, and urbanization should therefore be studied on such scales (McDonnell and Pickett 1990, Seress et al. 2014). What these landscape characteristics are, depend on study species and question, but in practice urbanization intensity is generally calculated based on easily quantifiable parameters in ecological studies, such as the relative proportion of buildings, hard surfaces, and vegetation cover (Seress et al. 2014). Although definitions may vary, cities are in essence epicenters for anthropogenic changes to the environment. In this thesis, I therefore use the terms 'cities', 'urbanization', and 'urban areas' interchangeably to refer to the general and intense land-use changes associated with modern human settlements (Grimm et al. 2008). The focus of my research is on the resulting effects on the ecosystem.

From an ecological standpoint, cities are still a very recent habitat type. Being characterized by fragmentation and loss of vegetation, together with an increase in several types of pollution (e.g., air, light, and noise), urbanization poses a challenging environment for most species to thrive in (Grimm et al. 2008, Seto et al. 2012). Cities tend to have been settled in areas with historically high natural productivity and urban areas are thus often located in biodiversity hotspots (Faeth et al. 2011, Ives et al. 2016). The loss and change of habitats caused by urbanization is therefore of particular concern since cities tend to impact valuable habitats. Moreover, urban nature today also provides the majority of the world's population with ecosystem services and everyday experiences of nature (Figure 2). Impoverished ecosystems in cities have therefore raised concerns about the so-called '*extinction of experience*', where people are further removed from nature and may eventually lose their connection to nature, and ultimately their will to conserve the environment in general (Pyle 1978, Dunn et al. 2006).

Simply put, cities are hotspots for anthropogenic changes, and studying the ecosystems that have formed here has potential to yield results highly relevant to conservation and society in general. Below, I summarize three key aspects that shape urban ecosystems, and their effect on wildlife, with particular focus on birds: diminished and altered vegetation, shifted food availability, and increased levels of various pollutants. I conclude with a summary of research on human-nature contact in an urban setting to contextualize these changes to the environment.

Vegetation

Vegetation is one of the most important factors in supporting urban biodiversity (Beninde et al. 2015). In addition, vegetation is one of the few biotic components of cities that is managed to an impactful degree, meaning it has special importance in conservation questions (Faeth et al. 2011). Natural vegetation is however sparse in cities: urbanization results in fragmented habitats interspersed in a matrix of hard surfaces and buildings, creating a mosaic-type landscape. Urban greenspaces can still host a variety of species, partly due to historical biodiversity, but also because urban parks can hold ecological values (Faeth et al. 2011, Nielsen et al. 2014, Ives et al. 2016). For example, city parks often contain old-growth trees, which in turn can provide important microhabitats and promote species richness of birds (Fernández-Juricic 2000, Nielsen et al. 2014). The general determinants for urban biodiversity are however patch-size and vegetation structure (Nielsen et al. 2014, Beninde et al. 2015). Namely, large areas of greenery, and vegetation complexity (e.g., dead wood, canopy layers, and closure) are positively associated with biodiversity in cities (Beninde et al. 2015, Felappi et al. 2020). These qualities are however not the most common characteristics of urban vegetation due to intense management regimes, exemplified by the large proportion of greenspace that urban lawns account for (Ignatieva and Hedblom 2018). A study of Swedish cities found that over 50% of all urban greenspace consisted of lawns, which is a much-used feature in city designs worldwide (Hedblom et al. 2017, Ignatieva and Hedblom 2018).

In turn, the decrease of vegetation (canopy layers in particular) and increase in hard surfaces lead to higher local temperatures in cities (Ziter et al. 2019). This effect is called the urban heat island (UHI) and is a well-documented consequence of decreased evaporation and increased heat retention from light absorption caused by the substitution of greenery (Oke 2006, Peng et al. 2012). The UHI effect subsequently impacts the remaining local vegetation and can alter the phenology of plants in cities, e.g., by advancing bud burst (Wohlfahrt et al. 2019). Phenological mismatches between plants and animals have been suggested to occur in urban ecosystems, similar to disruptions observed in response to climate change, but such mismatches are still not well-studied in an urban context (Both et al. 2009, Fisogni et al. 2020).

Climate change, in conjunction with the relatively hotter local temperatures caused by current city-planning, has also led to concerns about survival of urban trees (Esperon-Rodriguez et al. 2022). Based on this, arguments have been put forth to further increase the proportion of non-native plant species in cities (Sjöman et al. 2016). Other factors, such as aesthetic values and commercial availability, also influence the vegetational composition of cities (van Kleunen et al. 2015, Avolio et al. 2018). Consequently, over a quarter of plant species in cities worldwide today are non-native, making mixed plant origin a striking characteristic of urban

vegetation (Aronson et al. 2014). In fact, the global exchange of species leads to a homogenization of city nature, making the urban ecosystems more akin to each other across the world (Aronson et al. 2014). Additionally, since plants are typically sourced from commercial nurseries, urban flora can show unique traits from artificial selection, although little is known about the genetic diversity of urban plants today (Avolio 2023). Genetic diversity of urban trees is however likely low: for example, a single tree clone has been planted throughout 250 years in the city of Copenhagen (*Tilia* × *europaea*; Hansen et al. 2014). Taken together, urban vegetation is not only altered in amount and configuration but also holds several unique characteristics in terms of composition that are likely to affect the resources it provides to local animal populations.

Box 1: Responses to urbanization

The many changes to habitats that urbanization is associated with create a novel ecosystem, challenging for many species to thrive in. Certain species however, commonly referred to as urban exploiters, possess traits that are well-matched to the habitat characteristics of cities (Blair 1996). For example, avian urban exploiter species are typically omnivorous and thus able to utilize the variety of unique food sources found in cities (Croci et al. 2008). Other traits that are adaptive in urban environments are nesting on cliffs and gregarious behavior. In comparison, ground nesting birds and migratory species typically either belong to the group urban adapters, which can breed in urban environments and may thrive in suburban areas, or urban avoiders, which are typically not found in cities (Blair 1996, Croci et al. 2008). According to a global analysis, cities support approximately 20% of the world's bird species, meaning that a majority of species fall into the urban avoider category (Aronson et al. 2014). It is however important to note that it is not single traits of species, but several biotic and abiotic filters, that shape urban community assemblies (Kraft et al. 2015, Aronson et al. 2016). Factors such as climate, past land-use, urban configuration, local human facilitation (introduced species), and species interactions such as predation, can all influence which species are found in cities (Rodewald et al. 2013, Aronson et al. 2016, Haddou et al. 2022). Moreover, phenotypic variation can aid species in dealing with the habitat changes associated with urban environments (Watson et al. 2017) and recent studies have begun to reveal evolutionary processes of local adaptation to cities in arthropods and birds (Theodorou et al. 2018, Salmón et al. 2021). Urban evolutionary biology is still an emerging field with many unanswered questions (Szulkin et al. 2020), but it is important to note that although some processes can be rapid, modern cities are a very recent phenomenon from an evolutionary standpoint. In other words, we should not expect adaptation to drastically mitigate the risk of local extinctions of species posed by urbanization.

