Eesti Maaülikool
Estonian University of Life Sciences

URBAN ECOLOGY: NOVEL ECOSYSTEMS, NOVEL CHALLENGES

LINNAÖKOLOOGIA: UUED ÖKOSÜSTEEMID, UUED VÄLJAKUTSED

MARTA ALÓS ORTÍ

A Thesis
for applying for the degree of Doctor of Philosophy
in Applied Biology

Väitekiri
filosoofiadoktori kraadi taotlemiseks
rakendusbioloogia erialal

Tartu 2022

Eesti Maaülikooli doktoritööd

Doctoral Theses of the
Estonian University of Life Sciences

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Opponent: Dr. **Chiara Cortinovis**
Department of Geography
Humboldt-Universität zu Berlin
Berlin, Germany

Pre-Opponent: Dr. **Aveliina Helm**
Chair of Botany
University of Tartu
Tartu, Estonia

Supervisor: Dr. **Lauri Laanisto**
Institute of Agricultural and Environmental Sciences
Estonian University of Life Sciences
Tartu, Estonia

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

The present dissertation is based on a set of research papers, which are referred to in the text by their Roman numerals (from I to IV), namely:

Paper I. Pinho, P., Casanelles-Abella, J., Luz, A. C., Kubicka, A. M., Branquinho, C., Laanisto, L., Neuenkamp, L., **Alós Ortí, M.**, Obrist, M. K., Deguines, N., Tryjanowski, P., Samson, R., Niinemets, L., & Moretti, M. (2021). Research agenda on biodiversity and ecosystem functions and services in European cities. Basic and Applied Ecology, 53, 124–133. https://doi.org/10.1016/j.baae.2021.02.014

Paper II. Alós Ortí, M., Casanelles J, Chiron F, Deguines N, Hallikma T, Jaksi P, Kwiatkowska P, Moretti M, Muyshdont B, Niinemets Ü, Pinho P, Pinto MM, Saar P, Samson R, Tryjanowski P, Van Mensel A, Laanisto L. (2022). Negative relationship between woody species density and size of urban green spaces in seven European cities. Urban Forestry & Urban Greening, 74, 127650. https://doi.org/10.1016/j.ufug.2022.127650

Paper III. Rocha, B., Matos, P., Giordani, P., Lõhmus, P., Branquinho, C., Casanelles-Abella, J., Aleixo, C., Deguines, N., Hallikma, T., Laanisto, L., Moretti, M., **Alós Ortí, M.**, Samson, R., Tryjanowski, P., Pinho, P. Modelling the effects of broad scale air pollution and climate on urban ecosystem: through the lens of lichens. Environmental Pollution. *Under review.*

Paper IV. Casanelles-Abella, J., Müller, S., Keller, A., Aleixo, C., **Alós Ortí, M.**, Chiron, F., Deguines, N., Hallikma, T., Laanisto, L., Pinho, P., Samson, R., Tryjanowski, P., Van Mensel, A., Pellissier, L., Moretti, M. (2021). How wild bees find a way in European cities: pollen metabarcoding unravels multiple feeding strategies and their effects on distribution patterns in four wild bee species. Journal of Applied Ecology, 59, 457-470 https://doi.org/10.1111/1365-2664.14063

The author's contribution to the articles were the following:

	Paper I	Paper II	Paper III	Paper IV
Study design		*		
Data collection	*	*		*
Data analysis	*	*		
Manuscript preparation	*	*	*	*

LIST OF ACRONYMS

AGB: Above-Ground Biomass
B-EF/ES: Biodiversity-Ecosystem Functions/Ecosystem Services
DBH: Diameter at Breast Height (~1.3 m from the ground)
ESs: Ecosystem Services
EU: European Union
FD: Functional Diversity
GI: Green Infrastructure
IPBES: Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services
CBD: Convention on Biological Diversity
NBSs: Nature-Based Solutions
PCA: Principal Component Analysis
PM: Particulate Matter
RaoQ: Rao's Quadratic Entropy
PI: Proximity Index
SDG: Sustainable Development Goals
TD: Taxonomic Diversity
UGSs: Urban Green Spaces
UN: United Nations

1. INTRODUCTION

The present thesis is the result of four years of PhD studies where various taxonomic groups were explored in terms of taxonomic and functional diversity in urban ecosystems at a broad scale. My research was conducted within the framework of BioVeins, a European research project aimed at studying urban biodiversity of several taxa and ecosystem functions and services in European urban areas.

Three out of four European residents currently live in cities, and projections foresee a further increase of city dwellers in the upcoming years (UN, 2019). Urban areas are a patchwork of different land use and land cover types where surfaces unsuitable for most species (e.g. industrial and residential areas) occur simultaneously with green areas (e.g. parks, cemeteries) varying in size and isolation from other similar areas (Faeth et al., 2012). Urbanization process comes along with land use change, habitat fragmentation and other stressors that compromise biodiversity creating novel ecosystems with new species assemblages (Gaston, 2010; Swan et al., 2011). Therefore, functional diversity, providing the multifaceted ecosystem services and benefits in urban communities depends on biotic and abiotic factors acting as filters of the pre-existent traits Spasojevic et al., 2018), and those arriving by natural processes such as dispersal. Novel urban communities composition are guided by processes such as stochasticity, facilitation, competition or adaptation (Kondratyeva et al., 2020). The mechanisms by which species assemble in urban ecosystems may differ from those in natural and semi-natural rural ecosystems (Mason et al., 2011), and are still not fully understood, mainly due to more factors acting in urban community composition compared to rural environments (e.g. social preferences, economic constraints, urban heat island effect).

Urban green spaces (UGSs) are often seen as potential biodiversity hotspots compared to the surrounding area, as they constitute habitat for native and non-native species, and provide food and shelter for migrating wildlife (University of California, 2014; Derbi Lewis et al., 2016), creating ecological oases in the middle of the impervious surfaces and built structures of the urban fabric. Therefore, while urbanization and urban expansion pose a major threat for biodiversity outside cities, UGSs increase habitat heterogeneity and create new opportunities for maintaining and increasing biodiversity. However, which factors and how they influence urban taxonomic and trait diversity, species composition and distribution is not fully understood in urban ecology.

In this thesis we firstly propose a research agenda where we discuss five potential research directions aimed at improving our understanding of the links between biodiversity, ecosystem functions and services (B-EF/ES) in urban areas. Then, we explore the taxonomic and functional diversity of vegetation, lichens and wild bee species and how they respond to main urban abiotic factors (e.g. landscape metrics, air pollution) and availability of food resources.

We selected a wide range of UGSs from seven cities across a NE-SW gradient of mainland Europe, namely: Tartu (Estonia), Poznan (Poland), Antwerp (Belgium), Paris (France), Zurich (Switzerland), Lisbon and Almada (Portugal). In each city, we selected sites based on the land cover class 1.4.1. Green Urban Areas included in the pan-European Urban Atlas (EEA, 2012). We used random stratified sampling for the selection of sites. We included the UGS size (area in m^2) and calculated its connectivity with other similar elements of the urban fabric by using the Proximity Index (PI) within a 5km radius from the focal UGS. Then we created a matrix formed by two orthogonal gradients comprising the size and the resulting connectivity – both classified into 6 classes – and distributed the UGSs along the matrix, resulting in a maximum of 36 possible combinations of UGS size and connectivity in each studied city. We sampled taxonomic and functional diversity of woody vegetation, lichens and floral resources used by wild bee species using a standardized sampling design framework, thus getting comparable data from the same UGSs across the continental gradient.

BioVeins research agenda identified five main research directions, namely: i) use a trait-based approach in order to improve our understanding of B-EF/ES relationships; ii) improve urban habitat mapping; iii) use citizen science to involve city dwellers in B-EF/ES research; iv) consider multiple environmental gradients; and v) include neglected urban habitats and ecological niches in urban ecology research.

In the course of fieldwork (from 2018 to 2020) we identified 418 woody species in 225 UGSs, 140 lichen species in 219 UGSs both across 7 cities, and pollen from 135 plant species as part of the larval bee diet in 80 sites from 5 cities. Regarding urban vegetation, we found high proportions of non-native woody species in all the sampled cities (i.e. from 40 to 65% of the total species pool). Species richness, vegetative above-ground biomass (AGB) and canopy cover (m^2) were positively related to UGS size, while species density steeply decreased along the size gradient.

Urban vegetation, particularly herb and tree species, represent an important food source for wild bees and their larvae in cities. Urban bee species displayed different successful feeding strategies. Specialist bee species showed more consistent diets across cities (i.e. less variation in the diet along the latitudinal gradient) compared to more polylectic (generalist) bees. Diet composition in terms of taxonomic and preferred plant traits varied with the specialization degree. Most generalist species showed a more diverse and variable diet, with a higher proportion of exotic plant species compared to more oligolectic (specialist) bee species. The probability of occurrence of medium and high specialized bees decreased with increasing urban intensity.

Regarding lichen biodiversity, Lisbon, Antwerp and Tartu showed higher diversity and abundance compared to the other cities. Cities also presented dissimilarities in terms of functional structure of lichen communities, with some exceptions. For instance, solar radiation tolerance was high across all the cities (accounting for >75% of the total lichen abundance). In general, more abundant lichens displayed a medium or medium-high tolerance to arid conditions. Broad scale environmental drivers (air pollution and climate) explained ~15% of the total variation in taxonomic and trait-related metrics for urban lichens. The remaining variance (~85%) is explained by local factors (e.g. distance to the pollution source, management practices, etc.). Within the broad scale drivers, air pollution accounted for most of the variability on that scale (10.4%). However, climate was the driver of lichen functional diversity at the broad scale, although it only explained 7.1% of the broad scale variance.

While biodiversity loss is occurring at an unprecedented rate (Leclère et al., 2020), and urbanization increasing globally (UN, 2019), it becomes necessary to integrate biodiversity conservation strategies into urban planning. For this, we need to understand B-EF/ES relationships at multi-taxa level in order to promote multi-functional urban ecosystems. UGSs are commonly vegetatively diverse environments with heterogeneity of habitats that provide a variety of food and shelter for urban taxa, such as wild bees and lichens. This high species richness is due to the big proportion of non-native species that are commonly guided by local socio-economic preferences (e.g. ornamental purposes) rather than by natural processes (e.g. dispersal).

Plant selection and, therefore, species composition have an influence on several urban taxa. For instance, non-native plant species turned to be an important component of the larval bee diet, and herbaceous and tree species were the preferred plant growth forms – with different levels of diet conservatism across cities at the plant family and genus levels. Our results suggest that while municipalities tend to promote woody species richness, especially in bigger parks, they do so up to a certain threshold, that is city-dependent. Therefore, local anthropogenic factors play an important role in designing urban biodiversity (e.g. Matos et al., 2019; Munzi et al., 2007) and ecosystem services. However, broad-scale drivers also need to be considered since they account for an important proportion in taxonomic and functional diversity of several taxonomic groups (e.g. lichens). Woody species density, lichen diversity and larval bee diet composition revealed good indicators of how decision-makers integrate biodiversity in urban planning and management.

Comparable multi-taxa and multi-city studies provide a holistic understanding of urban biodiversity patterns and the relationship with ecosystem functioning and services. The presented taxonomic and functional diversity of urban green spaces at the continental scale can support the planning and management of urban ecosystems to promote biodiversity and ESs (e.g. pollination, air quality improvement) and, therefore, increase cities resilience and livability for both humans and nature.

2. REVIEW OF THE LITERATURE

2.1. Why study nature in cities?

Biodiversity loss has accelerated during the past decades and is now occurring at an unprecedented rate. Land-use change has been recognized as one of the main drivers of biodiversity decline globally (IPBES, 2019). Apart from agriculture, urban growth has been playing an important role in landscape transformation (Nuissl at al., 2021), converting natural and semi-natural ecosystems into more anthropogenic landscapes. Consequently, ecosystem processes have been altered by changing the biogeochemical circulation patterns (Kaye et al., 2006, Grimm et al., 2008, Zhang et al., 2009) leading to significant losses of various ecosystem services (ESs) (Foley et al., 2005, Lawler et al., 2014, Delphin et al., 2016, Eigenbrod et al., 2011, Xie et al., 2018). ESs are defined as the benefits that people obtain from nature (MEA, 2005) such as food and fiber provision, climate regulation, flood control and clean air, among others. This concept highlights the interactions between ecological processes and functions and human well-being.

Urban areas that include cities, towns, industrial settlements and other densely populated areas with high infrastructure offer most of the job, education, culture, commerce and social opportunities. Consequently, urban areas currently host 55% of the world population (nearly 75% if we focus only on European population) and this percentage is predicted to rise up to ca. 70% in the next 30 years (UN, 2019). Accordingly, cities will experience a further increase in terms of number and extent, making the world more urbanized in the near future. Comparing the urban areas between 2000 and their projected extent in 2030, cities are expected to grow 1.2 million km^2 (Seto et al., 2012). Nowadays, due to the high amount of people living in urban areas and in their proximate surrounding areas demand a high amount of different ESs (e.g. clean air, food, timber, temperature regulation, recreation areas). Some of the main issues harming city dwellers health and well-being are air pollution and urban heat island effect (i.e. higher temperature in cities compared to their rural surrounding areas).

Urban green spaces (UGSs) – one of the key components of the urban green infrastructure (GI) (i.e. ecological network that provides ecological and socio-economic benefits through natural solutions (EC, 2013) – have been shown to provide multiple ESs from which city dwellers benefit. They play a role in the reduction of pollution and noise levels (Van den Bosch et al., 2017; Gascon et al., 2016; Van Cauwenberg et al., 2011; Lee et al., 2011; Cohen et al., 2014; Klingberg et al., 2017), sequester carbon (Tsay et al., 2015; Anav et al., 2016; Proietti et al., 2016), regulate air temperature (Bowler et al., 2010; Manes et al., 2012) and control water runoff (Pataki et al., 2011), among other beneficial services provided to humans. Numerous studies have also showed how having natural environment nearby home has positive influences for human health and well-being by lowering morbidity and mortality (Hartig et al., 2014; James et al., 2015; Gascon et al., 2016; van den Bosch et al., 2017; Shanahan et al., 2015; Twohig-Bennett et al., 2018; Fong et al., 2018; Chen et al., 2019).

Existing urban areas in Europe are growing, and infrastructure in already existing urban areas is becoming more dense (Shaw et al., 2020). On one hand it means that urban nature is getting more fragmented and the remaining fragments become more isolated from each other (Braaker et al., 2014). But on the other hand, urban nature becomes more important for the people, as getting out of cities to experience nature is becoming less frequent (Remme et al., 2021). This means that urban nature has to provide most of the ESs and benefits for humans living in cities and towns, as this is the only nature that most of the people experience and are in contact with for most of the time.

However, our knowledge of urban nature is still relatively limited, especially from the functional perspective (Calfapietra et al. 2015). Habitat fragmentation and isolation affect the processes in urban ecosystems, from interactions and trophic links to ecosystem services benefiting humans, like pollution removal and climate mitigation (Pickett et al., 2001). There is quite a lot of research about ecosystem functioning for natural and semi-natural ecosystems and habitats, but because of the high fragmentation and often artificial nature of urban ecosystems, it is not possible to directly transfer this knowledge to urban nature.

Urban areas are stressful environments for nature, from both individuals and ecosystem point of view. Urban nature is generally affected by higher abiotic stress than in the surrounding areas – higher temperatures, more extensive drought periods, higher pollution rates (Calfapietra et al., 2015).

Urban heat island phenomenon was first described by Seneca in Ancient Rome, while the first written account was published for London already more than 200 years ago, in 1810 by Luke Howard (Yow, 2007). Since then urban heat island effect has been described in urban settlements all over the world. Climatic conditions in urban heat islands tend to be relatively similar to what is expected from the currently ongoing climate change in terrestrial natural habitats, as urban heat island effects are themselves contributing to climate change (McCarthy et al., 2010). For example in Brussels, it has been shown that while climate change brings on heat waves and other cases of extreme weather events, the urban heat island effect adds additional severeness to these effects (Lauwaet et al., 2016). Therefore, we can interpret urban green spaces (hereafter UGSs), especially in the developed regions, to be kind of "open labs", where the microenvironmental conditions allow us to study how nature is capable of adapting to the changes on local and regional scale that are imminent (Calfapietra et al. 2015).

Natural habitats and all the species living and interacting within, have evolved during long time periods, and typically in relatively stable conditions where habitat is abundant and continuous (Zobel et al., 2008). Urban ecosystems are, however, typically generated artificially in a very limited spatial scale, and the species put together are often not interacting in natural conditions due to biogeographical or ecological constraints (Teixeira et al., 2020). These novel ecosystems (*sensu* Hobbs et al., 2006) comprise native and non-native species that have likely never coexisted in the same ecosystems (Higgs 2017). A species is native to a given region or ecosystem when it has originated and evolved in that area and is, therefore, adapted to the specific conditions. Contrarily, non-native species – also known as exotic or alien species – occur in different habitats from their origin. Some non-native species are not well-adapted to the new conditions and may need human intervention to succeed (e.g. some ornamental plants). However, other species that find favorable conditions to thrive in the new habitat where they occur (e.g. no limiting factors like species-specific pathogens) can reproduce rapidly and become invasive, as they strongly compete and partly or fully replace native biota and may also cause economic, environmental, or human health harm. Some of the non-native species have been typically introduced intentionally in urban areas for potential provision of specific ESs, especially for the ornamental value in UGSs (Potgieter et al., 2019), thus considerably increasing biodiversity levels within city boundaries.

As a consequence, community composition of urban novel ecosystems is fundamentally different from their natural counterparts. In addition to the novel combinations of species, novel interactions also arise, especially in the unprecedented combinations of (anthropogenic) disturbances in urban ecosystems. Therefore there are significant knowledge gaps regarding the functioning of urban ecosystems, especially considering different aspects of various spatial scales, like fragmentation, dispersal and connectivity (LaPoint et al., 2015).

Fragmentation and connectivity are crucial factors in all terrestrial ecosystems worldwide due to the habitat loss processes, which result in more fragmented, less interconnected, and smaller ecosystems (Kowarik, 2011). However, in urban ecosystems the effects of fragmentation and isolation are not clear, as the vegetation in UGSs, providing shelter and resources for other species, has artificial composition. Due to focus on aesthetic and ornamental value of nature, urban planning often designs highly variable UGSs, with abruptly changing land-cover types and high heterogeneity in relatively small areas (Sack, 2013; LaPoint et al., 2015). This is why urban areas tend to have higher plant species richness than the surrounding rural areas (Teixeira et al., 2020), and this high diversity on both landscape and species level is upheld by intensive maintenance of UGSs, that mitigates the negative effects of low connectivity and fragmentation in urban environment at least for vegetation.

Thus, it is largely unclear how the fragmentation and connectivity affect other organisms inhabiting UGSs. From one hand there can be positive factors concurring with fragmentation (absence or lower abundance of herbivores and predators, lower competition etc.); but on the other hand, chronic environmental stress (air pollution, prolonged heat and drought, no natural enemies for herbivores and pathogens etc.) can have significant additional negative effects on urban biota. While different biotic groups have been affected differently in urban environments (see Savage et al., 2015 for ants; Vergnes et al., 2013 for mice; Santini et al., 2019 for mammals in general; Tremblay et al., 2009 for birds), the general conclusion is that locally distributed specialist species tend to be replaced by globally distributed generalist, often exotic species. As different biotic groups respond differently to stress and disturbance that is dominating UGSs, there is a need to study multiple biotic groups together in order to gain holistic insight on ecosystem functioning in urban environments (Pinho et al., 2016).

2.2. Taxonomic and functional diversity and their link to ecosystem functions and services

Urban ecology considers cities as socio-ecological systems (Pickett et al. 2001) where nature and people coexist and interact. Societies have altered ecological processes, threatening ecosystem functioning and the provision of ESs in urban areas. Nature-based solutions (NBSs), that are cost-effective interventions inspired and supported by nature, are aimed at promoting resilience as well as biodiversity and ESs provision with the consequent benefit for both nature and the socio-economic system in the urban century (EC, 2020; Elmqvist et al., 2019).

Urban areas generally harbor a great plant species richness (e.g. Kühn et al., 2006), mainly due to four main factors: i) the big proportions of exotic species, which range among 30-60% in European cities (Pyšek, 1998; Salinitro et al., 2018; Säumel et al. 2010), ii) socio-economic factors, iii) high landscape heterogeneity (i.e., wide variety of different land use and land cover types), and iv) high environmental heterogeneity (e.g., different soil and microclimate conditions) (Morgenroth et al., 2016). Despite some authors even considering urban areas as biodiversity hotspots compared to the surrounding rural areas (e.g. Shaffer, 2018), cities also have unfriendly characteristics for biodiversity resulting in altered ecosystem functions and the services provided (Tresch et al., 2019).

Urban stressors may also condition species assemblages and, as a consequence, the provision of ESs due to the species-specific response. Management practices (e.g. watering) of UGSs can facilitate plant species occurrence in urban ecosystems by counteracting urban stressors. It is known that the taxonomic and functional components of biodiversity support ecosystem functions and services in different natural ecosystems (e.g. Funk et al., 2017). However, in urban contexts this relationship is insufficiently investigated. Urban ecosystems differ from their rural counterparts in several ways due to the difference in biotic and abiotic conditions, including higher temperature, pollution levels and habitat fragmentation (Alberti, 2015; Aronson et al., 2016) that may have altered species distribution and community composition. In addition, human choices based on socio-economic features play a key role in species assemblages creating novel ecosystems and interactions. Consequently, urban ecosystems are challenging our traditional understanding on ecosystem functioning and the delivery of ESs (Alberti, 2015) as well as their link to human-made biodiversity. Therefore, multi-taxa and trait-based approaches are required to better understand these relationships and increase our capability to maximize GI multifunctionality and therefore, to create more resilient cities (Pinho et al., 2021; Tran et al., 2020).

2.3. Science, practice and policy for cities

The growing urban population and the human-caused disruptions to urban ecosystems constitute an important challenge to urban planners (da Silva et al., 2012). It is still unclear whether and how relevant urban ecology is in the context of urban planning. It is necessary to explore how UGSs can be effectively integrated into smart city planning, in order to maximize ecosystem benefits for all city dwellers, and support urban ecosystems functioning (Nitoslawski et al., 2019). What is clear is that concerns about ecological challenges such as biodiversity loss and global change effects are taking center stage in the current society. Several instruments and initiatives concerning biodiversity and global change effects have emerged at different spatial scales (e.g. IPBES, CBD, Millennium Ecosystem Assessment, among many others) in the frame of policy and science.

At the global scale, the Agenda for Sustainable Development 2030 (UN, 2015) included biodiversity conservation, urban sustainability and mitigation of the climate change effects among their 17 ambitious Sustainable Development Goals (SDG). Despite the global scale of the SDG, many of them need to be addressed at the urban level, therefore municipalities and regional governments play a key role in the implementation of the 2030 Agenda (Bentz, 2020). In this context, Siragusa et al., (2020) developed a set of indicators gathered in the European Handbook for SDG to facilitate local authorities to monitor their progress towards the SDG.

At the regional level, it has been recognized that strategically integrating GI into urban planning and decision-making processes is key to guarantee ESs provision, city resilience and biodiversity conservation in European cities (EC, 2013). However, the incorporation of biodiversity, ecosystem functions and services in land use planning is not fully accomplished yet (Basnou et al., 2020). Accordingly, and in the frame of the European

Green Deal and the EU Recovery Plan, the European Commission recently launched a new EU Biodiversity Strategy for 2030 (EC, 2020) with the objective of addressing the five main drivers of biodiversity loss (i.e. sea/land use changes, natural resources overexploitation, climate change, pollution, and invasive exotic species) and setting targets to restore degraded ecosystems and increase resilience. In regards to urban areas, the new EU Biodiversity Strategy aims to stop the UGS loss due to urban growth and to integrate NBSs in the urban planning process. With this in mind, the EC called on European cities with a population size of at least 20000 inhabitants to create Urban Greening Plans (UGPs) by the end of 2021. With these UGPs, municipalities should favor biodiversity in several ways: i) increase biodiversity in the different urban ecosystems (e.g. urban parks, green roofs, street trees, etc.), ii) increase structural and functional connectivity among UGSs, iii) other measures such as low the mowing frequency of UGSs and eliminate pesticides.

In science, urban studies have also increased especially since 2000 including research from several scientific disciplines exploring a wide variety of taxa inhabiting urban areas mainly from developed countries (Magle et al., 2012). A recent literature review found that the most studied taxa in cities are birds and mammals compared to others (e.g. arthropods) (Collins et al., 2021). This increase in scientific urban literature is in line with the growing concern about the response of urban ecosystems to environmental stressors and their link to biodiversity. Studies addressing urban biodiversity and ESs provision are becoming more and more common across different spatial scales (e.g. Capotorti, Alós Ortí et al., 2019; Kabisch 2015; McPhearson et al. 2014; Nilon et al., 2017).

Moreover, many research projects have emerged with the intention to increase and share ecological and mechanistic knowledge of urban ecosystems and to guide municipalities and stakeholders in the urban planning process and management practices oriented to increase multi-functionality of urban ecosystems and therefore more resilient cities. Well-known examples at the European level are Esmeralda (Enhancing ecosystem services mapping for policy and decision making), EnRoute (Enhancing resilience of urban ecosystems through green infrastructure), Green Surge (Green Infrastructure and urban biodiversity for sustainable urban development and the green economy) and BioVeins (Connectivity of green and blue infrastructures: living veins for biodiverse and healthy cities), among others.

More concretely, the main objective of the BioVeins project (ERA-Net BiodivERsA, Grant Number: BiodivERsA32015104, 2017-20) was to use functional diversity (FD) to highlight the mechanisms underpinning the link between UGSs, taxonomic diversity (TD) and ecosystem services (ESs) provisioning. It was an interdisciplinary project that involves the study of functional and taxonomic diversity of several urban taxa (i.e. vegetation, pollinators, lichens, soil biota, leaf bacteria, bats and nocturnal insects) and the related ESs provided, while considering also landscape configuration (i.e. UGS size and connectivity degree). BioVeins involved an overall 225 UGSs belonging to seven European cities along a latitudinal gradient (Fig. 1). City dwellers and stakeholders also had a place in BioVeins through a citizen science approach, in which citizens are engaged in data collection and become aware and informed about their surrounding nature and how it influences their life quality.

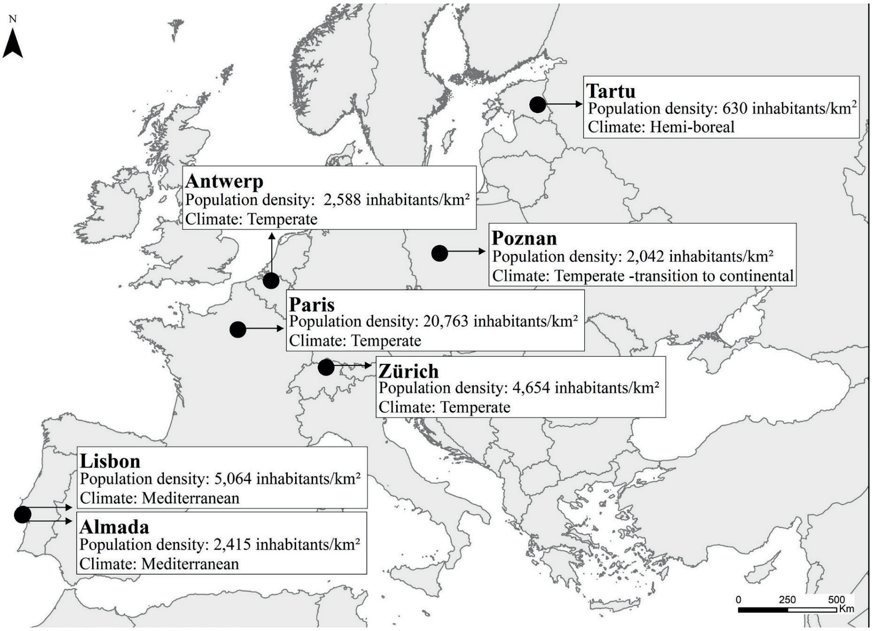


Figure 1. Location, demography and climate of the selected cities of BioVeins project (Paper II).

To date, partners of BioVeins project have produced several interdisciplinary scientific outcomes, namely:

1. Alós Ortí, M., Casanelles J., Chiron, F., Deguines, N., Hallikma, T., Jaksi, P., Kwiatkowska, P., Moretti, M., Muyshdont, B., Niinemets,

22 Ü., Pinho, P., Pinto, M.M., Saar, P., Samson, R., Tryjanowski, P., Van Mensel, A., Laanisto, L. (2022). Negative relationship between woody species density and size of urban green spaces in seven European cities. Urban Forestry & Urban Greening, 74, 127650. https://doi.org/10.1016/j. ufug.2022.127650 (Paper II)

2. Casanelles-Abella, J., Keller, A., Müller, S., Aleixo, C., Alós Ortí, M., Chiron, F., Laanisto, L., Myczko, Ł., Pinho, P., Samson, R., Tryjanowski, P., Van Mensel, A., Villarroya-Villalba, L., Pellissier, L., Moretti, M. (2022). Wild bee larval food composition in five European cities. Ecology, e3740. https://doi.org/10.1002/ecy.3740

3. Pinho, P., Casanelles-Abella, J., Luz, A. C., Kubicka, A. M., Branquinho, C., Laanisto, L., Neuenkamp, L., Alós Ortí, M., Obrist, M. K., Deguines, N., Tryjanowski, P., Samson, R., Niinemets, L., & Moretti, M. (2021). Research agenda on biodiversity and ecosystem functions and services in European cities. Basic and Applied Ecology, 53, 124–133. https://doi.org/10.1016/j.baae.2021.02.014 (Paper I)

4. Casanelles-Abella, J., Müller, S., Keller, A., Aleixo, C., Alós Ortí, M., Chiron, F., Deguines, N., Hallikma, T., Laanisto, L., Pinho, P., Samson, R., Tryjanowski, P., Van Mensel, A., Pellissier, L., Moretti, M. (2021). How wild bees find a way in European cities: pollen metabarcoding unravels multiple feeding strategies and their effects on distribution patterns in four wild bee species. Journal of Applied Ecology, 59, 457-470 https://doi.org/10.1111/1365-2664.14063 (Paper IV)

5. Casanelles-Abella, J., Frey, D., Müller, S., Aleixo, C., Alós Ortí, M., Deguines, N., Hallikma, T., Laanisto, L., Niinemets, Ü., Pinho, P., Samson, R., Villarroya-Villalba, L., & Moretti, M. (2021). A dataset of the flowering plants (Angiospermae) in urban green areas in five European cities. Data in Brief, 37, 107243. https://doi.org/10.1016/j.dib.2021.107243

6. Villarroya-Villalba, L., Casanelles-Abella, J., Moretti, M., Pinho, P., Samson, R., van Mensel, A., Chiron, F., Zellweger, F., & Obrist, M. K. (2021). Response of bats and nocturnal insects to urban green areas in Europe. Basic and Applied Ecology, 51, 59–70. https://doi.org/10.1016/j.baae.2021.01.006

Other scientific articles in the frame of BioVeins project are currently under peer-review process:

1. Rocha, B., Matos, P., Giordani, P., Lõhmus, P., Branquinho, C., Casanelles-Abella, J., Aleixo, C., Deguines, N., Hallikma, T., Laanisto, L., Moretti, M., Alós Ortí, M., Samson, R., Tryjanowski, P., Pinho, P. Modelling the effects of broad scale air pollution and climate on urban ecosystem: through the lens of lichens. Environmental Pollution. *Under review.* (Paper III).

2. Van Mensel, A., Wuyts, K., Pinho, P., Muyshondt, B., Aleixo, C., Alos Orti, M., Casanelles-Abella, J., Chiron F., Hallikma, T., Laanisto L., Moretti, M., Niinemets, Ü., Tryjanowski, P., Samson, R. Magnetic signal of urban trees' trunk bark catches the variation in particulate matter exposure within and across six European cities. Environmental Science and Pollution Research. *Under review.*

3. Muyshondt, B., Wuyts, K., Van Mensel, A., Smets, W., Lebeer, S., Aleixo, C., Alós Ortí, M., Casanelles-Abella, J., François, C., Giacomo, P., Laanisto, L., Moretti, M., Niinemets, Ü., Pinho, P., Tryjanowski, P., Woszczyło, P., Samson, R. Phyllosphere bacterial communities in urban green areas throughout Europe relate to urban intensity. FEMS Microbiology Ecology. *Under review.*

Other research papers that are currently in progress will be published in the upcoming years. Besides the scientific outcomes, more practical knowledge was provided to municipalities by creating an ID card of every studied UGS. Each ID card provided comprehensive information on plant cover, species biodiversity (richness and abundance of every studied taxa) and ecosystem services. We provided these ID cards to municipalities from the cities involved in BioVeins, thus contributing to shortening the gap between science and practice and promoting ecologically-informed decisions, as it was one of the strengths of the project.

3. OBJECTIVES AND HYPOTHESES OF THE STUDY

The main objective of the research presented in this thesis was to provide a holistic view of the taxonomic and functional diversity of several urban taxa occurring in urban green spaces (UGSs) from different European cities. In order to achieve this main aim, we outlined four specific objectives and seven associated hypotheses, namely:

1. Identify gaps of knowledge in urban ecology research and draw future trends aimed at fulfilling them.

Hypothesis 1: *Despite the recent progress in trying to understand biodiversity-ecosystem functions and services relationships in a multitude of urban taxa, there are key questions that still have no answer. We expect that answering these questions require applying holistic and comparable methodological approach.*

2. Provide a comprehensive description of the vegetation in UGSs that provides ESs to people and food and shelter for other urban taxa.

Hypothesis 2: *UGSs have generally high plant diversity, especially among woody plants, as management practices directly deal with designing the UGSs woody vegetation. However, we hypothesize that a significant proportion of this diversity is due to the presence of non-native species, and the planting of woody species does not follow ecological knowledge.*

Hypothesis 3: *Bigger UGSs have generally higher plant species richness, but this relationship is not strong, depending on the urban area location.*

Hypothesis 4: *Despite bigger UGSs hosting more woody species richness, the ecological potential of these urban ecosystems is not fully exploited from both taxonomical and functional aspect.*

3. Explore the lichen taxonomic and trait diversity as a response to the urban environmental conditions.

Hypothesis 5: *In spite of recent the efforts in improving abiotic conditions in cities, lichen communities in urban areas are still composed of stress tolerant species.*

Therefore, indicating that the urban environmental conditions have not changed significantly for the better.

4. Analyze how urban vegetation and urban intensity influence bee species foraging strategies.

Hypothesis 6: *Plant species selection in UGSs may have a significant role in the pollinator diet. More generalist wild bee species might have better chances than specialist species in surviving in an urban environment due to more rich and variable diet, because they are better adapted to foraging in alien plant species.*

Hypothesis 7: *Broader diets of wild bee larvae are associated with wider distribution ranges of bee species.*

4. MATERIAL AND METHODS

4.1. Sampling sites selection

We selected and studied urban green spaces (UGSs) from seven European cities distributed along a NE-SW gradient: Tartu (Estonia), Poznan (Poland), Antwerp (Belgium), Paris (France), Zurich (Switzerland), Lisbon and Almada (both in Portugal) (Table 1). These cities vary in terms of climate, population density and urbanization history.

Table 1. DMS coordinates, climate, extent and population density of the selected cities.

City	Coordinates	Climate	Area (km^2)	Population density (inhabitants/km^2)
Tartu	58° 22’ 40.89” N 26° 43’ 42.57” E	Hemi-boreal	38.8	630
Poznan	52° 24’ 34.33” N 16° 55’ 55.17” E	Temperate – transition to continental	261.8	2042
Antwerp	51° 15’ 36.70” N 4° 24’ 9.97” E	Temperate	204.5	2588
Paris	48° 51’ 52.97” N 2° 20’ 56.45” E	Temperate	105.4	20763
Zurich	47° 22’ 25.96” N 8° 32’ 42.33” E	Temperate	87.88	4654
Lisbon	38°42'49.75"N 9°8'21.79"W	Mediterranean	100	5064
Almada	38° 40’ 35.49” N 9° 9’ 54.37” W	Mediterranean	70.21	2415

For the sampling sites selection we based on the land cover class 1.4.1. Green Urban Areas included in the pan-European Urban Atlas (EEA, 2012) and followed a random stratified sampling design. We stratified patches of 1.4.1. Green Urban Areas of the 7 cities along two orthogonal gradients. First gradient accounted for the UGS size and second one of the connectivity with other green elements of the urban matrix that had a favorable habitat (i.e. other 1.4.1. Green Urban Areas; 3.1. Forests; and 1.1.2.3. Discontinuous low – and 1.1.2.4. very low – urban density with less than 30% and 10% of impervious surfaces, respectively). UGS size was given by the Urban Atlas, while connectivity degree was determined by means of the Proximity Index (PI) (Gustafson et al., 1992) computed in Fragstats v.4 (McGarigal et al., 2012) and calculated within a 5-km radius of each Green Urban Area, as it is the maximum possible with the available cartography. The PI measures the degree of connectivity/isolation of each UGS to neighbor green elements, providing higher values to less isolated UGSs (i.e. higher proximity) and lower values indicating more fragmented landscape. It is defined as:

$$PROX = \sum_{s=1}^{n} \left(\frac{a_{ijs}}{h_{ijs}^{2}} \right)$$

Where a_{ijs} refers to the area (m^2) of a UGS ijs within specified neighborhood (m) of a green element ij, and h_{ijs}^{2} refers to the distance (m) between the UGS ijs, based on patch edge-to-edge distance.

Then UGSs were classified in 6 classes (from A1 to A6) according to their area (in ha) (i.e. $0 \leq A1 < 0.2$; $0.2 \leq A2 < 1.2$; $1.2 \leq A3 < 2.4$; $2.4 \leq A4 < 4.8$; $4.8 \leq A < 9.6$; and $A6 \geq 9.6$) and 6 classes (from P1 to P6) according to the resulting PI values (i.e. $0 \leq P1 < 18000$; $18000 \leq P2 < 36000$; $36000 \leq P3 < 72000$; $72000 \leq P4 < 144000$; $144000 \leq P5 < 288000$; and $P6 \geq 288000$) (Table 2). This resulted in a distribution of all the 1.4.1. Green Urban Areas into a 6x6 matrix, where we randomly selected our study sites. This final site selection resulted in 225 UGSs distributed as follows: 34 in Tartu, 35 in Antwerp, 36 in Poznan, 36 in Paris, 35 in Zurich, 34 in Lisbon and 15 in Almada (Figs. A1-A6). All the urban taxa explored within the Bioveins framework (i.e. vegetation, pollinators, lichens, soil biota, leaf bacteria, bats and nocturnal insects) were sampled in the same UGSs when possible (e.g., resources availability).