Nutrition

Many insects are closely linked to specific host plants (Ehrlich and Raven 1964), which means the novel vegetation of cities is bound to impact arthropod populations (Chatelain et al. 2023). Low availability of arthropods has been proposed to have cascading effects to higher trophic levels, namely insectivorous birds, limiting their reproduction in cities (Chamberlain et al. 2009, Seress et al. 2020). Nevertheless, while natural food items such as caterpillars may be scarcer in cities, human activity is also linked to novel food sources, through food waste and direct provisioning, particularly to birds (Jones and Reynolds 2008, Stofberg et al. 2019). Given the scale of bird feeding in many countries (e.g., the United Kingdom with 150 000 tons of wild bird food sold annually; PFMA 2018), impacts on bird populations in proximity to human settlements are to be expected. Motivations for bird feeding often include a sense of stewardship and wanting to help birds (Cox and Gaston 2016, Brock et al. 2017). The reliability of food provided by humans is also likely positive to individuals that can utilize this resource (Box 1; Oro et al. 2013, Watson et al. 2023). The ecological effects from bird feeding can however be more complex than simply being a beneficial increase in food quantity. At a community level, bird feeding will favor species that can utilize the food provided, but the resulting population growth of some species may skew interspecific competition for other resources than food (e.g., nesting sites); bird feeding can thus indirectly have negative impacts on species that do not rely on the feeders (Shutt et al. 2021). Other studies have found direct negative effects on future reproduction from winter provisioning of blue tits (*Cyanistes caeruleus*), possibly caused by a sub-optimal nutritional status of adults caused by an unbalanced winter diet (Plummer et al. 2013a, 2013b). In terms of the urban ecosystem however, it is important to recognize that bird feeding may not be the most intense in highly urbanized areas since birds are typically fed in private gardens (PFMA 2018). Still, taken together with shifted urban diets from lower prey availability (Narango et al. 2018, Jarrett et al. 2020), a picture of a significantly altered nutritional landscape caused by human activities emerges.

Studying how interactions between organisms and the environment are formed through nutritional needs has a long history, although little is known about how urbanization shapes such interactions (Coogan et al. 2018). General findings in nutritional ecology however suggest that it is not necessarily a common currency (i.e., energy) that drives effects, but instead the relative composition of macronutrients (proteins, carbohydrates, and lipids), together with micronutrients (vitamins and minerals), that explain nutrition related patterns (Raubenheimer et al. 2009, Coogan et al. 2018). For example, the fat-provisioned blue tits mentioned above were likely not energy-limited, but instead lacked the needed composition of nutrients for successful breeding (e.g., fatty acids, Box 2; Plummer et al. 2013a, 2013b).

Urban birds have been shown to improve their breeding performance, close to that of rural conspecifics, when supplemented with food during nestling rearing, which underscores that some aspect of the urban diet is in fact deficient (Seress et al. 2020). Additionally, pollution from human activities has been proposed to impact the nutritional ecology of animals: heavy metal exposure could, for example, interact with nutrient uptake or requirements for birds (Eeva et al. 2003, Birnie-Gauvin et al. 2017). In summary, nutrient availability in cities differs vastly from most natural ecosystems, both through an increase of novel food sources (direct provisioning and food waste), but also through the decrease or shift in naturally occurring prey due to altered vegetation. Little is still known about how nutrition influences the ecology of urban birds or possibly interacts with other co-occurring anthropogenic changes to the environment.

Box 2: Polyunsaturated fatty acids

Fatty acids are a type of lipid, consisting of a carbon chain ending in a carboxyl group (COOH) and a methyl group (CH3; Figure 3). Based on the number of double bonds in the carbon chain, fatty acids can be divided into saturated fatty acids (no double bonds), monounsaturated fatty acids (one double bond), and polyunsaturated fatty acids (PUFAs; two or more double bonds). PUFAs are involved in several physiological processes in animals, including immune function and growth. For immune responses, the further subdivision of ω6 and ω3-PUFAs (based on the location of the first double bond) is important, as ω6-PUFAs are linked to pro-inflammatory responses, while ω3-PUFAs are linked to anti-inflammatory responses (Calder and Grimble 2002). Current human diets, which are available to urban birds through food waste, typically have high proportions of ω6-PUFAs compared to ω3 (Simopoulos 2011, Stofberg et al. 2019). Some bird food, such as sunflower seeds, also contain high levels of ω6 compared to ω3-PUFAs. Certain long-chained ω3-PUFAs, i.e., eicosapentaenoic acid (EPA; 20:5n3) and docosahexaenoic acid (DHA; 22:6n3), are especially important to avian development and growth: dietary access to these PUFAs can have stronger positive effects than food quantity on nestling growth and condition (Twining et al. 2016). DHA is, for example, involved in brain and muscle development and has been linked to cognition (Speake and Wood 2005, Lauritzen et al. 2016). However, only two PUFAs are strictly essential to birds and must be obtained through diet: the short-chained linoleic (18:2n6) and α-linolenic acid (18:3n3). Still, the efficacy to biosynthesize other PUFAs from these appears to vary between species (Twining et al. 2018, 2021b, 2021a), and dietary access to long-chained ω3-PUFAs can clearly be beneficial to birds.

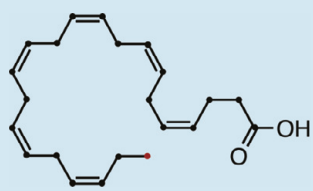

Figure 3. Molecular structure of docosahexaenoic acid (DHA). As indicated by the lipid number (22:6n3), DHA is long-chained (22 carbon), and polyunsaturated (6 double bonds) fatty acid, belonging to the ω3-group (first double bond located on the third carbon, counting from the methyl-end [red circle]).

Pollution

The intense human activity in cities leads to high concentrations of pollution. Pollution takes many different forms, including increased levels of artificial light and noise, but perhaps most notably: the release of chemical pollutants in ambient air. There are several types of airborne pollutants linked to human activities, including carbon monoxide (CO), nitrogen oxides (NO_X), sulfur dioxide (SO_2), ground-level ozone (O_3), and particulate matter (PM). Many air pollutants are directly generated from traffic and industries, with others forming as secondary pollutants from these, leading to particularly high levels in urban areas (Hill 2020). For example, a major source of NO_X is the combustion of fuels from traffic, which leads to high concentrations in urban areas. NO_X, together with volatile organic compounds (VOCs; of which motor traffic also is a major source), are precursors to ground-level ozone, which forms through reaction to sunlight, and is a major component of photochemical smog. Although less common, NO_X can also convert to nitrate particulates and then contribute to the levels of particulate matter, a general term for microscopic, airborne matter (e.g., $PM_{2.5}$: air-suspended particles, with a diameter of 2.5 μm or less). PM also has several direct anthropogenic sources, including the burning of fossil fuels and wood, as well as construction and road dust (Hill 2020).

Negative health effects caused by air pollution in cities are well-documented for humans, including increased risk for disease and death (West et al. 2016, World Health Organization 2022), but the effects of air pollutants on an ecosystem level are much less studied. Pollutants can impact both urban plants and wildlife, as well as the interactions between them: for example by interfering in plant-insect interactions, potentially obscuring chemical cues (Blande 2021). Conversely, increased herbivory has been documented on street trees highly exposed to air pollutants, likely through a suppression of phytochemical defense compounds (Meineke et al. 2023). Air pollutants also have direct impacts on wildlife, for example by negatively affecting avian reproduction, immune function, and increasing respiratory distress (Sanderfoot and Holloway 2017). Moreover, oxidative stress is generally increased for wild animals in urban ecosystems (Isaksson 2010). Oxidative stress is a state of imbalance between pro and antioxidants, causing damage to biomolecules and subsequently increasing risk for various diseases, and is recognized as a unifying consequence of exposure to chemical pollutants (Isaksson 2010). The relatively higher oxidative stress in urban areas suggests a general physiological toll from pollutants on wildlife residing in cities.

More than chemical pollution, urbanization is also linked to increased intensity of artificial light and noise pollution. Artificial illumination is strongly correlated to human settlements and currently less than 40% of Europeans are able to see the Milky Way due to artificial light at night, a type of pollution which is increasing in both extent and intensity (Falchi et al. 2016, Kyba et al. 2017). Light pollution can affect the phenology of vegetation and interact with temperature to advance reproduction in passerine birds (French-Constant et al. 2016, Dominoni et al. 2020). Light pollution has been suggested as a key driver of insect declines and is associated with lower abundances of caterpillars, linking back to food availability for birds (Owens et al. 2020, Boyes et al. 2021). Artificial light at night can also directly impact the physiology of birds by affecting immune function and hormone levels (Sanders et al. 2021, Ziegler et al. 2021). Light exposure correlates to behavioral changes as well, for example advanced onset of activity and singing in the morning, at least in some bird species (Da Silva et al. 2016, De Jong et al. 2017, but see Da Silva et al. 2017). The increased noise associated with urbanization, e.g., from traffic, has similarly been suggested to affect the behavior of birds, with urban birds changing their vocalizations in cities, seemingly to be heard over the disturbance of noise pollution (Halfwerk and Slabbekoorn 2009). Taken together, there are many forms of human-generated pollutants that can disturb individual organisms, or ecological processes in cities, with possibility of interactions between pollutants, or different effects between trophic levels. Comprehensive understanding of the specific pollutants and their potential interactions is vital to mitigate adverse effects on the urban ecosystem.