Table 2. Scheme of the stratification of the 1.4.1. Green Urban Areas from the European Urban Atlas according to their size (Area, ha) and connectivity (Proximity Index, PI). This scheme was used for each city separately. Final site selection was done randomly and covered the maximum of combinations possible.

Area (ha)|PI	0	18000	3600	72000	144000	288000	>288000
0	class	P1	P2	P3	P4	P5	P6
0.2	A1	A1P1	A1P2	A1P3	A1P4	A1P5	A1P6
1.2	A2	A2P1	A2P2	A2P3	A2P4	A2P5	A2P6
2.4	A3	A3P1	A3P2	A3P3	A3P4	A3P5	A3P6
4.8	A4	A4P1	A4P2	A4P3	A4P4	A4P5	A4P6
9.6	A5	A5P1	A5P2	A5P3	A5P4	A5P5	A5P6
>9.6	A6	A6P1	A6P2	A6P3	A6P4	A6P5	A6P6

4.2. Studying the vegetation of urban green spaces (Paper II)

4.2.1. Field Survey

We surveyed vascular plants in every selected site during the summer of 2018, 2019 and 2020 by using a method based on quadrats. We identified the woody plant species occurring within five quadrats of 5m x 5m each that we set in the centroid or as close as possible to it (Fig. 2a) (e.g. if the centroid was located in an impervious area or there was infrastructure, we set the quadrats in the closest suitable location) and measured different structural traits from them. It is worth mentioning that the centroid was the sampling area of every taxa studied in BioVeins (i.e. vegetation, pollinators, lichens, soil biota, leaf bacteria, bats and nocturnal insects) when possible (i.e., if the taxa-specific sampling protocol required characteristics not found in the centroid, the nearest suitable area was then selected). The structural traits measured in trees were: tree diameter at breast height (~1.3m height) (DBH), tree height, crown height and width; while for shrubs and hedges we recorded their height and canopy width and length (Fig. 2b). We used a clinometer and a DBH tape for the measurements. In addition, we identified the woody plants also at the site level (i.e. overall woody species richness at the site level) and the mean height of every woody species by assessing the mean height of all the individuals belonging to the same species. The herbaceous layer was sampled by setting one plot of 1m x 1m within each of the five quadrats. At the plot level, we recorded the herbaceous species richness, mean plant height and cover percentage.

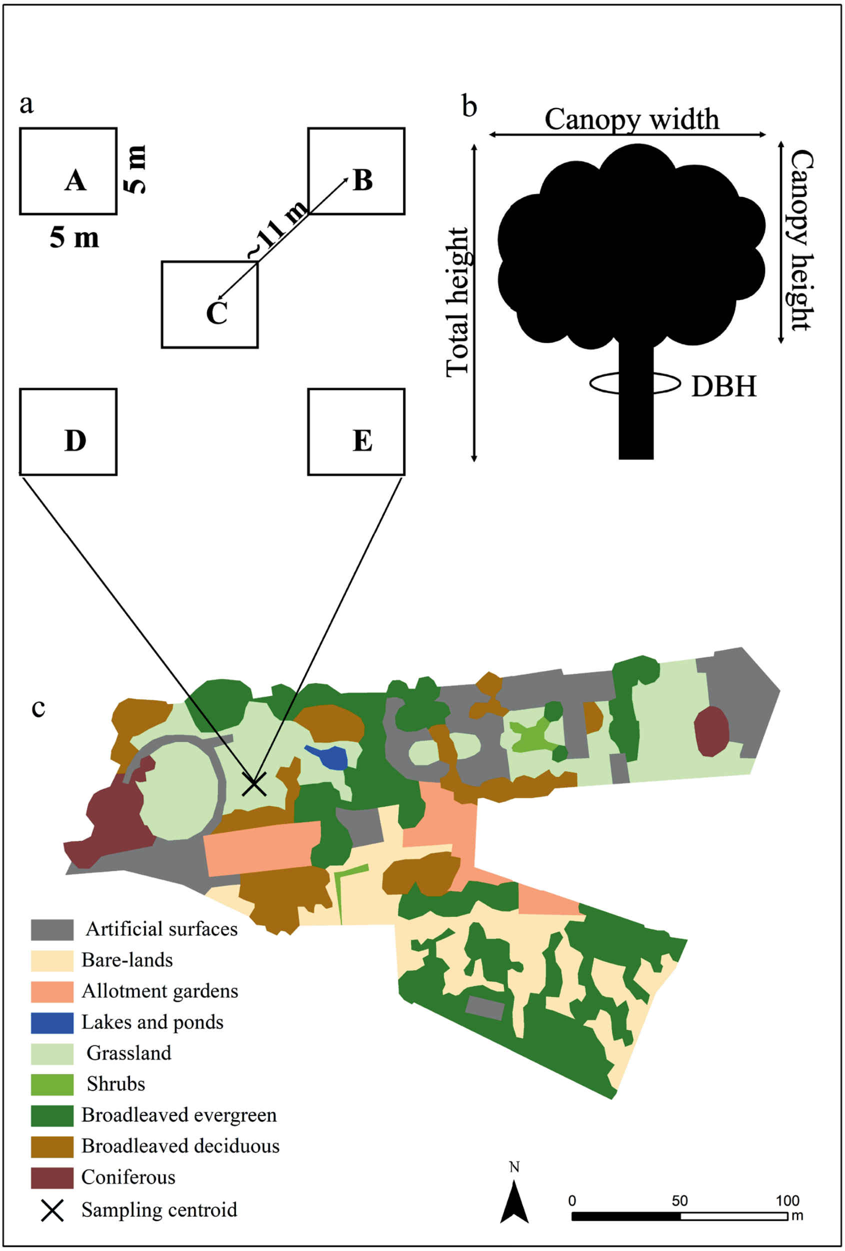


Figure 2. Sampling design (a), quadrat C is located in the sampling centroid of the urban green space (UGS). Plant traits measured for tree plants (b). Example of one of the studied UGSs in Lisbon (size = 31 868.26 m^2), land cover map and location of the sampling centroid (38°46’13.7” N, 9°10’33.9” W) (c) (Paper II).

4.2.2. Land cover classification

We distinguished nine different land cover types within each UGS (Fig. 2c) by photo-interpretation of high resolution aerial images (i.e. World Imagery basemap from 2015 at 0.5m resolution) using ESRI ArcMap 10.4 at a scale of 1:600. We differentiated among the different types of tree cover (i.e. coniferous, broadleaf evergreen and broadleaf deciduous trees) by inspecting different phenological periods in Google Earth Pro v.7.3.2.5776 and street view in Google Maps. Then validated the precision of our maps on the site during the vegetation surveys. As a result, we got high-accuracy land cover maps of the upper layer, which corresponds to tree cover and every other open surface.

4.2.3. Above-ground vegetative biomass

Structural traits measurements (Fig. 2b) were used in order to estimate the above-ground biomass (AGB) of trees by means of existing allometric models (Zianis et al., 2005; Tabacchi et al., 2011; Forrester et al., 2017). We firstly used species-specific allometric equations when available followed by genus-specific models and, finally, models built for broadleaf and coniferous trees. When more than one model existed for a given plant species, mean value of all the models was used. In order to avoid outliers derived from over- and under-estimations of AGB, we excluded plants with values of DBH and/or height outside the threshold for which the models were built. This resulted in an exclusion of 15 UGSs. Tree cover maps resulting from photo-interpretation were used in order to extend the AGB calculation from the individual to the site level.

4.2.4. Data analysis

We produced a comprehensive list of woody species at the site scale and their distribution and proportion of native vs. non-native species at the city level. We followed Tutin et al., (1964–1980) and Euro+Med PlantBase (2006) for the determination of the species biogeographic status (i.e. native or non-native in a given area).

The overall variables considered in the statistical analyses are gathered in Table 3. We conducted all the analyses in R v. 3.6.1 (R Core Team, 2019) using the following packages: Hmisc v.4.4-1 (Harrel 2020), corrplot v.084 (Wei et al., 2017), nlme v. 3.1-152 (Pinheiro et al., 2021), ggplot2 (Wickham, 2016), factoextra v. 1.0.7 (Kassambara et al., 2020) and FSA v.0.8.32 (Ogle et al., 2021).

Table 3. Description of the variables included in the analysis, their units, type of variable, scale of measure and data source (Paper II).

Variable	Description	Units	Scale	Source
UGS size	Urban Green area extent	m^2	UGS	Urban Atlas 2012
AGB	Tree above-ground biomass derived from allometric models	kg	Tree	Zianis et al., 2005; Tabacchi et al., 2011; Forrester et al., 2017
Canopy cover	Absolute coverage of tree canopies	m^2	UGS	Photo-interpretation
Canopy percentage	Relative coverage of tree canopies	%	UGS	Photo-interpretation
Mean height woody layer	Species-specific mean height of the woody layer	m	UGS	Vegetation survey
DBH	Diameter at breast (~1.3m) height	cm	Tree	Vegetation survey
Woody species richness	Woody species richness	n species	UGS centroid	Vegetation survey
Species density	Amount of woody species per unit of UGA	n/m^2	UGS	Vegetation survey

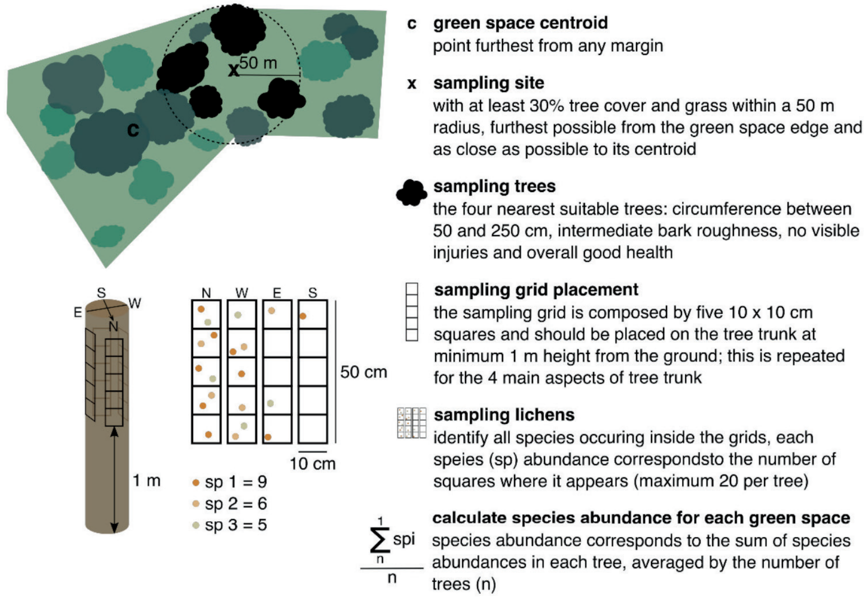
Firstly, we did run linear regression models to explore the relationships among UGS size as explanatory variable and vegetation features (i.e. woody species richness, woody species density, canopy cover and AGB) at two different spatial scales: i) regional, by considering all the cities together, and ii) local, each city separately. Secondly, we tested the above-mentioned relationships through linear mixed effect models considering the different cities as random factors in order to explore the city-based differences in these relationships. As plant species assemblages in UGSs are generally driven by socio-economic preferences rather than by natural mechanisms (e.g. seed dispersal), we did not expect that connectivity had a role in shaping woody diversity. Still, we did analyze its effect on woody species richness, as we did with UGS size, and confirmed our expectations ($p>0.05$). Therefore, we did not further explore this relationship.

4.3. Taxonomic and trait diversity of urban lichens communities (Paper III)

Global change drivers such as air pollution and climate change are intense stressors in urban areas conditioning humans and ecosystems health. In the "urban century" it becomes necessary to efficiently monitor these drivers and create effective policies able to face this challenge. Lichens are well-known good ecological indicators of human disturbances, but little is known about how global drivers affect biodiversity at the city scale. For this reason, we investigated how air quality and climate affect urban lichen diversity in the 7 European cities involved in the BioVeins project. We identified 140 lichen species in 219 UGSs and calculated several biodiversity-based metrics.

4.3.1. Lichens sampling

We sampled epiphytic lichens from tree barks using the European Standard Method (Asta et al., 2002; Cristofolini et al., 2014). As displayed in Figure 3, in each UGS we collected samples from four trees located within a 50m-radius buffer (sampling site) with at least 30% tree and grass cover. Suitable sampling trees fulfilled the following requirements i) did not show any sign of disease either branches or injuries lower than 2m high, ii) straight growth form (the maximum trunk deviation allowed was 20º from the vertical axis), and iii) had a trunk perimeter from 50 to 250cm at 1 to 2m from the ground (height to which we sampled the lichens).



c green space centroid
point furthest from any margin

x sampling site
with at least 30% tree cover and grass within a 50 m radius, furthest possible from the green space edge and as close as possible to its centroid

sampling trees
the four nearest suitable trees: circumference between 50 and 250 cm, intermediate bark roughness, no visible injuries and overall good health

sampling grid placement
the sampling grid is composed by five 10 x 10 cm squares and should be placed on the tree trunk at minimum 1 m height from the ground; this is repeated for the 4 main aspects of tree trunk

sampling lichens
identify all species occuring inside the grids, each speies (sp) abundance correspondsto the number of squares where it appears (maximum 20 per tree)

$$\frac{\sum_{n}^{1} spi}{n}$$

calculate species abundance for each green space
species abundance corresponds to the sum of species abundances in each tree, averaged by the number of trees (n)

Figure 3. Selection of sampling site inside a UGS and sampling scheme for epiphytic lichens, according to the European Standard Method (Asta et al., 2002; Cristofolini et al., 2014) (Paper III).

Then, we placed a five 10cm x 10cm grid (Fig. 3) facing the four cardinal points of every selected tree, covering a sampling area of 2000cm^2 per tree and 8000cm^2 per UGS. We identified the lichens that fell within the grid either on the site or later in the laboratory. We determined the species abundance by counting the amount of squares in a tree (i.e. 10cm x 10cm plots) in which a given species occurred and then averaging at the site level. Nomenclature followed (Nimis et al., 2021).

4.3.2. Biodiversity metrics

We measured both the taxonomic and functional diversity of lichens. On the one hand, we accounted for the taxonomic diversity by means of eight taxonomic metrics: species richness, amount of rare species, Shannon diversity Index, Inverse-Simpson Index, species abundance, and community homogeneity by means of Bray-Curtis, Jaccard and Horn-Morisita indices (Barwell et al., 2015). On the other hand, we assessed functional diversity and functional structure by exploring seven traits (Table 4) that are related to environmental change drivers in urban areas influencing growth, survival and fitness of lichens.

Table 4. Lichen species traits and related functional groups used in the study, described following (Nimis and Martellos, 2021) (Paper III).

Trait	Functional group	Description
growth form	*crustose*	thallus firmly and entirely attached to the substrate by the lower surface. Does not include leprose growth form.
	foliose broad-lobed	thallus partly attached to the substrate, with distinct upper and lower surfaces and broad lobes
	foliose narrow- lobed	thallus partly attached to the substrate, with distinct upper and lower surfaces and narrow lobes
	fruticose	thallus attached to the substrate by one single point and with rounded or flattened branches
	leprose	thallus like crustose but surface thallus with a granular mass appearance and always decorticated
	squamulose	thallus composed of small scales
main photobiont type	*cyanobacteria*	lichens with cyanobacteria
	green algae	lichens with green algae other than Trentepohlia
	trentepohlia	lichens with Trentepohlia (green algae)
substratum pH tolerance	*low*	occurs in very acid substrata
	medium-low	occurs in acid substrata
	medium	occurs in subacid to sub neutral substrata
	medium-high	occurs in slightly basic substrata
	high	occurs in basic substrata
solar irradiation tolerance	*low*	occurs in very shaded situations
	medium-low	occurs in shaded situations
	medium	occurs in sites with plenty of diffuse light but scarce direct solar irradiation
	medium-high	occurs in sun-exposed sites
	high	occurs in very high direct solar irradiation

aridity tolerance	*low*	hygrophytic
	medium-low	rather hygrophytic
	medium	mesophytic
	medium-high	xerophytic
	high	very xerophytic
eutrophication tolerance	*low*	occurs in sites with no eutrophication
	medium-low	occurs in sites with very weak eutrophication
	medium	occurs in sites with weak eutrophication
	medium-high	occurs in sites with rather high eutrophication
	high	occurs in sites with very high eutrophication
poleotolerance	*low*	occurs in undisturbed forests
	medium-low	occurs in natural or semi-natural habitats
	medium	occurs in moderately disturbed areas
	high	occurs in heavily disturbed areas

The selected traits respond to one or both the environmental stressors analyzed (pollution and climate). Firstly, growth form and the main photobiont type are influenced by both climate and air quality (Aptroot et al., 2007; Koch et al., 2019; Matos et al., 2015). Substratum pH tolerance is related to air pollution since the deposition of pollutants alters the pH of barks and, consequently, lichen communities (Larsen et al., 2007; Llop et al., 2012). The same applies to eutrophication tolerance that reflects the tolerance to nitrogen-based compounds (Giordani et al., 2017; Llop et al., 2012; Pinho et al., 2011). Solar irradiation and aridity tolerance are directly related to climate (Munzi et al., 2014). Finally, poleotolerance refers to the capacity of lichens to resist human disturbances (Rocha et al., 2019) often associated with air pollution. We characterized the traits of 131 lichen species out of 140, since 9 of them could only be identified to genus level and were therefore omitted from the species-based analysis. We calculated the functional richness, understood as the amount of functional groups in a UGS and Rao's quadratic entropy (RaoQ) that accounts for the functional dispersion of species, weighted by their relative abundances. Moreover, we computed the community weighted mean (CWM) to measure the functional structure of lichen communities.

4.3.3. Environmental change drivers

We retrieved climatic and pollution data for all the selected 219 UGSs using available large scale datasets. We used the CHELSA database (Karger et al., 2017, 2018) to retrieve broad scale climatic data. Concretely, we selected 19 variables related to climate, i.e., precipitation and air temperature, annually and seasonally during the past decades (from 1979 to 2013) and at 1km resolution. We used EMEP (Fagerli et al., 2019) to retrieve broad scale air pollution data. For this, we got data for 2018 at 11km resolution about the 7 most abundant pollutants in cities: Reduced Nitrogen (NH_3 and NH_4) and oxidized nitrogen deposition (both at $mg.m^{-2}$), SO_2, NOx, $PM_{2.5}$ and PM_{10} air concentration (all of them at $\mu g.m^{-3}$). Since the environmental variables selected come from broad scale datasets (i.e. the display little variance within each city), we added an additional factor called ‘other’ in order to account for the variability that was not explained by air pollution and climate. It helped to represent city-specific features (e.g. urbanization ,management practices) that vary at the broad scale.

4.3.4. Data analysis

We firstly performed two principal component analysis (PCA), one including the 19 climatic variables and another one with the 7 air pollution variables in order to avoid redundancy in our datasets. The resulting meaningful variables were used for the subsequent analysis. We conducted all the analyses in R software v. 4.0.3 (R Core Team, 2020) using the following packages: Vegan (Oksanen et al., 2011) and dbFD (Laliberté et al., 2014). We did run Spearman correlation tests to explore the directions and intensity of air pollution and climate with lichen biodiversity. We represented through boxplots the distribution patterns of taxonomic diversity, functional diversity and functional structure among the 7 cities. We performed linear models to test for the relationships of the biodiversity-based metrics with climate and air pollution. We then included the variable ‘other’ (see subsection 4.3.3.) in our models as a fixed and random factor.

4.4. Plant-pollinator interactions in urban ecosystems (Paper IV)

It is well known that land use change is the main cause of global biodiversity loss. However, several studies have demonstrated how urbanization may benefit some taxa (Kurucz et al., 2021) compared to others (McKinney, 2008). Urban vegetation provides ESs directly (e.g. temperature reduction or pollution mitigation) and indirectly by maintaining and fostering ecosystem functions and processes (e.g. pollination) (Prendergast et al., 2022). Particularly, urban plants provide food and shelter to wild bees and other insect pollinators. The availability of floral resources in cities has an influence on wild bee community composition and species distribution depending on the species-specific diet preferences. In this study we focused on four common cavity-nesting urban bee species: *Chelostoma florisomne* (Linnaeus, 1758), *Hylaeus communis* (Nylander, 1852), *Osmia bicornis* (Linnaeus, 1758) and *Osmia cornuta* (Latreille, 1805) surveyed in 80 UGS from 5 out of the 7 cities involved in Bioveins, namely: Tartu (n=12), Poznan (n=12), Antwerp (n=12), Paris (n=12) and Zurich (n=32) (Fig. 4).

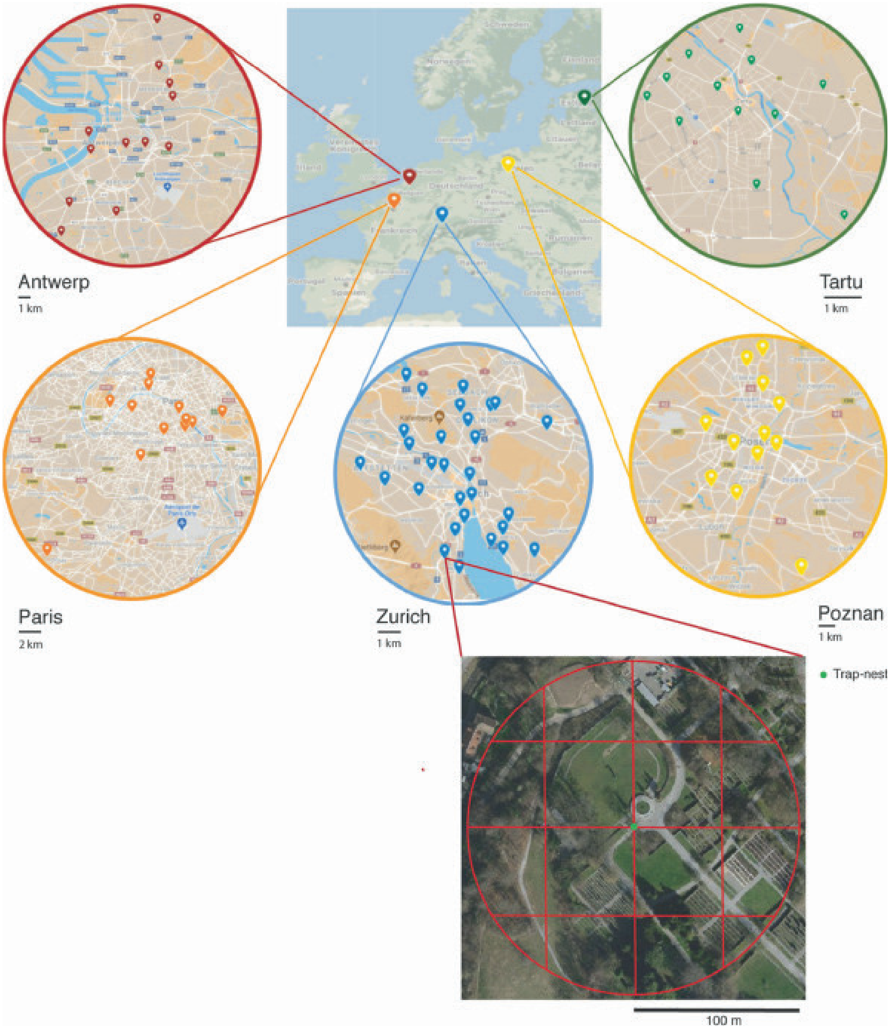


Figure 4. Maps of the study sites in each of the five cities (Antwerp, Greater Paris, Poznan, Tartu and Zurich) and an example of how the sampling was conducted. For the site Zu006 (located in Zurich), we show the trap-nest location (green dot), the 100 m radius buffer around it and the 16 cells dividing the buffer (Paper IV).

4.4.1. Trap nests

In order to explore the larval diet composition of the four wild bee species, we installed a trap-nest (Fig. 5) in each UGS during January 2018. Trap-nest structure is designed in a way that ensures covering the requirements of the cavity-nesting bee community. We installed the trap-nests in trees at the centroid or as close as possible to it at 2.5 - 3.5m height and facing to SE or SW ensuring direct sunlight. In two cases (one in Tartu and one in Zurich) no trees around the centroid were present and we put the trap-nest in another vertical structure (e.g. light post). We removed the 80 trap-nests in October 2018, transported them all to Zurich, where they were kept at 5°C and then at ambient temperature in order to simulate spring-like conditions until February 2019. Once the larvae bees had hatched, we identified them to the species level.

Figure 5. Installed trap-nests (left) and photographs of four nests where bee data was collected (right) for *C. florisomne, O. cornuta, O. bicornis* and *H. communis*.

4.4.2. Floral resources sampling

In order to determine the bee distribution and larval diet composition of the four selected solitary bee species and as described in Casanelles-Abella (2021), we sampled the floral resources in a buffer of 100 m radius around each trap-nest three times during the flowering season of 2018 (in April, May and June) and identified the pollen of each occupied nest. In each buffer we set a grid of 16 cells (Fig. 4) where we recorded two functional traits (i.e., plant growth form and blossom type) of every flowering plant (Table A1). The selected functional traits indicate the accessibility of the food resources by bees and thus, indicators of plant-bee interactions. In addition, we extracted 464 pollen samples from the trap-nests and they were identified to the species level through DNA metabarcoding performed by AllGenetic laboratories (AllGenetics & Biology SL; A Coruña, Spain). We then classified the plant species according to their biogeographic status (i.e., whether native or non-native) and also according to the previous functional traits (Table A1). Metabarcoding procedure is a novel approach which consists of extracting and amplifying the DNA by using Polymerase Chain Reaction (PCR) and sequencing it by means of next-generation sequencing to generate thousands to millions of reads. Unlike barcoding techniques, DNA metabarcoding includes extensive simultaneous sequencing of samples.

4.4.3. Environmental drivers of bee species distribution

We selected three environmental variables representing different aspects of the urban environmental gradient and having an influence on bee diet and distribution. These drivers were: thermal stress (derived from remote sensing-based metrics), amount of habitat (derived from high resolution land cover maps, see section 4.2.2.) and resource availability (from floristic inventories, see section 4.4.2.). We used remote sensing-based indices as proxies of the thermal stress. Specifically, we calculated land surface temperature (LST), the urban index (UI), the color index (CI), the normalized difference water index (NDWI) and the normalized difference vegetation index (NDVI) at different spatial scales (i.e. 50, 100, 200, 400, 800 and 1600 m radius from the trap-nest). We calculated the proportions of artificial surfaces, bare-lands, grasslands, coniferous trees and deciduous broad-leaved trees at different spatial scales (i.e. 8, 16 and 32 m radius from the trap-nest) (see section 4.2.2.) to account for the amount of habitat. Moreover, we used the UGS size and connectivity degree (see section 4.1.).

4.4.4. Data analysis

For each bee species, we calculated the different proportions of plant families, genus and species that compound bee larval diet and calculated the Shannon diversity index at the three taxonomic levels. Moreover, we accounted for the plant trait preferences in bee larval diet composition. We conducted all the analyses in R software v.4.0.2 (R Core Team, 2021) using the following packages: V.phylomaker v.0.1.0 (Jin et al., 2019) to explore the phylogenetic tree of the plant species present in the pollen of the studied bees, mgcv v.1.8-30 (Wood, 2011), RandomForest v.4.6-14 (Liaw et al., 2002) and gbm v.2.1.5 for the distribution models.

We performed a principal component analysis (PCA) with the explanatory variables that allowed us to define sets of meaningful variables and reduce the dimensionality of our dataset. We did run Pearson correlations to explore the associations among the taxonomic and plant trait preferences and the urban intensity gradient, habitat amount and availability of floral resources. We performed such correlations at both the city and regional scale. We also investigated the diet consistency (i.e., variability) by performing pairwise comparisons of binary trophic interaction matrices between the bee species and the plant family, genus and species. Then, we calculated Pearson correlations of the matrices between pairs of cities for each bee species and plant taxonomic level. In addition, we performed species distribution models (SDMs) to investigate the bee distribution patterns using city as a fixed factor. We built occurrence matrices with the presence of each bee species across sites. We used predictive power in order to identify the statistical relevance of every environmental predictor and chose those predictors displaying correlations <0.7 in order to avoid collinearity. The models that we used were: generalized linear models (GLMs), generalized additive models (GAMs), gradient boosting machines (GBMs) and random forests (RFs). We calibrated GLMs with first-order polynomials, GAMs with a spline smoothing term of intermediate complexity (k = 4), RFs with a node size of 5 and 1000 trees, and GBMs with an interaction depth of 1, a shrinkage of 0.001 and 1,000 trees. We divided the species list into two datasets for model calibration (including 80% of the data) and for model evaluation (including 20% of the data) and repeated the process 5 times. We assessed the model performance with the True Skill Statistic (TSS; Allouche et al., 2006). We considered a predictive model to be acceptable when TSS>0.4. We used the acceptable model to predict the probability of occurrence of each bee species in every studied city.

5. RESULTS

5.1. Drawing future research directions for urban ecology (Paper I)

Following an expert discussion approach based on the scientific questions and knowledge exchange between the multidisciplinary members of the BioVeins project, we identified several gaps of knowledge in urban ecology research (Hypothesis 1 - understanding B-EF/ES relationships require applying a holistic and comparable methodological approach). As a result, we proposed five main research directions (Fig. 6) aimed at filling existing gaps of knowledge related to the links between biodiversity, ecosystem functions and services (B-EF/ES) in urban areas.

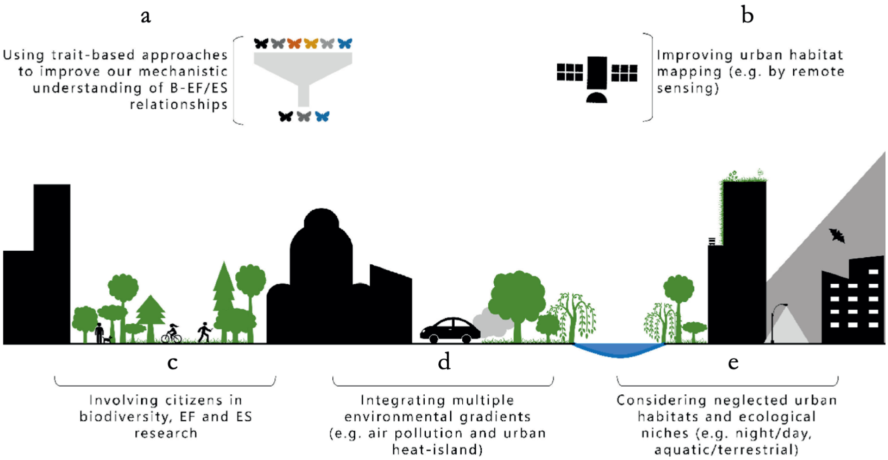


Figure 6. Conceptual research agenda to improve our understanding of relationships between biodiversity and ecosystem functions and services (Biodiversity-Ecosystem functions/Ecosystem services, B-EF/ES) in cities. The five topics highlighted by text sections are discussed in detail in the main text (Paper I).

Firstly, we recognized that applying a trait-based approach is a successful strategy to determine ecosystem processes and, therefore, ecosystem services provision (Dias et al., 2013). We propose using a trait-based approach (Fig. 6a) in order to better understand the link between B-EF/ES in urban ecology studies. For instance, our results from Paper IV showed how plant diversity and occurrence of certain plant traits could affect bee species diversity and consequently pollination. For this, we suggest firstly recognizing the significant traits and socio-environmental filters (e.g. human choices on plant species composition in UGSs) behind the relationships among B-EF/ES. In addition, we stress the importance of considering the future effects of global change when identifying relevant traits.

The second research line (Fig. 6b) arises from the need of spatially and temporally accurate maps of the different kinds of habitats existing in urban areas. We call for habitat mapping techniques that incorporate information related to management practices, habitat size and the full range of land use/land cover types. Moreover, we consider remote sensing as a cost-effective way to create standardized habitat maps with a proper spatial resolution (i.e. allowing us to better characterize the different habitat types) and that are temporarily replicable (i.e. valuable to study long-term processes).

Following on from our knowledge and experience acquired during the development of the BioVeins project, we identified citizen science (Fig. 6c) as a cost-effective way to increase our understanding of the mechanisms that underpin B-EF/ES relationships. So, our third research direction focuses on the importance of including city dwellers in urban ecology studies, emphasizing the need of standardized sampling protocols and error reporting practices in order to make citizen science effective. We also point out the relevance of promoting bottom-up initiatives (e.g. public participation geographic information system, PPGIS) to include city dwellers in urban ecology research.

Several socio-environmental features (i.e. vegetation composition, UGSs configuration, temperature, pollution, soil moisture, etc.) affect urban biodiversity and its relationship with EF and ES. However, their synergistic effect is still poorly understood and, therefore, we consider that there is a need for a holistic understanding of the B-EF/ES relationships. As a result, we propose to integrate multiple environmental gradients in future urban ecology research (Fig. 6d). Accordingly, we need to account for the multiple components (i.e. ecological, socio-cultural and economic drivers) affecting B-EF/ES relationships in urban ecosystems.

Finally, we highlight the importance of considering all kinds of habitat and niches in the urban environment as a continuum (Fig. 6e) since many urban taxa need more than one of them to carry out vital functions. However, many urban ecology studies are bounded by some land use-land cover types (green vs. blue infrastructures), vertical components (above vs. belowground taxa/processes), time of the day (day vs. night) and habitat type (e.g. green roof vs. meadow). Therefore, our fifth research direction is in line with the first one (Fig. 6a): using trait-based approaches. Due to the stochastic changes associated to the urban environment -and the potential increase by future global change-, using trait-based approaches may aid to understand how species respond to these changes at different spatial and temporal scales. It allows us to better understand and predict intraspecific trait variability and phenotypic plasticity in current and future urban conditions.

5.2. Characterization of the vegetation in urban green spaces (Paper II)

5.2.1. Plant diversity

We identified 418 woody species belonging to 76 families in the selected 225 UGS from the 7 studied cities. We provided a comprehensive list (Table A3) of taxa, their occurrence and distribution at regional scale as well as their biogeographic status (i.e. native or non-native at the local scale). The most abundant plant types were deciduous broadleaved trees, specifically *Acer platanoides* and *Quercus robur*, while the most widespread coniferous trees were *Taxus baccata*. We found a marked heterogeneity in terms of most common plant taxa across the latitudinal gradient (Table 5). We also identified high but heterogeneous proportions of non-native woody species across cities, ranging from 40% in Antwerp to 65% in Lisbon and Paris (Hypothesis 2 - high plant diversity in UGSs is due to the presence of non-native species, and the planting practices do not follow ecological knowledge). The most abundant non-native species was *Robinia pseudoacacia*, an invasive species from North-America that was present in all the studied cities.

Table 5. Woody species richness per city: total woody species (n species), average and range (minimum and maximum) of species richness; percentage of non-native species; most predominant woody plant taxa per city; and number of UGSs investigated (Paper II).

	Woody species richness					
City	n	Mean	Range	Non-native species (%)	Most common genus and species (n UGSs)	UGSs (n)
Almada	65	9.5 ± 1	4-18	54	*Pinus* spp. (13), *Olea europaea* (12)	15
Antwerp	74	8.9 ± 0.6	1-18	40	*Acer* spp. (25), *Quercus robur* (17),	35
Lisbon	102	8.2 ± 0.6	3-19	65	*Pinus* spp. (18), *Olea europaea* (17)	34
Paris	231	27.2 ± 3.3	3-101	65	*Acer* spp. (27), *Taxus baccata* (24)	36
Tartu	116	15.3 ± 1.4	4-48	61	*Acer* spp. (28), *Betula pendula* and *Quercus robur* (23)	34
Zürich	137	12 ± 1.2	2-27	64	*Acer* spp. (26), *Carpinus betulus* (19)	35
Poznan	56	6.1 ± 0.3	3-11	54	*Acer* spp. (27), *Acer platanoides* (21)	36

Paris and Tartu harbor the UGSs with the highest woody species richness (i.e. 101 and 48, respectively) and displayed the highest average of woody species per site (i.e. 27.2 and 15.3, respectively) compared to Poznan (i.e. 11 woody species in the richest UGS and an average of 6.1 species per site) (Table 5). The minimum amount of woody species in an UGS was quite homogeneous across the different cities.

5.2.2. UGS size and plant diversity metrics

We explored the relationship among the size of UGSs and two plant diversity metrics, specifically the overall woody species richness and the woody species density (i.e. number of woody species per unit area) (Fig. 7) at two spatial scales (UGS and centroid). We found UGS size and species richness to be positively related at the regional scale (Fig. 7a, black regression line). However, this positive relationship was city-dependent and turned out to be significant and generally weak in Paris

(R^2=0.40), Antwerp (R^2=0.34), Lisbon (R^2=0.18) and Tartu (R^2=0.17) (Fig. 5a, colored regression lines) (Hypothesis 3 - bigger UGSs have generally higher plant species richness, but this relationship is not strong, depending on the urban area location.). We also tested this regression at the centroid level (i.e. UGS size and centroid species richness) without finding any significant relationship.