Human-nature relationship

While one can study biotic and abiotic effects shaping urban ecosystems in isolation, it is important to keep in mind that cities are an environment type designed and managed by humans, with human interests at hand. Hence, the relationship between people and nature in many ways sets the frame for the urban ecosystem. Although nature conservation often positively influences local residents by creating ecosystem services (e.g., vegetation improving air quality), there is also potential for conflicts between urban nature and people (Felappi et al. 2020). On a local level, this can be between the need for visibility in parks due to security concerns, while animal populations benefit from thick undergrowth and low levels of light at night, as discussed above (Beninde et al. 2015, Felappi et al. 2020). On a planning level, studies suggest land-sparing, i.e., concentrating nature in large parks rather than intermingling it with other infrastructure, is beneficial for supporting urban biodiversity (Soga et al. 2014, Ekroos et al. 2020). Here, the conflict of interests could arise on a societal level, where a city designed to concentrate nature in specific areas is likely to lead a shift in access to nature and ecosystem services towards higher socio-economic strata, the so-called '*luxury effect*' (Hope et al. 2003). This is of importance since there are several, and increasingly well-documented, positive effects of access to nature on human health (Hartig et al. 2014). For example, the number of trees close to city homes has been found to positively and significantly impact how local residents evaluate their well-being (ten trees on the city block had a similar magnitude of effect as being seven years younger; Kardan et al. 2015). Other studies have shown the importance of greenspace in the vicinity of schools for children's cognitive development (Dadvand et al. 2015). This effect has in part been explained by a decrease in air pollutants associated with higher proportions of greenspace, but other mechanisms are at play too: exposure to a diverse microbiota increases the immune function of children (Roslund et al. 2020) and access to nature has positive effects on the mental well-being of both adults and children (Fuller et al. 2007, Hartig et al. 2014, Chawla et al. 2014). Moreover, perceived biodiversity enhances the effects on well-being spending time in e.g., a city park, will have (Fuller et al. 2007, Dallimer et al. 2012). Similarly, our appreciation of urban landscapes increases if we hear a diversity of birdsong (Hedblom et al. 2014).

With the current extent of urbanization (Figure 2), most of the world's population relies on urban nature for local ecosystem services, and everyday interactions with nature, to reap the benefits described above. As stated before, this is an important prerequisite to consider when studying the urban ecosystem, which is designed to meet human preferences. Moreover, it is also important to recognize urban nature from a conservation perspective, as it has been argued that decimated urban ecosystems will decrease the public's will to further conserve nature in general, since people cannot relate to biodiversity in their everyday lives (the '*pigeon paradox*'; Dunn et al. 2006).

A similar trend, called the '*extinction of experience*', suggests the removal of everyday nature could alienate people in a downward spiral, where few previous nature interactions decrease the likelihood of gaining future experiences (Pyle 1978, Soga and Gaston 2016). Being exposed to nature, especially at an early age, is a key factor for engaging in environmental questions later in life (Chawla 1999), and local stewardship is another important motivation for conservation, as people tend to care most about nature in their vicinity (Shwartz et al. 2012, Brock et al. 2017). Thus, the relationship between people and urban nature is a fundamental aspect of the local ecosystem and is also consequential for both human well-being and biodiversity conservation in general.

In summary, gaining a better ecological understanding of our cities is highly relevant and has received growing attention during the last decades (Marzluff 2017). Today, the impacts of urbanization on plants and wildlife are increasingly well-documented and the emergence of larger and longer-term studies has helped identify general effects of urbanization. There are however still many questions that remain to be answered in our progression towards fully understanding the urban ecosystem. These include isolating and disentangling specific pollutants and adverse effects on wildlife linked to urbanization. Exploring how the effects vary in intensity and importance throughout the urban landscape is also key, as well as investigating potential interactions between them. Lastly, combining methodologies from several different fields is needed to fully understand the ecological consequences of urbanization. In this thesis, I aim to provide new knowledge to the field by exploring these questions with multiple methods and study-species, striving to create an encompassing picture of the urban ecosystem.

Material and methods

Study sites

All fieldwork was carried out in the province of Scania, in southern Sweden. The biological fieldwork (*Chapters I-IV*) was primarily focused on city-center parks within Malmö, the third largest city of Sweden with approximately 350 000 inhabitants (Figure 4). The study parks range in size from 3 to 45 ha and are characterized by a mixture of trees, managed lawns, and smaller waterbodies, as well as infrastructure such as paths, paved roads, and lampposts. Based on the local municipality tree database, there are over 150 tree species in the parks, a majority of which are non-native to Sweden. The parks are however dominated by native trees in absolute numbers, such as European beech (*Fagus sylvatica*), while non-native trees account for around 23%.

In *Chapters I*, *III,* and *IV*, a rural reference site was used: the nature reserve of Skrylle, located approximately 26 km northeast of the city of Malmö. The nature reserve spans 500 ha; our study sites are located within a part dominated by native forest, consisting mainly of European beech, silver birch (*Betula pendula*), and common oak (*Quercus robur*), with some patches of European spruce (*Picea abies*), interspersed by small gravel roads, and divided by one larger, trafficked, and illuminated tarmac road. Within the site, we have monitored a nest box population of 370 boxes for blue and great tits since 2017, used in *Chapters III* and *IV*. In Malmö, we monitored a population, consisting of 400 boxes in five parks, that was established in 2013 and used in *Chapters II-IV* (Figure 4).

Figure 4. Map over the study cities in southern Sweden and nest box populations. Left panel shows the study parks of Malmö and the 400 nest boxes within (black dots). Right panel shows the nature reserve of Skrylle and the 370 nest boxes located there.

Chapter VI included 14 urban and rural schools located within and around three cities in Scania: Malmö (described above), Helsingborg with 115 000 inhabitants, and Lund with 95 000. The schools were selected to vary in urbanization degree and socioeconomic factors of the surrounding areas. To ensure anonymity of the teachers and children in the participating schools, their exact locations are not disclosed. The experiment in *Chapter V* was conducted in the Aerosol laboratory of the Department of Design Sciences at Lund University.

Study species and relevant taxa

In this thesis, I aimed to study multiple trophic levels of the urban ecosystem and I therefore did not focus on a single study species, instead, my thesis encompasses several taxa. Even so, most chapters (*II-V*) focused on avian ecology or physiology. Being a conspicuous and popular taxon, birds are commonly studied in the field of urban ecology and therefore, there is a solid and growing body of urban avian research to expand on (Marzluff 2017).

Chapters II-IV focused on the great tit (*Parus major*), a small passerine (approximately 18 g) common in woodlands throughout Eurasia (Figure 5). The great tit can however be found in a wide variety of habitats, including cities, and is considered an urban adapter (see Box 1; Croci et al. 2008), making it one of the most well-studied species in urban avian ecology (Chamberlain et al. 2009). Being cavity nesters, great tits are also easily studied during breeding using nest box populations; a contributing factor to their well-documented life-history, which has been pivotal to several advances in population ecology and evolutionary biology (e.g., Perrins 1965, Boyce and Perrins 1987, Visser et al. 1998, Charmantier et al. 2008). During breeding great tits primarily rely on caterpillars (Lepidoptera) and spiders (Araneae) as food sources, to the extent that the peak in caterpillar biomass generally modulates great tit breeding phenology (van Noordwijk et al. 1995, Naef-Daenzer et al. 2000). During winter, their diet widens, and they are commonly seen on bird feeders foraging e.g., sunflower seeds.

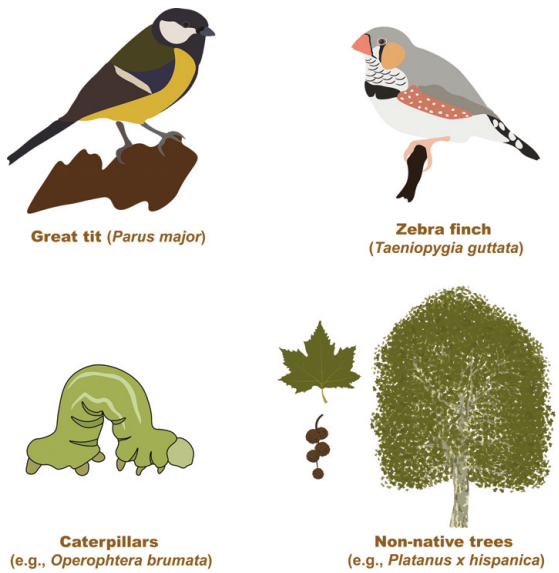

Figure 5. Illustrations of study species and relevant taxa: great tits (*Parus major*), zebra finches (*Taeniopygia guttata*), caterpillars (Lepidoptera), and non-native trees.

In *Chapter V*, the zebra finch (*Taeniopygia guttata*) was used as a study organism. Slightly smaller than a great tit, zebra finches commonly weigh around 14 g and are native to Australia. Zebra finches are gregarious and granivorous and are often found foraging in flocks on grasslands in the wild. They are also a well-studied species and a commonly used avian study organism for laboratory studies (Griffith and Buchanan 2010).

While not a taxonomic group, the classification of 'non-native' was used for trees in *Chapters I*, *II,* and *IV*. Several definitions of 'non-native origin' have been

proposed for plants, with varying cut-off points based on time since introduction, geographical barriers crossed, and mode of transport (human-aided or not; Essl et al. 2018). It is however important to note that from an ecological perspective 'nativeness' is a continuous scale, being determined by factors such as phylogenetic distance to local species and time since introduction (Brändle et al. 2008, Burghardt and Tallamy 2015, Kärvemo et al. 2023). What the term really refers to is the length of co-evolutionary history between a given species and other species within the ecosystem, which is highly important for facilitating biodiversity (Ehrlich and Raven 1964). In line with this, the single systematic review (as of writing) of literature investigating non-native plants and biodiversity in urban areas, showed that the negative impact of non-native plants is general regardless of exact definition (Berthon et al. 2021). Here, we defined the cut-off point for native and non-native plants to the 13th century and on a country level (Sweden). Thus, we used a conservative definition, which is based on the time-period for large-scale European sea travel (Essl et al. 2018), to avoid overestimating effects which could occur if only comparing the most recent introductions with the rest of the ecosystem. Given the scale of plant introductions, with 25% of urban plant species being non-native globally (Aronson et al. 2014, van Kleunen et al. 2015), general and applicable ecological knowledge is much needed. To this end, 'non-native' serves as a highly relevant demarcation and group of species, although large variation is of course also found between individual non-native species (Berthon et al. 2021).

Caterpillars, the larvae of butterflies and moths (Lepidoptera), are staple in the diet of many insectivorous bird species during breeding (Naef-Daenzer et al. 2000). Caterpillars were studied in *Chapter I* through shake-sampling of branches and collection of frass, the feces of caterpillars. Moreover, being a preferred and important prey for breeding great tits, the life-history of caterpillars is of importance to *Chapters II-IV* as well. Herbivorous caterpillars are closely linked to the phenology of their host plants, relying on cues from temperature and photoperiod for hatching (van Asch and Visser 2007). Species feeding on trees typically emerge synchronous to bud burst, as a mismatch of only a few days can have negative impacts on caterpillar populations, with leaves quickly increasing in phytochemicals while water and nitrogen content decreases (van Asch and Visser 2007). The synchrony of caterpillars leads to peaks in the biomass of common species, such as the winter moth (*Operophtera brumata*), which in turn insectivorous birds, relying on caterpillars for food, modulate their own breeding phenology to match (van Noordwijk et al. 1995). Winter moth caterpillars are very common in late spring (from approximately April-June) and are found in the canopy of deciduous trees such as oaks (*Quercus spp.*) in Sweden. The caterpillars pupate in the top layer of the soil in summer; in late autumn the adults emerge, giving the winter moth its name (Cuming 1961). Females are flightless and climb tree stems to deposit eggs on the bark after attracting a mate through pheromones. Caterpillars use silk threads to balloon as a mode of dispersal (Cuming 1961).

Overview of methodologies

To address my research questions in a complete manner, I not only studied multiple taxa, but I also used a multitude of methods, drawing from different fields of study. With cities being hotspots for many changes to the environment, as well as junctures between people and nature, the urban ecosystem needs to be viewed from multiple perspectives to be fully understood (Öberg 2011). *Chapters I* and *II* were observation based, relying on traditional ecological methods: nest box population monitoring, direct and indirect arthropod sampling, together with microhabitat vegetation and phenology measures. In *Chapter III*, a field experiment was performed, combining measures of nestling growth with physiological markers (hemoglobin and fatty acid levels; see below). *Chapters IV* and *V* also relied on physiological measures, here focusing on both oxidative stress and nutritional physiology in birds. Moreover, both these chapters included air pollutants: in *Chapter IV* ambient air pollutants (NO_2 and $PM_{2.5}$) were quantified through point measures and related to the microhabitat, and *Chapter V* used exposure to air pollution (ozone) as a treatment in a fully controlled laboratory experiment. Lastly, *Chapter VI* was based on qualitative methods, with questionnaires, semi-structured interviews, and brief fieldnotes, analyzed together with demographic variables. In other words, my thesis as a whole takes an interdisciplinary approach, combining methods from the fields of Ecology, Physiology, Sociology, and Aerosol technology to answer the question of how urban ecosystems function, and impact both wildlife and people.

Laboratory analysis and biomarkers

Fatty acid analysis

We quantified the composition of fatty acids (FAs) circulating in the blood plasma of great tits in *Chapters III*, *IV*, and for a subset of the zebra finches in *Chapter V*. Given the relatively rapid turnover rate of blood, circulating fatty acids largely mirror dietary intake, but the composition is also influenced by physiological processes such as selective mobilization and biosynthesis of FAs (Box 2).

Oxidative stress biomarkers

We used several biomarkers of oxidative stress in *Chapters IV* and *V*, estimating both antioxidant capacity and oxidative damage, to capture the full response to air pollutants and other potential oxidative challenges. In *Chapter IV*, we used the ferric reducing antioxidant power (FRAP) assay for avian plasma as a measure of total non-enzymatic antioxidant potential (Benzie and Strain 1996). Uric acid (the end-product of protein catabolism) can influence the FRAP measure but is unlikely to be of ecological relevance in terms of oxidative stress physiology (Cohen et al.

2007, Costantini 2011). We therefore measured and corrected for uric acid, using the uricase/peroxidase method (Salmón et al. 2018). In *Chapter V*, we used the total concentration of the key cellular antioxidant glutathione (GSH) in red blood cells, together with the levels of its oxidized form (GSSG), as a measure for oxidative defense (Baker et al. 1990). Additionally, we also used the OXY-adsorbent assay (Costantini et al. 2006), which measures the antioxidant barrier of plasma by simulating a pro-oxidant attack, using hypochlorous acid (HOCl). To estimate oxidative damage, we quantified malondialdehyde (MDA) in plasma, an end-product of lipid peroxidation, used in *Chapter IV*. In *Chapter V*, we measured reactive oxygen metabolites (ROMs: i.e., hydroperoxides) in the plasma, using the dROM assay (Costantini et al. 2006).