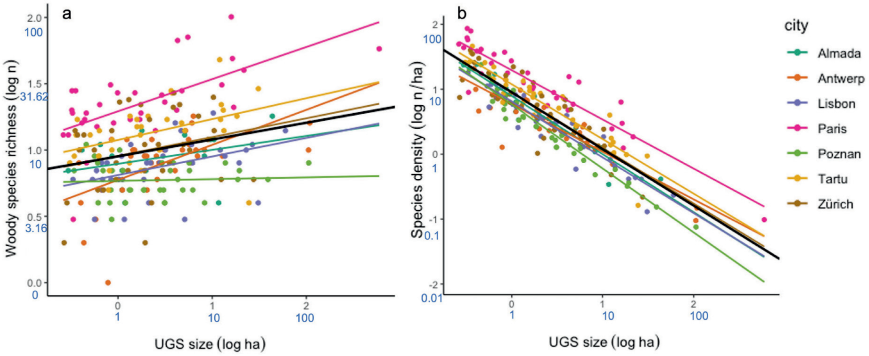


Figure 7. The relationship between the woody species richness (a) and woody species density (b) with the size of UGS. Both scatter-plots on log-scale (black numbers) and absolute scale (blue numbers). Each dot is one UGS. The species richness data (a) comprises all the woody species found in each urban green space. The overall relationship is described by the black regression line. Estimates of the linear mixed effect model: β = 0.16, SE=0.02, t= 6.7, $p < 0.0001$). The woody species density data (b) comprises all the woody species found in each urban green space. The overall relationship is described by the black regression line. Estimates of the linear mixed effect model: β = -0.84, SE=0.02, t= -34.8, $p < 0.0001$). Regression coefficients and significances of simple linear models can be found in Supplementary Table S2 of Paper II.

We obtained a well-defined negative regression between UGS size and woody species density at regional (R^2=0.77) (Fig. 5b, black regression line) and city level (R^2 ranging from 0.72 in Zurich to 0.95 in Poznan) (Fig. 5b, colored regression lines) (Hypothesis 4 – the ecological potential of UGSs is not fully exploited from both taxonomical and functional aspects). The average of species density at the site level was: Antwerp 4 spp./ha, Lisbon 4.7, Poznan 4.7, Almada 6.5, Zurich: 9.5, Tartu 10.6, Paris 23.2.

5.2.3. Tree cover and aboveground biomass

We found significant positive regressions among UGS size and two vegetation parameters (Fig. 8). Firstly, tree canopy cover in absolute terms turned out to have a positive and city-dependent relation with size, displaying regression coefficients from 0.80 in Lisbon to 0.97 in Paris. Regarding tree cover percentage, we found UGSs with an average of 40% of their extent covered by trees in Almada to 74% in Tartu (Table 6). Tree AGB was also positively related with the size of the UGS, independently of the city. This relationship showed a wide range of regression coefficients among cities, from 0.43 (Lisbon) and 0.45 (Zurich and Tartu) to 0.76 in Paris.

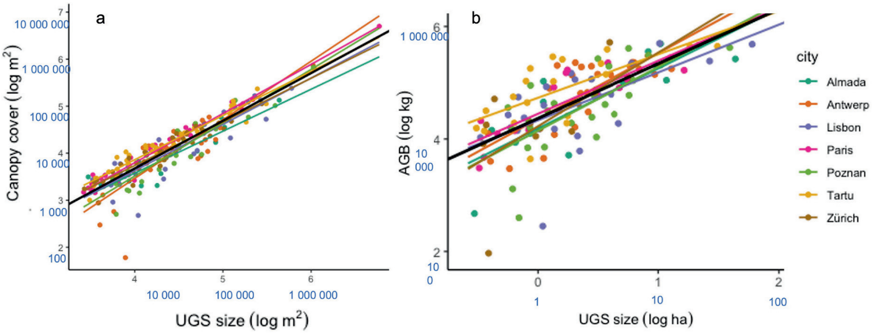


Figure 8. The relationship of UGS size with canopy cover (a) and AGB (b) per city. Both plots are on log-scale (black numbers) and absolute scale (blue numbers). Each dot represents an UGS. The overall relationships are described by the black regression lines. Estimates of the linear mixed effect model a: $\beta = 1.03$, SE=0.03, t= 34, $p < 0.0001$; b: $\beta = 0.98$, SE=0.08, t= 11.9, $p = 0.08$). Regression coefficients and significances of simple linear models can be found in Supplementary Table S2 of Paper II.

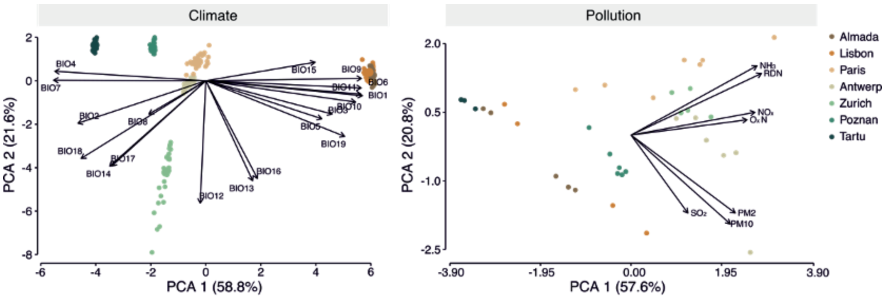
Table 6. Percentage of tree canopy cover, mean above-ground biomass, mean height of the woody layer and diameter at breast height (DBH) of tree plants in the seven cities.

City	Canopy cover (%)	Mean AGB (tons)	Mean height (m)	DBH (cm)
Almada	40	133	8.2 ± 0.4	35 ± 3.3
Antwerp	50	120	11.3 ± 0.4	23 ± 2.5
Lisbon	50	105	9.3 ± 0.2	31 ± 1.5
Paris	67	111	9.8 ± 0.2	24 ± 2.6
Tartu	74	148	9.8 ± 0.2	36 ± 2.1
Zurich	56	78	10.5 ± 0.3	20 ± 2.3
Poznan	45	92	10.7 ± 0.5	26 ± 1.5

5.3. Taxonomic and trait diversity of urban lichens communities (Paper III)

5.3.1. Air quality and climate gradients at the broad scale

Our PCA results showed well-defined gradients of climate and air pollution across the 7 studied cities. Firstly, PCA of temperature and precipitation (Fig. 9a) explained 80.4% of the overall climate variability. First axis displayed the temperature distribution in the different cities. Consistently with the latitudinal gradient, Portuguese cities (Lisbon and Almada) displayed the highest temperature values followed by Paris, Antwerp, Zurich, Poznan and Tartu. According to the second PCA axis, which represented the precipitation variables, Zurich displayed the highest precipitation amounts compared to the rest of the cities that presented similar characteristics.



(a) (b)

Figure 9. Principal Components Analysis showing the ordination of sampling sites (N=219) along climate (a) and air pollution (b) gradients. In the climate PCA (a), the first axis (PCA 1) represents a temperature gradient while the second one (PCA 2) represents a precipitation gradient. Variables BIO1 to BIO 12 represent temperature-related variables, while the remaining represent precipitation-related variables. In the air pollution PCA (b), the first axis (PCA 1) represents a gradient of increasing air pollution while the second one (PCA 2) distinguishes between sites polluted by N-based compounds on one side and sulfur dioxide and particulate matter on the other. Vectors represent the seven-air pollution deposition/air concentration variables retrieved from EMEP, for the year 2018. Pollutant's deposition: reduced nitrogen and oxidized nitrogen. Pollutant's air concentration: NH3 – ammonia, SO2 - sulfur dioxide, NOx - nitrogen oxide. $PM_{2.5}$ and PM_{10} are atmospheric particulate matter of less than, respectively, 2.5 and 10 µm in diameter (Paper III).

The PCA of air pollution explained 78.4% of the total variance in air pollution (Fig. 9b). The distribution of UGSs along the first axis (PCA1) follows a gradient of overall pollution concentration, while the PCA2 displays the most abundant type of pollutants, from N-based compounds to sites mostly polluted by SO_2 and PM. The overlap of some UGSs in Fig. 9b is due to the lower spatial resolution of air pollution data (i.e. 11km) compared to climate variables(i.e. 1km) (see section 4.3.3.). PCA1 showed UGSs sited from Paris, Antwerp and Zurich as the most polluted compared to sites in Poznan, Lisbon, Almada and Tartu in the opposite extreme of the gradient. Regarding the pollution composition (PCA2), N-based compounds are more abundant in UGSs from Paris, Antwerp and Zurich and SO2 and PM are more widespread in Almada, Lisbon and Poznan.

5.3.2. Taxonomic and trait diversity of urban lichens

Our results showed similarities between some of the diversity metrics. Therefore, and in order to avoid redundancy, here we present our results of species richness, abundance, Shannon and Jaccard indices. Nonetheless, results of all the metrics are available in Figure S1 of the original manuscript (Paper III). We identified 140 lichen species (from which 9 could be identified only to the genus level) across 219 UGSs from the 7 studied cities. As displayed in Figure 10, UGSs from Tartu, Zurich and Lisbon were the richest and more biodiverse compared to Poznan where the lowest values were found. The same pattern was found in species abundance. According to Jaccard index scores, cities were taxonomically dissimilar among them, especially Almada (Jaccard = 0.91) compared to Lisbon, Paris and Zurich.

Our trait-based results show a dominance of lichens with a foliose narrow leaf growth form in all the cities while the least frequent growth form was fruticose (Fig. 10) but also leprosy and squamulose (see Fig. S1 from the original manuscript – Paper III). In general, the most abundant urban lichens at the continental scale are highly resistant to solar irradiation and present medium and medium-high tolerance to aridity (Fig. 10) (Hypothesis 5 - urban environmental conditions have not changed significantly for the better). This was true for all the cities except for Poznan, with few nuances in Almada, where lichens less tolerant to irradiation (i.e. medium tolerance) and with a medium-low tolerance to arid conditions were also rather common (25% and 13%, respectively). Lichens in Poznan were all medium-highly tolerant to aridity. The tolerance to eutrophication showed different patterns. The most tolerant lichens were found in Poznan, Paris, Zurich and Lisbon, accounting in most cases for more than 50% of the total species pool. In Antwerp, lichen species with medium-high and high eutrophication tolerance were more common. As seen in Figure 10, Tartu was the most heterogeneous city in terms of functional traits (i.e. highest functional diversity) and Almada displayed the highest functional dispersion (i.e. RaoQ). Contrastingly, Poznan showed the lowest values in terms of functional richness and functional dispersion. The rest of the cities displayed rather medium values of functional diversity in their lichen communities.

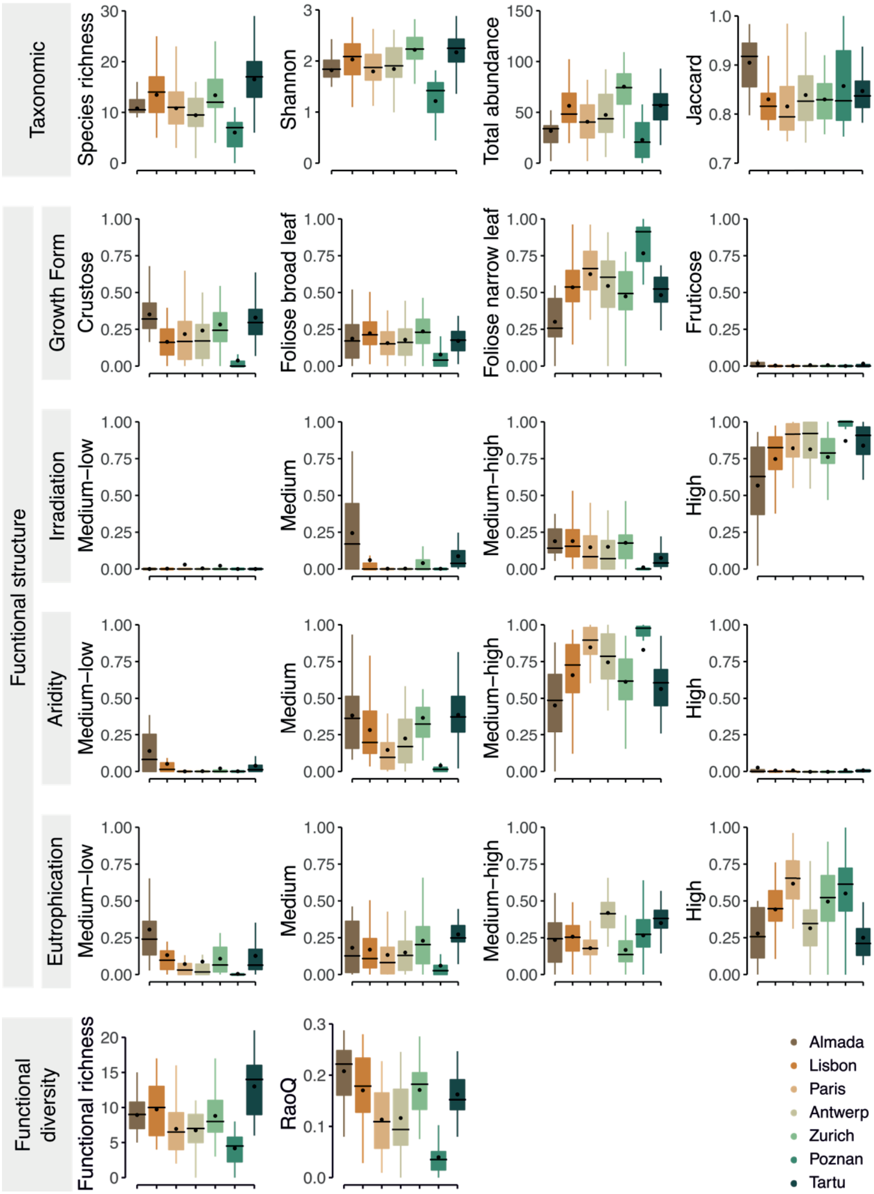


Figure 10. Boxplots representing the distribution of taxonomic, functional structure and functional diversity metrics in the seven European cities, ordered here from the warmest (Almada to the coldest (Tartu), as indicated in the first axis of the PCA (Fig. 9a). Shannon, Jaccard and Rao's Q indices values range from 0 to 1. The functional structure, represented here by the CMW of each functional group (Table 3) belonging to the same trait (growth form, tolerance to irradiation, tolerance to aridity, tolerance to eutrophication) ranges also from 0 to 1 (the sum of all functional groups from the same trait is 1 at site level). Boxes display first to third interquartile ranges, the black lines the median, the dots the average, and the whiskers the maximum and minimum (N=219) (Paper III).

5.3.3. Broad scale air pollution and climate as driver of the taxonomic and trait variance

Our results showed that the four selected drivers at the broad scale (i.e. air pollution type, pollution concentration, precipitation and temperature) explained an average of 14.4% (considering all diversity metrics). Local scale (within-city) drivers must represent most of the variance (the remaining 85.6%). Among the broad scale drivers, we found air pollution accounting for most of the variance when grouping by metric type, especially when considering the overall functional diversity (21.3%) and some functional groups (e.g. tolerance to aridity) (Fig. 11b). Regarding broad scale climate, it did not explain more than 7% of the variance in any of the considered metrics, with the only exception of the overall functional diversity (7.1%). The variance of the functional structure of lichen communities was better explained by air pollution than by climate with a very small difference in the irradiance tolerance (Fig. 11b).

Overall taxonomic variance was mainly explained by air pollution (7.8%) (Fig. 11b), although each taxonomic metric showed differences individually (Fig. 11a). Shannon index and total abundance were considerably explained by climate. Functional richness variance was explained by air pollution (24.3%), while for RaoQ both broad scale drivers were important (Fig. 11a). Regarding the functional structure, air pollution was the main broad scale driver explaining the variance of most of the metrics (e.g. 12.8% crustose lichens, 17.9% medium tolerance to aridity), although climate turned to be important in explaining the variability of some traits such as the medium-high tolerance to solar irradiance and medium-low aridity tolerance (Fig. 11a). Eutrophication tolerance was mainly explained by air pollution compared to climate (Fig. 11a,b) although for the medium-high tolerance level, both drivers were equally important.

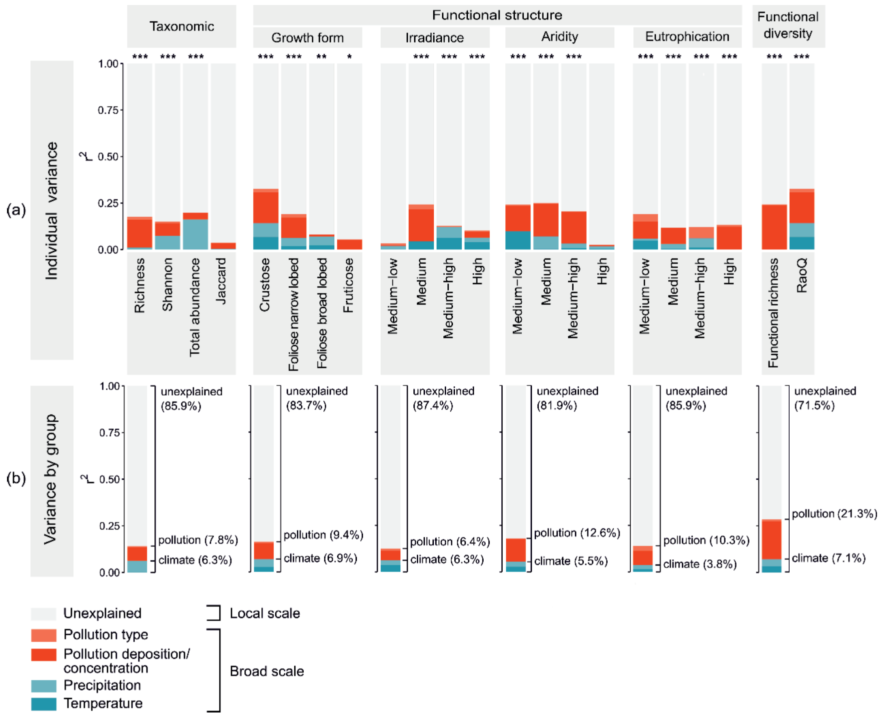


Figure 11. Variance partitioning of broad scale drivers for each (a) lichen biodiversity metrics and (b) the average variance partitioning for each group of metrics. Metrics are grouped into taxonomic and trait-based, the latter sub-divided into functional diversity and functional structure by trait (growth form and tolerance to irradiance, aridity and eutrophication). Significance of the model is indicated in superscript: * = p < 0.05; ** = p < 0.01; *** = p < 0.001 (Paper III).

5.4. Plant-pollinators interactions (Paper IV)

5.4.1. Taxonomic and trait-based diet preferences

We identified a total of 135 plant species from 93 genera and belonging to 41 families in the larval diet composition of the four studied bee species through the metabarcoding technique. There was a general preference for native plant species (55%) and for some functional traits in larval diet. Herbs (42%) were the most commonly found plant growth form and dish-bowl (56%) was the preferred blossom type. We found an heterogeneity in the amount of plant taxa across the diet of the four studied species (Fig. 12) at the regional level that was coherent with their diet specialization degree (Hypothesis 6 - more generalist wild bee species might have better chances than specialist species in surviving in an urban environment due to more rich and variable diet). In the nests of the most oligolectic bee species (*C. florisomne*) we identified pollen from just 4 plant species, the nests of the intermediate polylectic species (*O. cornuta* and *O. bicornis*) had 33 and 51 plant species respectively, while the diet of the most generalist bee (*H. communis*) was composed by 81 plant species. Exotic plant species were more commonly found in the larval diet of *H. communis* than in other bee species.