Hemoglobin

In *Chapter III* we used hemoglobin, the oxygen binding protein of red blood cells, as a biomarker for physiological condition. Hemoglobin concentration has been shown to be a reliable proxy for overall condition in birds, when age and season are taken into account (Minias 2015). We used a medical grade whole-blood absorbance reader to measure the hemoglobin levels of great tit nestlings in the field.

Results and discussion

Non-native trees and food limitation (Chapters I-III)

The altered composition of urban vegetation is not without consequence: studies have suggested non-native plants drive insect declines, and plant origin has been found to be a deciding factor for hosted biodiversity (Tallamy et al. 2021, Berthon et al. 2021). The mechanism linking non-native plants to lower biodiversity is not fully clear but is likely connected to novel phytochemicals and shifted phenology (Cappuccino and Arnason 2006, Burghardt and Tallamy 2015). Non-native trees have also been linked to negative effects on avian populations, likely because these trees provide less food to birds in the form of arthropods (Narango et al. 2018, Wood and Esaian 2020). It is therefore likely that non-native plants contribute to food limitation in cities, something which is believed to affect many urban bird populations (Chamberlain et al. 2009, Seress et al. 2020). Diet shifts to less preferred food have been documented for urban birds (Pollock et al. 2017, Jarrett et al. 2020), but the nutritional consequences from this, e.g., suboptimal composition of lipids (see Box 2), remains largely unknown (Trautenberg et al. 2022). Moreover, the relative importance of plant origin, in comparison to other urban effects that can negatively influence animal populations, is not well-studied.

In *Chapter I*, we investigated the relative impact of origin and urbanization on tree phenology and arthropod abundances. Our results showed that non-native park trees were associated with significantly fewer arthropods compared to native trees, both in terms of tree-dwelling species and flying insects. Importantly, plant species origin showed a greater magnitude of effect, compared to the 'urban effect' (the differences between native urban and rural trees). As an example, we observed a later phenology of non-native trees, reaching bud burst on average 8 days later than native species (Figure 6); a greater and contrasting difference to the urban effect of 6-day advance in bud burst for native trees, likely caused by a heat island effect measured to 1.4°C. Given the magnitude of the observed origin effect, and the lack of any negative effect linked to urbanization in terms of arthropod abundance on native trees, the results from *Chapter I* suggest tree origin is a major contributing factor to the diminished arthropod communities of cities (Tallamy et al. 2021, Chatelain et al. 2023).

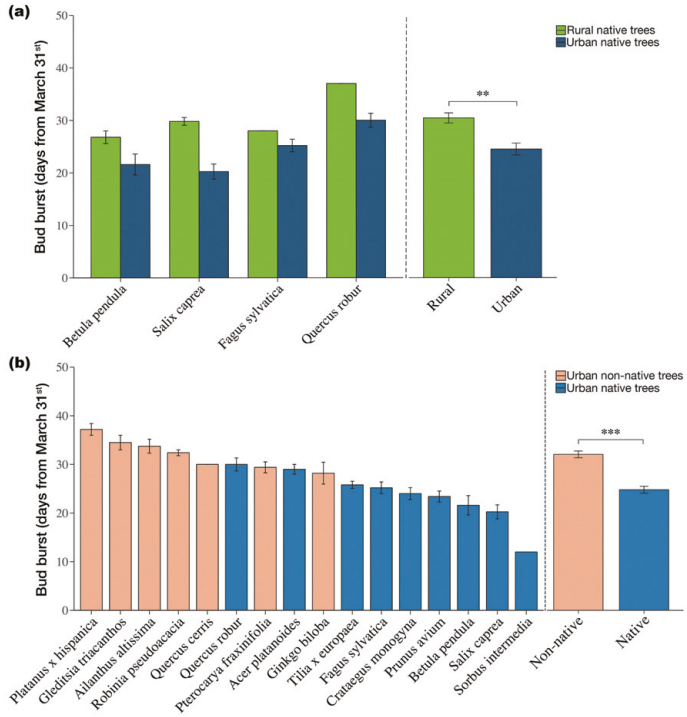

Figure 6. Bud burst phenology of native and non-native tree species in days from March 31st, depending on **(a)** environment (urban/rural) and **(b)** species origin (native/non-native). The bars show mean ±SE of raw data; the two right-most bars show mean values for all native and non-native species, respectively. Significance levels are indicated by asterisks (**p = 0.01 – 0.001, ***p < 0.001). Note that for *Quercus cerris*, rural *Fagus sylvatica,* and rural *Quercus robur* no error bar is visible since all individuals reached bud burst the same day. For *Sorbus intermedia*, only one individual was surveyed. Adapted from Figure 3 of *Chapter I*.

In *Chapter II* we expanded on these findings by including another trophic level: insectivorous birds. We set out to establish what constitutes a high-quality habitat in the urban ecosystem in terms of tree composition, specifically looking at the breeding performance of great and blue tits. We found that the probability of a breeding attempt declined with the number of non-native trees in the local territory (defined as a 35 m radius from the nest box; Jarrett et al. 2020). Moreover, we found that great tit nestling weight decreased with a higher number of non-native trees, which suggests the avoidance of these territories was adaptive and likely caused by low food abundance linked to the trees (*Chapter I*; Narango et al. 2018). Notably, we found that the negative effects associated with non-native trees were consistent across the 7 years that *Chapter II* encompassed, and regardless of when in the season the birds started breeding (Figure 7a).

The sampling for *Chapter I* was centered around bud burst and the breeding season of the great tits (van Noordwijk et al. 1995), and with only data from one year, a limitation of this study was thus its temporal scale. The results of *Chapter II* however corroborate the ecological significance of the lower arthropod abundances on non-native trees (*Chapter I*), and suggest the effect is constant across years (and habitats, see Narango et al. 2018, Wood and Esaian 2020).

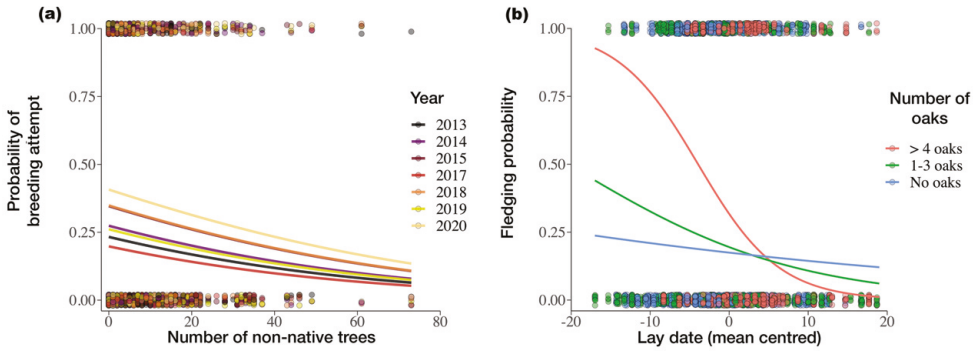

Figure 7. Correlations between local tree composition and **(a)** breeding probability of blue and great tits (*Cyanistes caeruleus* and *Parus major*) and **(b)** probability of a great tit surviving from egg to day 14 nestling, depending on local tree composition. The probability of breeding attempts decreased with increasing numbers of non-native trees in the vicinity of the nest box all years of the study (2013-2020). The chance of reaching fledgling age showed an interaction between the number of oak trees (*Quercus robur*) and onset of breeding: breeding earlier in oak-rich areas was especially positive for nestling survival. While modeled as covariates, oak numbers are separated into discrete groups for ease of visualization; corresponding trendlines represent the average model fit. Adapted from Figures 2a and 3a of *Chapter II*.