We found species-specific patterns in larval diet composition at the city level. Firstly, *C. florisomne* displayed a narrower taxonomic variety, having a clear preference for *Ranunculus* genus at the regional level with differences at the city scale (*R. acris* in Antwerp, *R. repens* in Tartu and *R. bulbosus* in Zurich). Secondly, we found a predominance of *Acer pseudoplatanus* in the larval diet of *O. bicornis* (abundances in Paris, 64% ; Poznan 44%; and Zurich, 33%) and *O. cornuta* (abundances in Antwerp, 37%; Paris, 21%; and Zurich, 24%), although in Antwerp *Quercus robur* displayed the highest abundance (70%) in larval diet of *O. bicornis*. Finally, *H. communis* presented less obvious preferences. In this case, most of the plant species showed an abundance between 1-14% with the only exception of *Styphnolobium japonicum* that was found to be predominante only in Paris (52%) and Poznan (32%). We found an abundance of dish-bowl or brush type blossoms, in the *O. cornuta* and *O. bicornis* larval diet from the *Sapindaceae*, *Salicaceae* and *Rosaceae* families (*O. cornuta*) and *Sapindaceae* and *Fagaceae* (*O. bicornis*) (Fig. 12).

5.4.2. Bee species distribution along the urban intensity gradient

The two main axes resulting from the PCA of the explanatory variables explained 38% and 11.6% of the total variation respectively (Fig. 13). The first axis involved remote sensing-based variables while the second axis was composed by local land cover metrics and the availability of floral resources (derived from the floral inventories). Large values of PC1 are associated with high UI, CI and LST, and lower NDVI. Large values of the second axis are related to more grassland and, therefore, less proportions of deciduous trees and artificial surfaces. Our linear model results showed NDVI to be positively related with family richness, species richness and pollen diversity in *H. communis* is every city but Poznan.

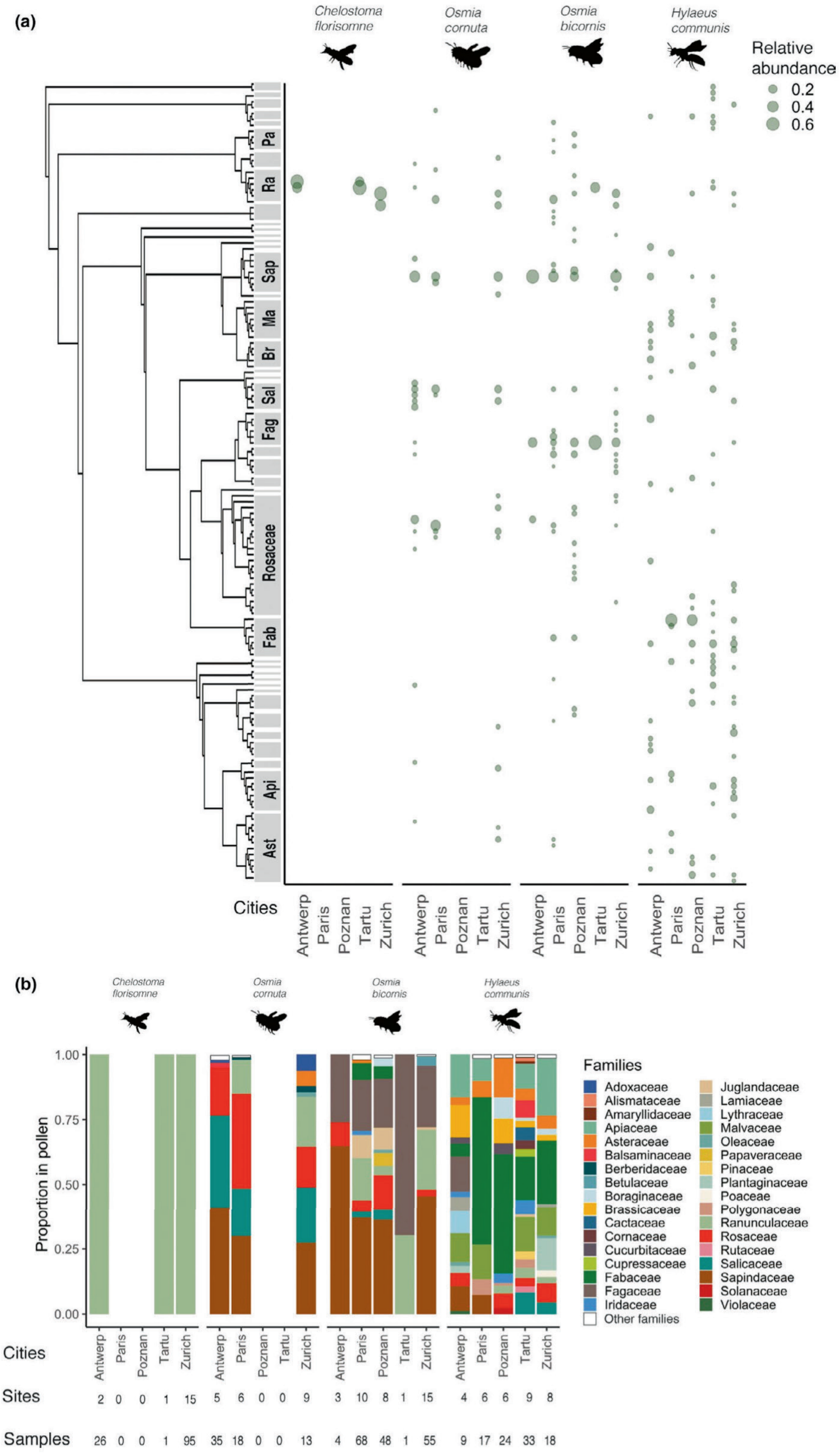

(a)
Chelostoma florisomne
Osmia cornuta
Osmia bicornis
Hylaeus communis
Relative abundance
0.2
0.4
0.6
Pa
Ra
Sap
Ma
Br
Sal
Fag
Rosaceae
Fab
Api
Ast
Cities
Antwerp
Paris
Poznan
Tartu
Zurich
(b)
Proportion in pollen
1.00
0.75
0.50
0.25
0.00
Families
Adoxaceae
Alismataceae
Amaryllidaceae
Apiaceae
Asteraceae
Balsaminaceae
Berberidaceae
Betulaceae
Boraginaceae
Brassicaceae
Cactaceae
Cornaceae
Cucurbitaceae
Cupressaceae
Fabaceae
Fagaceae
Iridaceae
Other families
Juglandaceae
Lamiaceae
Lythraceae
Malvaceae
Oleaceae
Papaveraceae
Pinaceae
Plantaginaceae
Poaceae
Polygonaceae
Ranunculaceae
Rosaceae
Rutaceae
Salicaceae
Sapindaceae
Solanaceae
Violaceae
Cities
Sites
2 0 0 1 15 5 6 0 0 9 3 10 8 1 15 4 6 6 9 8
Samples
26 0 0 1 95 35 18 0 0 13 4 68 48 1 55 9 17 24 33 18

Figure 12. Bee larval diet composition in the studied cities. (a) For each bee species, the collected plant species in each city where the bee species was recorded (three cities for *Chelostoma florisomne* and *Osmia cornuta*, five cities for *Osmia bicornis* and *Hylaeus communis*) are shown. The size of the circle represents the mean relative abundance of plant species contributing to pollen samples per city and bee species. (b) For each bee species, the proportion in the pollen of the different collected plant families in the studied cities is shown (mean relative abundance of plant species contributing to pollen samples per city and bee species). Only families with a proportion in pollen ≥ 0.01 are plotted, whereas the remaining ones are represented in the category 'Other families'. Note that the proportion in pollen for *O. bicornis* in Antwerp and Tartu was obtained using only four and one sample, respectively. For each bee and city, we provide the number of sites where pollen samples were taken, and the total number of samples. Information on the computation of the phylogenetic tree can be found in Text S2 and Figure S5 of the original publication (Paper IV). Data supporting (a) can be found in Table S8 of the original publication (Paper IV). Ast, Asteraceae; Api, Apiaceae; Fab, Fabaceae; Fag, Fagaceae; Sal, Salicaceae; Br, Brassicaceae; Ma, Malvaceae; Sap, Sapindaceae; Ra, Ranunculaceae; Pa, Papaveraceae.

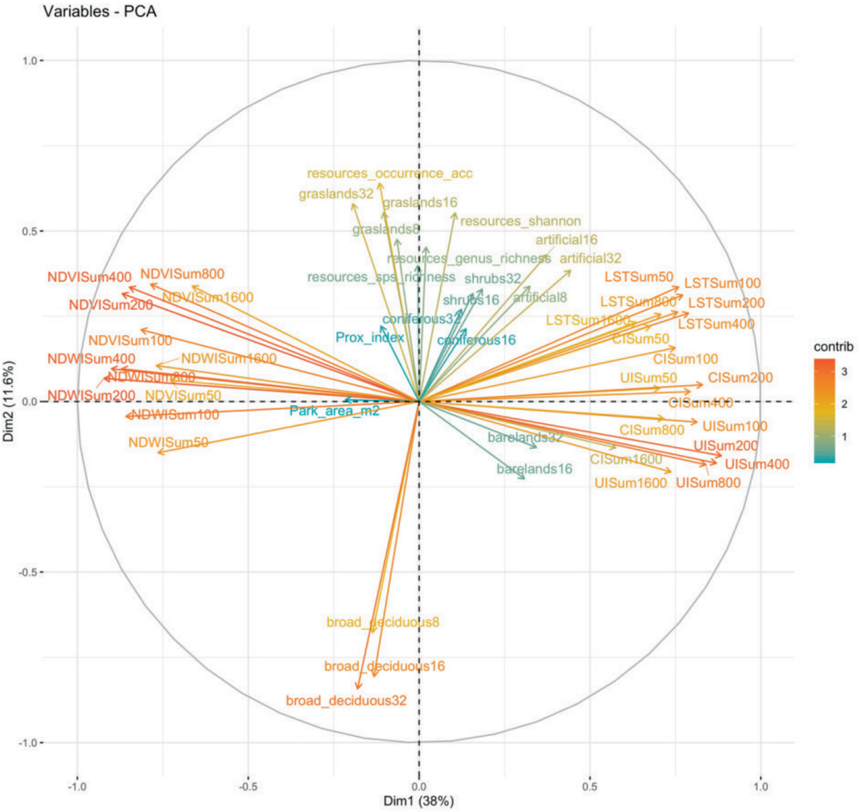


Figure 13. Results from the principal component analyses on the 53 explanatory variables. The color of each arrow indicates the contribution to the axis, with warm colors (red) indicating the highest contribution and cold colors (blue) indicating the lowest. LSTSum = Land Surface Temperature; NDVISum = Normalised Difference Vegetation Index; NDWISum = Normalised Difference Water Index; CISum = Color Index; UISum = Urban Index; artificial = artificial surfaces; coniferous = coniferous trees; shrubs = shrub vegetation; broad_deciduous = broad deciduous trees; grasslands = grassland vegetation; resources_shannon = Shannon diversity of the floral resources; resources_occurrence_acc = Sum frequency of all flowering plant species; resources_sps_richness = species richness flowering plants; resources_genus_richness = genus richness flowering plants. Numbers indicate the radius of the measuring buffer in meters (Paper IV).

Our distribution models evidenced two main distribution patterns along the urban intensity gradient (Fig. 14). On the one hand, the predicted probability of occurrence of *C. florisomne, O. cornuta* and *O. bicornis* was lower when increasing urban intensity gradient at the landscape scale (i.e. low values of NDVI and large values of UI, CI and LST) (Fig. 14a,b). At the local scale, their probability of occurrence increased with grassland cover (Fig. 14c,d). Despite *O. cornuta* and *O. bicornis* diet composition having large proportions of tree pollen, their maximum probability of occurrence happened where there were low proportions of broadleaved deciduous trees. On the other hand, *H. communis* showed a rather constant probability of occurrence along the urban intensity gradient at the landscape level (Fig. 14a,b) (Hypothesis 7 - broader diets of wild bee larvae are associated with wider distribution ranges of bee species). At the local scale, proportions of broadleaved deciduous trees had an influence on their predicted probability of occurrence (Fig. 14c,d).

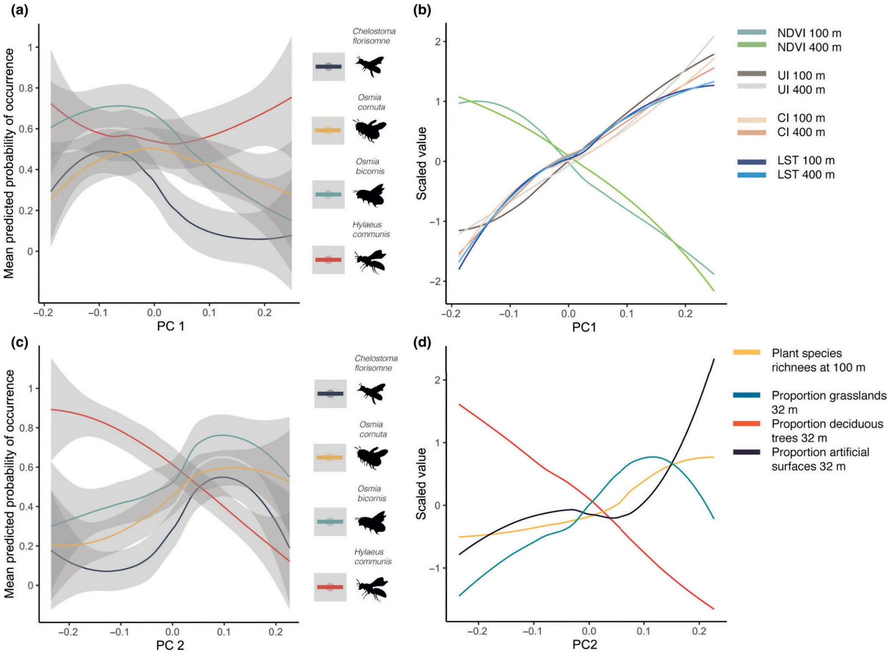


Figure 14. Bee distribution along urban gradients. (a and c) Loess smoothing of the mean predicted probability of occurrence of the four bee species in relation to the (a) first PCA axis (PC1) and (c) second PCA axis, performed on the explanatory variables, representing 38% and 11.6% of the variation, respectively. The mean predicted probability of occurrence results from the predicted probabilities of occurrence of the models with TSS > 0.4. Bands represent 95% confidence intervals. (b and d) Variation in the explanatory variables contributing the most to PC1 (b) and PC2 (d). (b) Larger values of PC1 correspond to higher values of impervious surfaces (urban index, UI), bare land (color index, CI) and land surface temperature (LST) and lower vegetation cover (normalized difference vegetation index, NDVI) at different landscape scales (i.e. 100 and 400 m). (d) Lower values of PC2 correspond to higher proportions of deciduous trees and lower proportions of grasslands and floral resources (plant species richness) at local scales. Other scales and variables have been omitted here for simplicity (see Figure S13). See also Figure S12 for more details on the PCA (Paper IV).

6. DISCUSSION

6.1. Drawing future research directions for urban ecology (Paper I)

This research was the result of a multidisciplinary discussion of the current knowledge and future trends of urban ecology. Specifically, we investigated five strategies (Fig. 6) to improve our knowledge on the link between biodiversity and ecosystem functions and services (B-EF/ES) in urban areas, namely i) using trait-based approaches, ii) improving urban habitat mapping, iii) promoting citizen science, iv) integrating multiple urban gradients, and v) considering often neglected urban habitats and ecological niches (Hypothesis 1 - understanding B-EF/ES relationships require applying a holistic and comparable methodological approach).

We proposed applying a trait-based approach to improve our knowledge on the link between B-EF/ES in urban ecology studies as well as to understand how species respond to urban distinctive conditions. In natural ecosystems, community composition is mainly shaped by natural processes such as dispersal ability, competition or the influence of abiotic factors. However, cities are more complex systems since the anthropogenic component creates specific conditions that shift our traditional knowledge of ecosystem functioning (Aronson et al., 2016). Novel species assemblages in urban ecosystems imply communities with novel trait composition. Vegetation traits have been demonstrated to play a key role in determining ecosystem functioning and green infrastructure multifunctionality (i.e., the provision of multiple ESs simultaneously) (Tiwary et al., 2016). For instance, canopy characteristics have been shown to have an important influence on multiple ESs (e.g., local climate regulation, Ziter et al., 2019; mitigation of extreme weather events, Lundholm et al., 2010; and PM removal, Hofman et al., 2016). Jeanjean et al. (2016) suggested that plant species selection in urban areas can lead to different reduction patterns in air pollution. Moreover, some species show adaptive trait variation as a response to changes in environmental conditions (Radchuck et al., 2019).

Exploring trait variation at the individual level allows for a better understanding of phenotypic plasticity and adaptations to the urban conditions, contributing to increase our knowledge on eco-evolutionary dynamics at a fine scale (i.e., genetic level) (Uchida et al., 2021). This is especially important in the frame of global change. Therefore, adopting trait-based approaches may improve our understanding on how species respond to current and projected urban stressors (see Paper III) (and thus, predict ESs provision under different environmental conditions and mitigate negative effects on urban nature) as well as contribute to strategically design more livable and resilient cities (e.g. promoting specific traits in order to cope with the city-specific demanded ESs) (Laughlin, 2014). In other words, it becomes necessary to understand how the functional trait diversity underpins ecosystem functions and services and to include this knowledge when developing urban plans and management practices (Luederitz et al., 2015; Schwarz et al., 2017). According to the literature (Isbell et al., 2011; Winfree et al., 2018), functionally redundant species may coexist in an ecosystem over the time, providing more stability to EF and the derived ESs.

Notwithstanding the existing land characterization instruments at large spatial scale (e.g. Natura 2000 network, European Urban Atlas, Corine Land Cover), there is a need for covering within-city habitat types at a very high thematic resolution. Despite the European Urban Atlas homogeneously mapping different land use and land cover types across European cities, the definition of habitat remains insufficient (i.e. it only comprises the three categories: Green Urban Areas, Forest, and Herbaceous Vegetation Association). Moreover, it does not consider socio-ecological features (e.g. management practices) either small areas and linear elements that are key to understanding the patterns of biodiversity (Pinho et al., 2016) and ESs provision (Capotorti, Alós Ortí, et al., 2019; Hand et al., 2017; Mexia et al., 2018).

Some cities (e.g. Paris and Zurich) have mapped their different habitat types at a very high spatial resolution. Nonetheless, their temporal and spatial resolution do not coincide, which limits their applicability in ecology research. Despite our outcomes from photo-interpretation of high resolution aerial images in Paper II contribute to fulfill this existing gap (i.e., we provided highly accurate land cover maps of 225 UGSs at a fine spatial scale), this technique is time-consuming and does not allow us to distinguish beneath-canopy surfaces). We point out the advantageous of remote sensing techniques for habitat characterization due to its spatial and temporal continuity, low resource consuming (i.e. economic cost and time) and the wide range of research opportunities (e.g. ESs distribution, cold- and hot-spots for biodiversity conservation, emergency warning systems) among others. In addition, it enables integration of multiple environmental gradients (e.g. temperature, humidity, vegetation type and cover) allowing for a more holistic study of urban biodiversity patterns, EF and ES. This combined with a trait-based approach provides a great opportunity to identify the potential socio-ecological filters involved in community composition and therefore, on EF and ES.

Finally, we also stress out the importance of citizen science in urban ecology studies for two main reasons. Firstly, since most of the world population lives in cities, it has been shown to be a great opportunity to enlarge and improve scientific datasets (Martin et al., 2019) by embracing a wide range of urban taxa, environmental features and providing data from inaccessible areas (e.g. private gardens). Secondly, involving citizens in scientific projects contributes to educating and concerning the public about environmental and ecological questions and challenges (Deguines at al., 2018; Deguines et al., 2020) as well as to social cohesion. For citizen science initiatives to be useful and successful, data quality needs to be carefully taken into account (Serret et al., 2019) (e.g. by means of data validation, sampling design, standardized sampling designs, error reporting protocols, feedback to the participants) (Silvertown, 2009).

6.2. Characterization of the vegetation in urban green spaces (Paper II)

In this research, we aimed at studying the woody communities composition and species distribution among UGSs in 7 European cities. We also investigated how woody species diversity, tree canopy cover and tree AGB vary across the size gradient. Our results showed how UGS size was positively related to woody species richness in four cities and negatively with woody species density in every studied city (Fig. 7). UGS size was also positively related to tree cover in absolute terms and tree AGB (Fig. 8). Our results indicate that there is more room to increase vegetation biodiversity in UGS and its associated ecosystem services in European cities through management practices.

6.2.1. Woody plant diversity

We identified 418 woody species from 76 families across 225 UGS in seven European cities (Table A3). Species composition in the studied

UGSs is 59% non-native. This proportion varies among cities, ranging from 40% in Antwerp to 65% in Lisbon and Paris (Table 4) (Hypothesis 2 - high plant diversity in UGSs is due to the presence of non-native species, and the planting practices do not follow ecological knowledge). The higher plant biodiversity in urban areas compared to natural ecosystems (e.g. Kühn et al., 2006) is mainly explained because of the high abundance of non-native species cultivated in cities. The most common non-native species in this research were *Robinia pseudoacacia* and A*esculus hippocastanum* (in 55 and 52 UGSs, respectively), while the most frequent native species were *Acer platanoides*, *Quercus robur*, *Taxus baccata* and *Carpinus betulus* (each of them found in, at least, 50 UGSs). Our results are in keeping with the existing literature (Crosby et al., 2021; Pauleit et al., 2002).

Urban ecosystems have many artificially planted species, such as ornamental trees. Species selection always comprises a trade-off among environmental, social and economic assets. *A. platanoides*, which was the most abundant species in our research, is an efficient species in pollution removal (particulate matter and O_3) and in storing C (Baraldi et al., 2019). However, its growing process harms impervious surfaces and other urban infrastructures (Scholz et al., 2016). Regarding *R. pseudoacacia*, which was found in all of our studied cities, it tolerates harsh environmental conditions and biological diseases and it is considered an invasive species in the European continent (Puchalka et al. 2021), but not as good in cooling temperature in cities as other native species (e.g. *Tilia cordata*) (Rahman et al., 2019). In addition, it has been shown that it is currently suffering the consequences of global warming and air pollution in urban areas (Wilkaniec et al., 2021). Unlike *R. pseudoacacia*, *A. altissima*, which is also a non-native and invasive species in Europe, was only found in Paris. It is a fast-growing species with a wide tolerance threshold for several urban stressors (i.e. urban heat island effect, drought and poor soil conditions). It has been found in many European urban areas according to previous studies (e.g. Casella et al., 2013), although its within-city distribution seems to be restricted to less or non-managed land cover types (e.g. ruderal areas and paved surfaces, Paź-Dyderska et al., 2020). Therefore, we claim that management practices, such as those applied to UGSs, may restrain its spread and, therefore, limit the ecological damage on native biodiversity.

This research has a high relevance in urban ecology studies since it contributes to knowing the species composition in UGSs, which is usually driven by human choices based on species impact on environmental and socio-economic features. Knowing the woody species composition is key for ecological research since it determines the resilience and effectiveness of urban ecosystems in ESs provision and biodiversity conservation. It takes an added value in the frame of the global change, its direct effect on temperature and the indirect consequences (e.g. increased pathogen threads) that will condition ecosystem functions and processes and, consequently, human health and well-being.

6.2.2. Woody diversity and UGS size

UGS size positive effect on biodiversity has been demonstrated in many studies in natural ecosystems (e.g. Cornelis et al., 2004). On the one hand, our research demonstrated that this relationship is not as clear and obvious in cities as it is in natural areas. We found this size-diversity relationship to be city-dependent and cannot be generalized to every urban area. In our studied cities, it was found to be significant and rather weak in four out of the seven studied cities (Antwerp, Lisbon, Paris and Tartu) (Hypothesis 3 - bigger UGSs have generally higher plant species richness, but this relationship is not strong, depending on the urban area location). However, increasing UGS size in order to increase biodiversity by planting more species, is not feasible in densely urbanized areas such as European cities. We also found differences in the size-diversity relationship at the regional and the city scale (i.e. it was significant when all the 225 UGSs were tested together and, at the city level, it occurred in four cities). It suggests that other features not considered in our study have also an influence on local biodiversity.

On the other hand, we found that the average and median of woody species richness in the sampled centroid of each UGS were always four and had no link with UGS size or city. As a consequence, we assume that it is the minimum amount in species selection by municipalities when planning and designing UGSs. Indeed, urban planning and policy do not fully consider the role of biodiversity in supporting ecosystem functioning and, therefore, ESs provision up to the point of some authors calling it 'biodiversity myopia' (Basnou et al., 2020). Moreover, we found a strong negative regression among UGS size and woody species density (i.e. species richness per unit area). This result, combined with the weak positive relationship found among UGS size and species richness, suggests that although park managers and urban planners in some cities tend to increase plant diversity when more room is available, they do so up to a limit. In other words, the already established UGSs have the potential of promoting more plant diversity (Hypothesis 4 - the ecological potential of UGSs is not fully exploited from both taxonomical and functional aspects). As demonstrated by previous studies (de Bello et al., 2010; Hector et al., 2005; Lundholm et al., 2010) the provision of multiple ESs can be maximized by increasing species richness and trait diversity. As our area-diversity results showed (Fig. 7), UGSs can be designed and managed to harbor more plant diversity, especially in larger UGSs. By increasing species-size relationships (Fig. 7a), species density across the size gradient (Fig. 7b) would get closer to a flat line. Studying species density in urban areas is a cost-effective indicator of how urban planning and policies are integrating biodiversity in urban ecosystems. More species richness implies enhanced ecosystem functioning and therefore, ESs provision. However, ecologically-informed decisions are needed to effectively promote biodiversity in UGSs, as species selection cannot be guided by socio-economic preferences only. In addition to taxonomic richness, functional diversity also plays a role in ecosystem processes (e.g. carbon, nutrient and water cycling) and ESs provided (Díaz et al., 2007). Key functional traits (e.g., canopy size) are closely related to multiple ecosystem processes (e.g., shading, evapotranspiration, water flow) and therefore, to the provision of several ESs (e.g., climate and water regulation) (de Bello et al., 2010). Combining taxonomic and trait approaches is especially important in ecosystems where non-native species are abundant (e.g., urban ecosystems), as communities with a high functional diversity are less prone to invasion (Funk et al. 2008). Although management practices of UGSs may contain the spread of invasive species, they may escape and succeed in less managed urban ecosystems and surrounding rural areas.

Regarding vegetation management practices, we found them to be consistent at the regional scale. Specifically, the average tree height in our studied cities ranged between 8 and 11m and large adult trees were preferred (i.e. DBH >20cm). These finding were more evident in cities from the upper extreme of the latitudinal gradient (i.e. Tartu) and, secondly in the lowest latitudes (i.e. Lisbon and Almada). In the case of Tartu, this may be due to the urban heat island effect that, together with management practices, has restrained the thermal limiting factor in plant growth (Chmielewski et al., 2001; Smith et al., 2019). Another combination of factors that foster tree growth in northern urban areas are the periodicity of rainy days (i.e. higher in high latitudes compared to southern areas) combined with the high CO_2 concentrations typical from urban areas (Pretzsch et al., 2017). In the case of Lisbon and Almada, climate conditions may act as a stressor for urban vegetation and therefore, be an environmental filter for plant species distribution and growth lessened by management practices.

6.2.3. Tree cover and AGB in UGSs

We analyzed the regression among UGS size and tree cover and AGB, finding a positive relationship in both cases and being size-canopy cover a city-dependent relationship (Fig. 8). For this, we used tree canopy cover in absolute terms instead of relative ones (i.e. percentage of tree cover) since relative canopy cover may mislead our results due to few trees covering big proportions of small UGSs. However, relative canopy cover provides useful information on management practices. Indeed, Table 5 suggests that municipalities consider other land cover types different from trees (e.g. open lawns, paved surfaces) when designing UGSs. Exploring tree cover in urban ecosystems is useful to better understand how cities face climate change (e.g. tree canopy cover has been shown to have a clear influence in cooling the urban environment, Chen et al., 2020; Zardo et al., 2017) as well as provide ES to city dwellers (Gillner et al., 2015; Mouratidis, 2019; Pataki et al., 2011) and provide habitat for other urban biota (Moudrý et al., 2021).

6.3. Air quality and climate regulation as drivers of lichen biodiversity (Paper III)

In this study we accounted for taxonomic and trait diversity of lichen communities in 219 UGSs from 7 European cities. We retrieved information of the most common urban stressors (climate and air pollution) and investigated their influence in lichen biodiversity, functional structure and functional diversity at local and continental scale. As we hypothesized, the variance of the taxonomic and trait-based metrics was mainly influenced by local (within-city) drivers compared to broad scale (between cities). Air pollution turned out to have a bigger effect on lichen communities than climate features at the broad scale.

Our results showed a clear and dominant influence of local scale drivers (an average of 85.6% of the overall variance and always >50% if we focus on the individual metrics) in shaping lichen communities in urban areas. Because we found that less than 15% of lichen metrics variance was due to broad-scale factors, we claim that in order to efficiently use lichens as ecological indicators in urban areas across broad gradients (e.g. at the continental or global scale), both broad and local scale environmental drivers must be considered together. The taxonomic and trait-based metrics responded differently to the environmental drivers considered (air pollution and climate).

A recent report about the air quality (Ortiz et al., 2020) states that NOx, PM and sulphur-based pollutants from industrial activities and transport have declined in Europe in the past decades. However, air pollution levels are still too high for lichen communities to reflect this recent trend in air quality improvement in European cities (Sicard et al., 2021; Stevens et al., 2020) (Hypothesis 5 - urban environmental conditions have not changed significantly for the better). Despite NH_3, NH_4 pollution in Europe has also declined -although in a small proportion- it is foreseen that this trend will overturn and reduced nitrogen pollution will increase (Amann, 2012) also in urban areas (Ortiz et al., 2020). Indeed, our results suggest that urban lichen communities are currently dominated by species resistant to eutrophication. Similar patterns were also found in previous studies conducted in urban areas (Llop et al., 2012; Llop et al., 2017). Our results confirm that lichens are good ecological indicators of air quality, given that the less polluted cities (Tartu and Almada) harbored a bigger proportion of eutrophication-sensitive lichens. In addition, RaoQ results indicated a bigger functional dispersion in these cities, pointing out that lichens dwelling in less polluted cities display a wider variety of functional strategies. Therefore, lichens with low tolerance to air pollution can succeed in cities with good air quality. Consequently, lichens can be used to monitor the success of air quality improvement strategies also at the broad scale.

Several studies have shown that broad scale climate has an influence in functional diversity in lichens (e.g. Concostrina-Zubiri et al., 2014; Di Nuzzo et al., 2021; Hurtado et al., 2020a; Hurtado et al., 2020b; Matos et al., 2015), but mainly in natural and semi-natural ecosystems. Our results showed that broad scale drivers had more influence on taxonomic and functional diversity compared to functional structure metrics, suggesting that trait-based metrics do not respond the same way to broad scale climate in urban areas (i.e. climate features explained 5.5% out of the 14.5% of the variance at the broad scale). Therefore, local scale drivers could play a more significant role in lichen functional traits. Our results show that functional richness is the best metric to monitor the effects of air pollution in such continental urban gradients. In addition, air pollution concentration was considerably more important than air pollution type across all the considered metrics. Consequently, we assume that lichens respond to air pollution intensity, regardless of the type of pollutant in question (Llop et al., 2017; Varela et al., 2018).

Among the considered climate variables (precipitation and temperature), precipitation had a bigger effect in lichen taxonomic diversity and growth form. Both variables were equally important in aridity and solar irradiation tolerances. Our results indicate that the considered taxonomic and trait-based metrics cannot be used to directly monitor the effects of climate in lichen communities in urban areas at the continental scale. Therefore, we agree with previous studies (Branquinho et al., 2015) as for future research should consider other metrics and/or uncouple air pollution (the main driver) from climate effects to better explore the latter. Previous studies at the city level have revealed that local environmental drivers have an effect in shaping lichen communities (Davies et al., 2007; Koch et al., 2019; Matos et al., 2019; Munzi et al., 2007). Accordingly, our multi-city research indicates that in urban areas across a continental-scale gradient, broad scale environmental drivers are overshadowed by local scale drivers. Local scale drivers such as local air pollution sources (e.g. UGS in the surroundings of industrial activities and high-traffic road), UGS management practices, history and phorophyte species should be included to understand the lichen communities response to the main environmental drivers. As far as we know, this is the first time that the response of lichen biodiversity metrics in urban areas across a large scale gradient are explored, distinguishing among broad and local scale drivers. Additional multi-city studies following a standardized field survey are necessary to increase our knowledge on urban ecosystem functions and processes.

6.4. Plant-pollinators interaction (Paper IV)

In this research we investigated larval diet and species distribution of four common urban bees that differ in terms of feeding behavior (i.e. from oligolectic to generalist species). We installed trap-nests, used metabarcoding techniques, mapped the availability of habitat and sampled the floral resources to accurately model wild bee species distribution in UGSs from 5 European cities. More specialized bees showed less floral variety in their diet and a higher sensitivity to urban intensity.

6.4.1. Taxonomic and trait-based diet preferences

Our results confirmed our hypotheses 6 (more generalist wild bee species might have better chances than specialist species in surviving in an urban environment due to more rich and variable diet) and 7 (broader diets of wild bee larvae are associated with wider distribution ranges of bee species): highly specialized bees showed more consistent (i.e. less variable) diets that were mainly composed of pollen from native plants compared to more generalist bee species. In addition, ad diets were also more consistent at high plant taxonomic ranks (i.e. family). Larval diet consistency of *C. florisomne, O. cornuta* and *O. bicornis* at plant family level has also been found in other ecosystems (e.g. Haider et al., 2014). Diet consistency at the family level seems to be common among bee species, since it has also been found in several previous studies (e.g. *Bombus* spp. in Wood et al., 2003; *Osmia* spp. in Haider et al., 2014 and Vaudo et al., 2020). At the plant species level, the consistency in bee diet was rather low (except for the oligolectic *C. florisomne*) maybe because of the concrete functional traits (Vaudo et al., 2020) that lead plant-insect interaction in more generalist bee species can be more consistent at the genus or family level. It has been shown how a wide variety in diet composition is an important feeding strategy to succeed in urban areas for different animal taxa (Fournier et al., 2020). It has also been reported intraspecific differences in functional traits among rural and urban animal populations (e.g. bumblebee, Eggenberger et al., 2019). Our results showed that herbaceous species that are widespread in urban areas (e.g. *Taraxacum officinale, Bellis perennis, Trifolium pratense, T. repens*) (Baldock et al., 2019; Kanduth et al., 2021; Larson et al., 2014) were very low represented in the diet of the four studied bees. However, pollen from woody species (independently if native or non-native species) were broadly preferred. Indeed, other studies (e.g. Somme et al., 2016) also found urban trees being a valuable food resource for wild bees. Therefore, we claim that maintaining and promoting different plant growth and habitat types in cities is an effective way for wild bee conservation.

Even if generalist bee species have a wider distribution range in urban ecosystems, intermediate specialized species can also entail a successful strategy to thrive in cities. This is in line with our results for *O. cornuta* and *O. bicornis*. Their success in our studied cities is in part due to the species selection that municipalities apply in urban ecosystems. Specifically, the success of intermediate polylectic bee species may be fostered if the cultivated plant taxa match with their diet preferences. This is common in many European cities, where municipalities tend to facilitate plant families such as Rosaceae, Fagaceae, Salicaceae (Ossola et al., 2020) that, combined with the occurrence of spontaneous native and non-native species, provides a wide variety of floral resources. Highly specialized feeding strategies, as in *C. florisomne*, can also have success in urban areas if their nutritional requirements are met (e.g. if specific floral resources are broadly distributed in urban ecosystems). However, changes in park management practices or urban policies that consequently modify the vegetation composition of UGSs and the availability of floral resources, can make these oligolectic bee species more vulnerable.

6.4.2. Foraging strategies shaping wild bee species distribution

Our results demonstrate that highly specialized bee species are more susceptible to environmental changes than generalist species. Therefore, the feeding strategy defines the response to urbanization (e.g. bumblebees, in Goulson, 1999; wild bees, in Deguines et al., 2016). Other factors such as stress tolerance or dispersal ability (Harrison & Winfree, 2015) have an influence on the distribution patterns along the urban gradient. The degree of specialization will condition the probability of successfully occupying new areas. Some UGSs can host high bee species richness, including specialists (Baldock, 2020; Salisbury et al., 2015). In order to foster diversity of wild bee communities in UGSs, habitat provision and floral resources availability are key elements to be included in urban planning. Mapping existing habitats (see section 4.4.3.) and floral resources distribution through field surveys (Baldock et al., 2019; Casanelles-Abella et al., 2021) or by using inventories (Ossola et al., 2020) is a useful tool to achieve this. These maps can be used to better identify hot and coldspots of foraging and promote specific actions for urban biodiversity conservation. Promoting plant species richness with specific traits rather than the abundance of few species individuals has been successfully applied in semi-natural ecosystems (e.g. agroecosystems, Sutter et al., 2017).

6.5. Final remarks

A holistic overview of the outcomes from Papers II, III and IV, suggest that UGSs have a valuable ecological potential to provide ESs that is currently not fully exploited. Urban planners and park managers have therefore an opportunity (and responsibility) to enhance multifunctionality of UGSs and thus, increase the effectiveness of urban GI. There are several directions proposed in Paper I that need to be addressed in order to increase our knowledge on key questions of urban ecology and the provision of ESs from which urban planning may also benefit.

Vegetation is the key component of UGS as plants provide ESs directly (e.g., heat mitigation and improved air quality) and indirectly by supporting other organisms living in urban environment (e.g., bee species) and, consequently, the ESs they provide (e.g., pollination). Different degrees of diet specialization in bee species implies different capacities to vary their feeding habits according to the availability of food resources (Paper IV). Contrary to highly specialized bee species whose diet is based on native plants, more generalist species are able to use pollen from native and exotic species and from different growth forms (i.e., from the herbaceous or the woody layer). As found in Paper II, UGSs can harbor populations of these more generalist pollinator species due to the high proportions of exotic plant species in the overall species pool. Therefore, the unexploited ecological potential of UGSs (especially the larger ones) should be used to increase native plant diversity and therefore, support populations of sensitive pollinator species that display more restricted feeding preferences.