The causal link between avian breeding performance and local trees being food limitation was hypothetical in *Chapter II* (but based on literature: Chamberlain et al. 2009, Seress et al. 2020). To establish whether urban great tits were food-limited during breeding, and to disentangle what aspect of the diet might be lacking, we performed the field experiment of *Chapter III*. Here, we divided broods into a general food provisioning treatment, and nestlings within broods to a specific nutrient supplement, aiming to test the polyunsaturated fatty acid DHA as a limiting nutrient in urban ecosystems (Box 2; Twining et al. 2016). Our results revealed positive effects of DHA supplementation on nestling development, significantly increasing wing-length, and showing a near-significant trend of mass, but only in urban broods (Figure 8). Moreover, DHA supplementation increased the hemoglobin levels (a proxy for physiological condition; Minias 2015), but again only in urban nestlings. Despite a higher depletion of the *ad libitum* provisioned mealworms in urban areas, the added food availability did not seem to benefit the nestlings. Instead, our findings in *Chapter III* suggest urban birds are limited by diet composition and quality.

Being involved in the development of skeletal muscle and brain tissue (Speake and Wood 2005), a scarcity of DHA could limit growth but possibly also cognitive development (Lamarre et al. 2021). Urban birds have been suggested to be under selection for increased cognition (Sol et al. 2013, Salmón et al. 2021) and our results of higher circulating DHA in breeding urban adults could indicate that the fatty acid is of particular importance in cities.

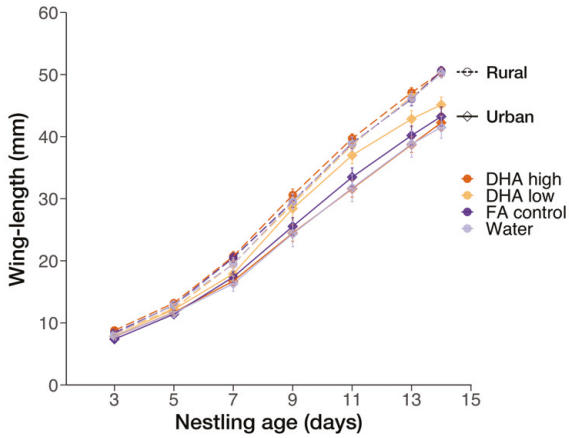

Figure 8. Growth of urban and rural great tit (*Parus major*) nestlings depending on experimental fatty acid supplementation. Wing-length differed significantly between habitats but increased with DHA supplement at a low dosage for urban nestlings (solid yellow line). Error bars are ±SE. Adapted from Figure 2a of *Chapter III*.

Given the results of *Chapters I-III*, a likely explanation for the lower reproductive performance of urban birds is a lack of arthropod species containing specific nutrients. DHA only occurs in low levels in the natural diet of great tits (Andersson et al. 2015), and conversion from precursors such as EPA is therefore the most likely source of DHA in our study system (Box 2; Twining et al. 2018, 2021b). Since spiders contain relatively high levels of EPA, they are probable candidates as principal sources of DHA to great tit nestlings, although further studies are needed (Naef-Daenzer et al. 2000, Andersson et al. 2015). Availability of nutrients is however not only mediated by prey abundance, but also by timing: phenological mismatches may occur on a nutritional plane, where peaks of biomass can be decoupled from peaks of specific nutrients (Twining et al. 2022). In both *Chapter I* and *II* we found indications of phenological mismatches taking place in the urban ecosystem: in *Chapter I*, we observed caterpillar biomass peaking on non-native trees prior to bud burst. For comparison, the biomass peak linked to native trees tended to occur 1-2 weeks after bud burst. In *Chapter II*, the effects of native vegetation on avian breeding performance varied within and between years.

An example of one of these temporal interactions is the effect of oak trees on fledging probability (survival from egg to day 14 nestling), which varied in strength depending on the birds' breeding onset (Figure 7b). Breeding earlier than the year average was especially positive in oak-rich territories, but the local number of oak trees however also correlated to breeding onset itself, appearing to significantly delay the egg laying of great tits (*Chapter II*). Oak trees typically modulate great tit breeding phenology in forest populations and are late in their food peak compared to other native trees (*Chapter I*; van Noordwijk et al. 1995). In contrast to forest populations, the response of delayed breeding appears maladaptive in urban environments, based on the correlation to fledging probability discussed above (Figure 7b). How these potential phenological mismatches impact the nutritional ecology of urban birds is unknown, although mismatches can be amplified across trophic levels (Both et al. 2009). Thus far, phenological mismatches have typically been studied in the context of climate change (e.g., Both et al. 2009, Twining et al. 2022), but with both plant composition and local temperature impacting the phenology of urban plants, similar shifts are likely to take place in urban environments (*Chapter I*, Dallimer et al. 2016, Fisogni et al. 2020). Urban phenological mismatches remain to be further explored but may prove increasingly relevant with progressing climate change.

Taken together, *Chapters I-III* showed that the composition of urban vegetation is a key factor in the urban ecosystem. Specifically, we found non-native trees to have strong and consistently negative impacts on higher trophic levels. Urban birds are limited in their reproduction by specific nutrients, rather than food quantity *per se*, which highlights the need for biodiversity in the urban areas, but also that detailed knowledge of biological processes is required to truly understand the urban ecosystem. From a practical perspective, it is important to underscore that *Chapters I-III* were carried out in city parks, which both host a significant portion of urban biodiversity and ecosystem services (Nielsen et al. 2014, Stott et al. 2015). Parks also constitute more benign habitats for vegetation than e.g., streetscapes, where non-native plants (preferably carefully selected) are still required under current city designs. Increasing native vegetation in the urban environment where it is possible, together with efforts to minimize heat island effects (and thereby the risk for phenological mismatches), are two general recommendations that can be derived from the findings in *Chapters I-III*.

Multiple anthropogenic factors (Chapters IV and V)

While *Chapters I-III* primarily focus on biotic effects in cities, there is also a multitude of abiotic factors that define the urban ecosystem. A current challenge in the field of urban ecology is to disentangle these factors from each other, which is both important to fully understand the ecosystem and to provide clear conservation advice. Environmental gradients have been useful in identifying responses of plant and animal populations to urbanization in general (McDonnell and Pickett 1990), but less so in shedding light on the mechanisms behind them (Sprau et al. 2017). Moreover, many anthropogenic factors co-occur and have the potential to interact, e.g., temperature and artificial light at night (Dominoni et al. 2020, Tougeron and Sanders 2023). Understanding interactions between two or more factors that potentially magnify negative effects on urban organisms is particularly important (Côté et al. 2016), since some factors may be more manageable to mitigate than others (for example, it might be easier to dim artificial light in warm areas of a city, than lowering the ambient temperature). To this end, physiological biomarkers can be particularly useful. Not only does physiology respond more rapidly to environmental changes than e.g., life-history (Isaksson 2020), but documenting mechanistic responses can also help in generalizing results and identify species with shared traits, that might be particularly vulnerable to a given anthropogenic factor or interaction.

In *Chapters IV* and *V*, we explored multiple anthropogenic changes to the environment and their interactions in relation to avian physiology. *Chapter IV* was observational, using *in situ* variation of environmental factors related to urbanization: tree composition, temperature, artificial light, and air pollutant concentrations (NO_2 and $PM_{2.5}$). The results of *Chapter IV* suggest that a gradient approach is too coarse to fully identify physiological impacts linked to the local environment. This was exemplified by oak trees and the local level of the air pollutant $PM_{2.5}$ both being associated with decreased antioxidant capacity of great tit nestlings, although, in terms of environmental variation, high $PM_{2.5}$ levels were associated with more urbanized areas, while oak trees were not (Figure 9). Given this relationship, the effects of $PM_{2.5}$ and oak trees on avian antioxidant capacity were effectively masked in a generalized analysis of the environment (i.e., principal component analysis). We however found little evidence for the hypothesized interactions between anthropogenic factors in *Chapter IV*. Instead, most effects found were directly linked either to vegetation or air pollution, both of which also appeared to influence the nutritional status of the nestlings, with correlations to the ratio of circulating ω6:ω3-PUFAs in nestlings, which bears consequence to immune function (see Box 2).

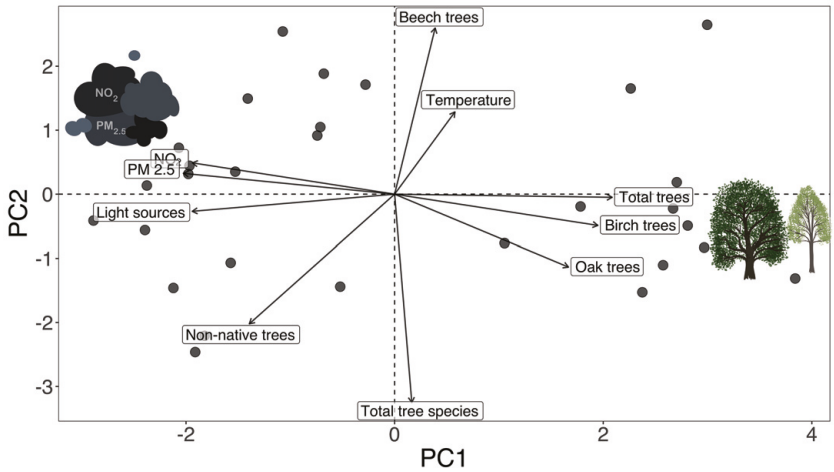

Figure 9. Graphical representation of the two principal components (PCs) summarizing the most variance of microhabitat characteristics linked to urbanization, based on a principal component analysis (PCA). Note that air pollutants and the density of oak trees loaded at opposing directions of PC1. Adapted from Figure 2 of *Chapter IV*.

In *Chapter V*, we performed a controlled experiment aiming to shed light on the potential interaction between air pollution, altered diet (specifically ω6 and ω3-PUFAs), and increased disease prevalence, in their combined effect on avian physiology. Our results showed that zebra finches given a diet high in ω6-PUFAs, which is typical for anthropogenic food and the commonly provisioned sunflower seeds (Simopoulos 2011, Reynolds et al. 2017), had a relatively high ratio of the oxidative stress measure GSH/GSSG in ambient air (Figure 10). A recycling of the GSH/GSSG ratio (reducing GSSG back to active form GSH, through an upregulation of the enzyme glutathione reductase) could indicate a response to meet an oxidative challenge, incited by ω6-PUFAs through their pro-inflammatory properties (Calder and Grimble 2002). The birds that were fed an ω3-diet, typically found in flax seeds, or arthropods such as caterpillars (Andersson et al. 2015), showed a comparatively lower GSH/GSSG ratio under ambient air. Under the additional oxidative pressure of ozone exposure, however, both diet groups displayed an intermediate level of GSH/GSSG. The decrease in the ratio of antioxidants of ω6-fed birds when exposed to additional pro-oxidants likely indicated a depletion of defenses and the beginning of oxidative stress, while ω3-fed birds appeared able to upregulate their antioxidants in response to the air pollutant. While we did not find statistical support for a three-way interaction, this pattern does appear partly driven by the birds that were administered lipopolysaccharide (LPS) to simulate an infection (Figure 10). Immune responses are known to cause oxidative damage (Armour et al. 2020), which we also observed in response to the LPS treatment, regardless of diet. In simple terms, ω3-fed birds appeared more prepared to meet further oxidative challenges than ω6-fed birds, for example from infection.

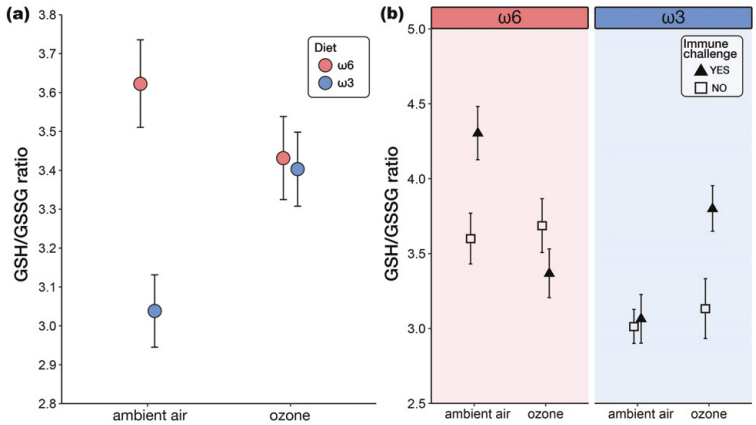

Figure 10. The significant interaction between diet treatment (ω6 versus ω3 PUFAs) and ozone exposure on the oxidative stress measure GSH/GSSG-ratio: reduced (GSH) over oxidized (GSSG) glutathione. Panel **(a)** shows general values for diet groups, while **(b)** shows values of immune challenge subgroups. Means ±SE of predicted values from models are shown. Note the different y-axis scales. Adapted from Figure 2 of *Chapter V*.

Urbanization has previously been shown to affect the ω6:ω3-PUFA ratio in birds, specifically lowering levels of ω3-PUFAs (Andersson et al. 2015). Our findings in *Chapter IV* suggest this effect is driven by specific environmental factors. Given the findings of *Chapter II* on annual variation however, we are careful to not extrapolate the results of *Chapter IV* (a one-year study) too far, in terms of the generality of effects from individual factors. Nevertheless, quality of food is often more important than quantity (*Chapter III*, Twining et al. 2016), and without dietary access to optimal food sources, birds are less likely to handle the multiple habitat changes associated with human activities and cities. A potential link between infection and diet is particularly interesting, since bird feeding could both alter the nutritional status of birds as well as increase the risk for disease transmission (Moyers et al. 2018, Lawson et al. 2018, but see Watson et al. 2023). I do however note that we found less evidence for synergistic interactions (enhancing effects) between anthropogenic factors in both *Chapters IV* and *V* than expected. It has previously been proposed that the magnifying effect of multiple anthropogenic factors might be overstated since interactions often are assumed to be synergistic (Côté et al. 2016). Indeed, as we observed for antioxidants in *Chapter IV*, certain changes to the environment can be antagonistic in their effect on organisms, obscuring their individual impact. Identifying such patterns and linking organismal responses to specific environmental factors is central to understanding the urban ecosystem, being a crucible of human-driven changes. Antagonistic interactions are also important to understand in terms of conservation, since efforts to alleviate negative impacts otherwise risk having less effect than expected.

Cities are however heterogeneous landscapes and factors such as e.g., air pollution and ambient temperature can vary in intensity at local scales. To identify which of the numerous potential interactions might bear ecological relevance in urban areas, further mapping of the actual co-occurrence of environmental factors across several cities would make for much-needed guidance. In summary, moving the field of urban ecology forward requires a multidimensional view of the environment to identify specific factors for conservation and planning prioritization (*Chapter IV*, Côté et al. 2016).

Value of urban wildlife to humans (Chapter VI)

The preceding sections (*Chapters I-V*) focus on urbanization's impact on plants and wildlife, but do not consider *why* the urban environment is configured the way it is, nor the root cause for the changes to local habitats. Understanding the forces that shape urban nature requires knowledge about people's perceptions and attitudes towards it, as well as their need for and utilization of local ecosystem services. Bird feeding is for example often motivated by a sense of stewardship and will to help local animals (Cox and Gaston 2016, Brock et al. 2017), although as discussed above, this may not always be the outcome (*Chapter III*, Plummer et al. 2013b). Bird feeding still provides a valuable ecosystem service by connecting people to local wildlife (Cox and Gaston 2016) and has been proposed as a way to ameliorate the disconnect to nature, which is believed to impact especially urban children (Beck et al. 2001, Soga and Gaston 2016, White et al. 2018).

In the last chapter of my thesis, *Chapter VI*, we explored how children's relation to nature is shaped. Using bird feeding as an intervention to increase nature interaction, we aimed to evaluate its effectiveness in connecting urban children to nature, and at the same time identify which factors modulate this connection. In contrast to the studies proposing a disconnect from nature caused by urbanization (Dunn et al. 2006, Soga and Gaston 2016), we did not find that children from urban schools differed in their species knowledge or attitude towards birds compared to those in rural schools. We instead found that other area factors modulated knowledge and attitude towards nature: higher education levels in attendance areas were correlated to better species knowledge of the children. Higher income correlated to children participating in more nature-based activities, which in turn positively influenced attitudes towards nature and the bird feeding intervention itself (Figure 11). This snowballing effect of previous nature experiences increasing the positive sentiment toward other activities, and nature in general, is in line with the extinction of experience hypothesis (Pyle 1978, Soga and Gaston 2016), although we did not see the predicted decline in attitude towards nature linked to urbanization. Interestingly, we instead found that the characteristics of the local nature (yards closest to where the children lived) interacted with the impact of the bird feeding intervention, so

that children with less nature close to their homes gained more in terms of species knowledge from the project. Additionally, we found a large variance between schools in terms of the impact of the intervention, which is likely caused by the teachers' role in facilitating the project (Chawla 1999).

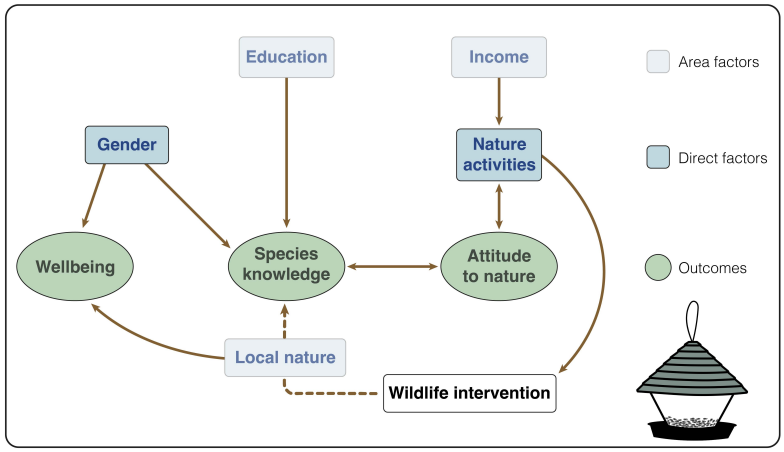

Figure 11. Direct and indirect factors modulating children's species knowledge and attitude toward birds, as well as self-perceived well-being. Solid arrows indicate significant correlations and dashed arrows interactive effects. Adapted from Figure 2 of *Chapter VI*.

While not formally included in *Chapter VI*, preliminary analysis of interviews performed with participating teachers indicated that low-quality habitats (no birds) and too few resources (time and/or personal) were common themes for challenges in the project. Interestingly, in schools with a relatively high diversity of birds, local nature was seldom noted as an important aspect of a successful project, but rather the connection to research was highlighted as making the project 'real' and more motivating for the pupils. Although not acknowledged, local habitat qualities that support avian populations, such as bird-friendly trees (*Chapter II*, Narango et al. 2018), are clearly needed for these types of projects to be meaningful and could in addition buffer against the potential negative nutritional influence from bird feeding (*Chapters III* and *V*, Plummer et al. 2013b). In conclusion, *Chapter VI* shows that a wildlife interaction, such as bird feeding, can positively influence children's species knowledge, but this knowledge, and ultimately attitude towards nature, is modulated by several other factors. Bird feeding does not improve connection to nature *per se*, but with the correct role models and context, it can be an important avenue for children to learn about wildlife, especially in areas with less nature and lower socioeconomic levels. These patterns do not appear directly coupled to urbanization, although diverse local nature is a prerequisite for wildlife interventions to be successful, together with sufficient support to teachers.

Conclusion

The urban ecosystem is a crucial intersection of humans and nature. For plants and animals, cities represent some of the most altered habitats in the world, with numerous novel challenges and resources. For people, a majority will experience and rely on the resulting urban nature for everyday interactions and ecosystem services. In this thesis, I have used an interdisciplinary approach, aiming to further our understanding of how anthropogenic changes to the environment affect local ecosystems, and in turn, how the urban ecosystem may influence us. I found that plant origin, namely the introduction of non-native trees, has strong negative effects on both arthropods and birds in cities (*Chapters I* and *II*). The magnitude and consistency over years of these effects indicate that vegetation composition is one of the main drivers hampering urban animal populations. The diminished and altered urban vegetation contributes to a lack of nutrients for wildlife, which cannot be compensated for by an increase in quantity of low-quality food sources, at least not for breeding birds (*Chapter III*). Furthermore, an unbalanced diet may lead to a reduced capacity to mount a physiological response to counter other anthropogenic factors, such as air pollution (*Chapter V*). Still, bird feeding can provide people with a link to local wildlife and help foster a connection to nature. As I showed in *Chapter VI*, an eroded connection to nature, which can take the form of poor species knowledge or negative sentiments towards birds, is however not necessarily linked to urbanization. Socioeconomic factors and access to local nature appeared as the actual drivers, which highlights the need to account for societal questions when studying urban nature, and the importance of city-planning which allows all children access to nature. In accordance with these findings, I suggest that urban ecology should move beyond sweeping definitions of the environment and instead look further into the variance that exists within cities. Identifying main drivers and isolating their effects is fundamental to making informed decisions in city-planning and can also help discover otherwise overlooked ecological patterns (*Chapter IV*). These patterns may take the form of interactions between co-occurring changes to the environment, although it is important to note not all interactions will amplify negative impacts. The field of urban ecology would benefit from mapping actual co-occurrence of factors to identify relevant interactions. Future studies should also further investigate the phenological interactions, and possible mismatches, taking place in urban environments.

Urbanization continues, especially in the Global South, which calls for more research in cities outside Western countries (where most studies have been performed so far), to account for local conditions and climate. Nonetheless, as urbanization begins to slow in the West, the time-window also narrows for building the often advocated for, but yet to be seen, green and sustainable cities here. Based on the results I have presented, increasing the amount and proportion of native vegetation in cities is a measure that would benefit many urban animals. Reducing the ambient temperatures of cities is likely also of importance, especially as climate change progresses. Perhaps most importantly, however, is to build cities that allow future generations to learn about species and enjoy nature near their homes.

Exotic Dangers in the Urban Forest

- A poem written by Sam Illingworth, for the podcast The Poetry of Science, inspired by *Chapters I* and *II*.

In concrete jungles
nature's pillars catch
the city's heat,
foreign tones of green
that hug the sky with
firm, unrooted ease.
Washing ashen cloaks
with verdant, leafy lungs,
gifting shade
and life
and joy.
Hidden in our hubris
these unfamiliar buds
misstep the local beats,
delaying bursts
of slumbering boughs
and creeping feed –
a brooding doubt
to native, perching wings.

Acknowledgements

I write my thanks to collaborators, colleagues, and comrades, as I sit in the middle of summer in the din of a warm city. It is hard not to get caught up in one's subject in periods of writing like this, and I will admit to spending most of my breaks watching the swifts effortlessly dive between the buildings of my block, as I wait for the greenfinch that keeps me company to return to my windowsill (note: I only endorse year-round bird feeding in periods of thesis writing). But, as I find comfort in watching the wildlife and patches of swaying trees in the distance, shouts and laughter from the playground below remind me that a city is nothing but its people. Similarly, science is nothing but the collaboration of peers and colleagues, teachers and students. For this thesis, I have many to thank:

First and foremost, I thank *Caroline Isaksson*. From the very start of my undergraduate studies, your research inspired me to learn about the urban ecosystem. More importantly, your kind and humane approach to science, and the people within, is what made me even consider starting a PhD in the first place. I will always be grateful for your support and supervision.

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