Environmental conditions are also an important limiting factor that influences the fitness of organisms in urban environment. As indicated by Paper III, common urban stressors (i.e., heat and air pollution) are still beyond acceptable levels. It is worth to mention that, although lichen communities in Paper III were sampled in the centroid of UGSs, which is considered the area with the least influence from the outside, they displayed high abundance of traits related to eutrophication tolerance (associated to N-based pollutants). Moreover, lichens were generally highly tolerant to solar radiation and aridity. The high tolerance to urban stressors of ecological indicator communities found in Paper III combined with the results of plant traits from Paper II suggests that increasing vegetated surfaces and promoting and preserving mature trees in UGSs may be a good strategy to mitigate heat stress (i.e., increased evapotranspiration, shadow and irradiation reflection) and reduce air pollution levels (i.e., deposition). UGSs in Tartu are a good example of this. We found there the highest percentage of canopy cover in UGSs (i.e., 74% on average), highest values of tree AGB (i.e., averaging ~150 tons per UGSs), largest trees (i.e., average DBH was 36cm) (Paper II) and lichen taxonomic and functional diversity (Paper III) was also higher compared to other cities (e.g., Poznan: 45% canopy cover, ~90 tons of AGB and 26 cm mean DBH). Land cover maps produced in Paper II showed that relative canopy cover is generally rather low in UGSs (e.g., 40% in Almada, 45% Poznan and 50% in Lisbon and Antwerp). Therefore, following our previous recommendation of increasing native plant taxonomic and functional richness (and, consequently, canopy cover and AGB) can be compatible with other land use types demanded in urban UGSs (e.g., sport facilities or open lawns for recreational use).

7. CONCLUSIONS

The present thesis is developed in the frame of the European project BioVeins (ERA-Net BiodivERsA, Grant Number: BiodivERsA32015104). One the one hand, it identifies the main gaps of knowledge in urban ecology, drawing potential research ways to effectively fulfill them. On the other hand, it explores taxonomic and functional diversity of several taxonomic groups (woody vegetation, lichens and insect pollinators and their diet) in urban green spaces differing in landscape configuration from seven European cities along a NE-SW gradient.

Under the predicted scenario of an increasingly urbanized world and the growing awareness of the imminent climate change effects, urban ecology offers an open door to explore and implement Nature-Based Solutions that contribute to creating more resilient cities for both nature and people. In this context, cities act as open labs providing the perfect scenario to study ecological features and their response to socio-economic drivers.

Based on the results obtained from the published and submitted papers (Paper I-IV in the main text), the following conclusions can be drawn:

1. Urban green spaces are multifunctional components of the urban Green Infrastructure and provide important social, environmental and economic benefits. Woody vegetation, as the main element of UGSs, provides not only key ESs for humans, but also habitat and food resources for other urban taxa. Urban planners and policy makers have the opportunity to increase biodiversity in large UGSs and therefore create more habitat heterogeneity and variety of food sources from which other organisms may benefit (e.g. oligolectic pollinators) as well as improve urban abiotic conditions (e.g., microclimate and air quality, measurable through lichen communities).

2. Lichen communities reflect that UGSs are currently not fully relieving local harsh environmental conditions (i.e., air pollution and heat stress). More effort is needed in the implementation of measures aimed at ameliorating urban stressors at the city level,

especially in the frame of growing urban population and climate change effects. UGSs have an unused potential to act as an oasis where environmental stressors are alleviated, with consequent benefits for urban nature and city dwellers. Lichens can be used as a cost-effective way to monitor the effectiveness of the adopted measures and strategies.

3. Feeding specialization strategies of urban bee species have an effect on distribution patterns. Bee species with different feeding specialization strategies can thrive in urban ecosystems, although more generalist feeding behavior entails a wider distribution and a more variable diet according to the floral resources availability. More specialized bees with narrower diets are more sensitive to urban intensity and floral resource turnover.

4. Trait-based approaches, including taxonomic and functional diversity, arose as an effective way to increase and improve our knowledge about the link of biodiversity with ecosystem functions and thus, ecosystem services. The outcomes of this thesis (Papers I-IV) contribute to create ecologically informed urban policies and planning strategies, which is necessary to increase resilience in cities and support ecosystem functions and services.

Urban biodiversity patterns respond to biotic (e.g., vegetation type) and abiotic factors (e.g., UGS size, air pollution concentration) in European cities. Although UGSs are generally rich in terms of species richness, several environmental and anthropogenic drivers may act as a filter for some species, thus favoring some species success (e.g., more generalist species) and limiting others (e.g. specialized or sensitive species). The mechanisms that underpin biodiversity patterns and their relationship with ecosystem functions and services are complex and still not totally understood.

Potential future outcomes of BioVeins project (see section 2.3), thus comprehensive multi-taxa and multi-city studies at the broad scale providing comparable data (i.e. using standardized sampling protocols) are needed to provide a comprehensive and holistic view of urban biodiversity patterns (both in terms of taxonomic and functional diversity) and the derived ESs. This is especially important given the high demand of different ESs in urban areas but also to mitigate the effects of the unprecedented threats that nature is facing (i.e. habitat fragmentation, invasive species, extreme events, etc.) and halt global biodiversity loss. Numerous ESs depend on the interactions among different taxonomic groups (De Bello et al., 2010; Cardinale et al., 2012). How these interactions influence ecosystem functioning and ESs is still poorly understood.

The multi-taxa nature of BioVeins (i.e., vegetation, pollinators, lichens, soil biota, leaf bacteria, bats and nocturnal insects) aimed at unraveling these interaction networks by exploring taxonomic and functional diversity as key elements of ecological processes that underpin the provision of ESs. For instance, pollination relies on interactions between the diversity of plants, pollinators and the organisms they interact with (e.g. predators; Kremen et al. 2007). Moreover, carbon and nitrogen cycling as well as several soil functions involve multiple interactions between plants, herbivores, carnivores and soil biota (Bardgett et al., 2003; Brussaard et al., 2007). Therefore, a combination of taxonomic and functional approaches involving multiple taxa, such as being developed in BioVeins, is a promising way to address B-EF/ESs relationships in urban ecosystems from a holistic perspective. Finally, scientifically informed policies are necessary to create urban planning strategies that effectively integrate socio-economic development with nature conservation in urban areas. In other words, science and practice need to come together in order to identify and use the potential of urban novel ecosystems to face the novel challenges.

REFERENCES

Alberti, M. (2015). Eco-evolutionary dynamics in an urbanizing planet. Trends in Ecology and Evolution 30, 114–126. http://dx.doi.org/10.1016/j.tree.2014.11.007.

Allouche, O., Tsoar, A., Kadmon, R. (2006). Assessing the accuracy of species distribution models: Prevalence, kappa and the true skill statistic (TSS). Journal of Applied Ecology 43, 1223–1232. https://doi.org/10.1111/j.1365-2664.2006.01214.x

Amann, M. (2012). Future emissions of air pollutants in Europe-Current legislation baseline and the scope for further reductions. Internation Institute for Applied Analysis (IIASA), Austria.

Anav, A., De Marco, A., Proietti, C., Alessandri, A., Dell'Aquila, A., Cionni, I., Friedlingstein, P., Khvorostyanov, D., Menut, L., Paoletti, E., Sicard, P., Sitch, S., Vitale, M. (2016). Comparing concentration-based (AOT40) and stomatal uptake (PODY) metrics for ozone risk assessment to European forests. Global Change Biology 22, 1608-1627.

Aptroot, A., Van Herk, C.M., (2007). Further evidence of the effects of global warming on lichens, particularly those with Trentepohlia phycobionts. Environmental Pollution 146, 293-298.

Aronson, M.F.J., Nilon, C.H., Lepczyk, C.A., Parker, T.S., Warren, P. S., Cilliers, S.S., et al. (2016). Hierarchical filters determine community assembly of urban species pools. Ecology 97, 2952–s063.

Asta, J., Erhardt, W., Ferretti, M., Fornasier, F., Kirschbaum, U., Nimis, P.L., Purvis, O.W., Pirintsos, S., Scheidegger, C., van Haluwyn, C., Wirth, V., 2002. Mapping lichen diversity as an indicator of environmental quality, in: Nimis, P., Scheidegger, C., Wolseley, P. (Eds.), Monitoring with Lichens- Monitoring Lichens. Kluwer Academic Publisher, The Netherlands, pp. 273-279.

Baldock, K.C.R. (2020). Opportunities and threats for pollinator conservation in global towns and cities. Current Opinion in Insect Science 38, 63–71. https://doi.org/10.1016/j.cois.2020.01.006

Baldock, K.C.R., Goddard, M.A., Hicks, D.M., Kunin, W.E., Mitschunas, N., Morse, H., Osgathorpe, L.M., Potts, S.G., Robertson, K.M., Scott, A.V., Staniczenko, P.P.A., Stone, G.N., Vaughan, I.P., Memmott, J.

(2019). A systems approach reveals urban pollinator hotspots and conservation opportunities. Nature Ecology and Evolution 3, 363–373. https://doi.org/10.1038/s4155 9-018-0769-y

Baraldi, R., Chieco, C., Facini, N.O., Rapparini, F., Morrone, L., Rotondi, A., Carierò, G. 2019. An integrated study on air mitigation potential of urban vegetation: From a multi-trait approach to modeling. Urban Forestry & Urban Greening 41, 127-138. https://doi.org/10.1016/j.ufug.2019.03.020.

Bardgett, R.D., Wardle, D.A. (2003). Herbivore-mediated linkages between aboveground and belowground communities. Ecology 84, 2258–2268.

Barwell, L.J., Isaac, N.J.B., Kunin, W.E. (2015). Measuring β-diversity with species abundance data. Journal of Animal Ecology 84, 1112-1122.

Basnou, C., Baro, F., Langemeyer, J., Castell, C., Dalmases, C., Pino, J. (2020). Advancing on green infrastructure approach: integrating biodiversity, ecosystem functions and services into landscape planning in the Province of Barcelona, Urban Forestry and Urban Greening 55, 126797. https://doi.org/10.1016/j.ufug.2020.126797

Bentz, S., 2020. The 2030 Agenda. Through the eyes of local and regional governments' associations 'Platforma' and the Council of European Municipalities and Regions (CEMR).https://platforma-dev.eu/wp-content/uploads/2020/07/CEMR-PLATFORMA-SDGs-2020.pdf

Bowler, D.E., Buyung, A.L., Knight, T.M., Pullin, A.S. (2010). Urban greening to cool towns and cities: a systematic review of the empirical evidence. Landscape Urban Planning 97, 147-155.

Braaker, S., Ghazoul, J., Obrist, M. K., Moretti, M. (2014). Habitat connectivity shapes urban arthropod communities: the key role of green roofs. Ecology 95, 1010-1021.

Branquinho, C., Matos, P., Pinho, P. (2015). Lichens as ecological indicators to track atmospheric changes: future challenges. Indicators and surrogates of biodiversity and environmental change. CSIRO Publishing, Melbourne, CRC Press, London, 77-87.

Brussaard, L., de Rutier, P.C., Brown, G.G. (2007). Soil biodiversity for agricultural sustainability. Agriculture Ecosystem & Environment 121, 233-244.

Calfapietra, C., Peñuelas, J., Niinemets, Ü. (2015). Urban plant physiology: adaptation-mitigation strategies under permanent stress. Trends in Plant Science 20, 72–75.

Capotorti, G., Alós Ortí, M.M. Cop, R., Fusaro, L., Mollo, B., Salvatori, E., Zavattero, L. 2019. Biodiversity and ecosystem services in urban green infrastructure planning: A case study from the metropolitan area of Rome (Italy). Urban Forestry & Urban Greening 37, 87-96 https://doi.org/10.1016/j.ufug.2017.12.014

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P. et al. (2012) Biodiversity loss and its impact on humanity. Nature 486, 59–67.

Casanelles-Abella, J., Frey, D., Müller, S., Aleixo, C., Alós Ortí, M., Deguines, N., Hallikma, T., Laanisto, L., Niinemets, Ü., Pinho, P., Samson, R., Villarroya-Villalba, L., & Moretti, M. (2021). A dataset of the flowering plants (*Angiospermae*) in urban green areas in five European cities. Data in Brief 37, 107243. https://doi.org/10.1016/j.dib.2021.107243

Casella, F., Burro, M. (2013). *Ailanthus altissima* (tree of heaven): Spread and harmfulness in a case-study urban area. Arboricultural Journal 35, 172-181. https://doi.org/10.1080/03071375.2013.852352

Chen, J., Jin, S., Du, P. (2020). Roles of horizontal and vertical tree canopy structure in mitigating daytime and nighttime urban heat island effects. International Journal of Applied Earth Observation and Geoinformation 89, 102060. https://doi.org/10.1016/j.jag.2020.102060

Chen, X., de Vries, S., Assmuth, T., Dick, J., Hermans, T., Hertel, O., Jensen, A., Jones, L., Kabisch, S., Lanki, T., Lehmann, I., Maskell, L., Norton, L., Reis, S. (2019). Research challenges for cultural ecosystem services and public health in (peri-)urban environments. Science of The Total Environment 651, 2118-2129.

Chmielewski, F-M., Rötzer, T. (2001). Response of tree phenology to climate change across Europe. Agricultural and Forest Meteorology 108, 101-112. https://doi.org/10.1016/S0168-1923(01)00233-7

Cohen, P., Potchter, O., Schnell, I. (2014). The impact of an urban park on air pollution and noise levels in the Mediterranean city of Tel-Aviv, Israel. Environmental Pollution 195, 73-83.

Collins, M.K., Magle, S.B., Gallo, T. (2021). Global trends in urban wildlife ecology and conservation. Biological Conservation 261, 109236. https://doi.org/10.1016/j.biocon.2021.109236

Concostrina-Zubiri, L., Pescador, D.S., Martínez, I., Escudero, A. (2014) Climate and small scale factors determine functional diversity shifts of biological soil crusts in Iberian drylands. Biodiversity and Conservation, 23, 1757-1770, doi:10.1007/s10531-014-0683-9.

Cornelis, J., Hermy, M. (2004). Biodiversity relationships in urban and suburban parks in Flanders. Landscape & Urban Planning 4, 385-401. https://doi.org/10.1016/j.landurbplan.2003.10.038

Cristofolini, F., Brunialti, G., Giordani, P., Nascimbene, J., Cristofori, A., Gottardini, E., Frati, L., Matos, P., Batic, F., Caporale, S., Fornasier, M.F., Marmor, L., Merinero, S., Zapata, J.N., Torra, T., Wolseley, P., Ferretti, M. (2014). Towards the adoption of an international standard for biomonitoring with lichens-Consistency of assessment performed by experts from six European countries. Ecological Indicators 45, 63-67.

Crosby, M.K., McConnell, T.E., Holderieath, J.J., Kjartasson, B.Þ, Traustason, B., Jónsson, Þ.H., ... Oddsdóttir, E.S. (2021). Urban street tree characteristics and benefits in city centre, Reykjavik, Iceland. Trees, Forest and People 4, 100066. https://doi.org/10.1016/j.tfp.2021.100066

da Silva, J.O., Kernaghan, S., Luque, A. (2012). A systems approach to meeting the challenges of urban climate change. International Journal of Urban Sustainable Development 4, 125-145

de Bello, F., Lavorel, S., Díaz, S., Harrington, R., Bardgett, R., Berg, M. et al. (2010) Functional traits underlie the delivery of ecosystem services across different trophic levels. Biodiversity and Conservation 143, 2873–2893.

de Bello, F., Lavorel, S., Díaz, S., Harrington, R., Cornelissen, J. H., Bardgett, R. D., et al. (2010). Towards an assessment of multiple ecosystem processes and services via functional traits. Biodivers. Conserv. 19, 2873–2893. https://link.springer.com/article/10.1007/s10531-010-9850-9

Davies, L., Bates, J.W., Bell, J.N.B., James, P.W., Purvis, O.W. (2007). Diversity and sensitivity of epiphytes to oxides of nitrogen in

London. Environmental Pollution 146, 299-310, doi:10.1016/j.envpol.2006.03.023.

Deguines, N., de Flores, M., Loïs, G., Julliard, R., Fontaine, C. (2018). Fostering close encounters of the entomological kind. Frontiers in Ecology and the Environment 16, 202–203.

Deguines, N., Julliard, R., de Flores, M., & Fontaine, C. (2016). Functional homogenization of flower visitor communities with urbanization. Ecology and Evolution 6, 1967–1976. https://doi.org/10.1002/ece3.2009

Deguines, N., Prince, K., Prevot, A.C., Fontaine, B. (2020). Assessing the emergence of pro-biodiversity practices in citizen scientists of a backyard butterfly survey. Science of The Total Environment 136842.

Delphin, S., Escobedo, F.J., Abd-Elrahman, A., Cropper, W.P. (2016). Urbanization as a land use change driver of forest ecosystem services. Land Use Policy 54, 188-199.

Derby Lewis, A., Bouman, M.J., Winter, A.M., Hasle, E.A., Stotz, D.F., Johnston, M.K., Klinger, K.R., Rosenthal, A., Czarnecki, C.A. (2019). Does Nature Need Cities? Pollinators Reveal a Role for Cities in Wildlife Conservation. Frontiers in Ecology and Evolution 7:220. doi: 10.3389/fevo.2019.00220

Dias, A.T.C., Berg, M.P., de Bello, F., Van Oosten, A.R., Bila, .K., Moretti, M. (2013). An experimental framework to identify community functional components driving ecosystem processes and services delivery. Journal of Ecology 101, 29–37.

Díaz, S., Lavorel, S., Chapin, F.S., Tecco, P.A., Gurvich, D.E., Grigulis, K. (2007). Terrestrial Ecosystem in a Changing World, (Eds.) Canadell, J., Pataki, D.E., Pitelka, L.F. Springer, Berlin. pp 79-91.

Di Nuzzo, L., Vallese, C., Benesperi, R., Giordani, P., Chiarucci, A., Di Cecco, V., Di Martino, L., Di Musciano, M., Gheza, G., Lelli, C., et al. (2021). Contrasting multitaxon responses to climate change in Mediterranean mountains. Scientific Reports 11, doi:10.1038/s41598-021-83866-x.

EC, European Commission. 2013. Green Infrastructure (GI) — Enhancing Europe‘s Natural Capital. Communication from the Commission to the European Parliament, The Council, The European Economic and Social Committee and The Committee of the Regions, Brussels Com (2013) 249 final.

EC, European Commission. 2020. Directorate-General for Research and Innovation. Naumann, S., Calfapietra, C., Bulkeley, H., et al., Nature-based solutions : state of the art in EU-funded projects, Freitas, T. (editor), Vandewoestijne, S.(editor), Wild, T.(editor), Publications Office, 2020, https://data.europa.eu/doi/10.2777/236007

EC, European Commission. 2020. EU Biodiversity Strategy for 2030: Bringing nature back into our lives. Communication from the Commission to the European Parliament, The Council, The European Economic and Social Committee and The Committee of the Regions, Brussels COM(2020) 380 final. https://eur-lex.europa.eu/resource.html?uri=cellar:a3c806a6-9ab3-11ea-9d2d-01aa75ed71a1.0001.02/DOC_1&format=PDF

EEA, European Environmental Agency. Urban Atlas (2012). Available online: https://land.copernicus.eu/local/urban- atlas/urban-atlas-2012?tab=download

Eurostat. (2020). Urban Audit. Retrieved from: https://ec.europa.eu/eurostat/web/gisco/geodata/reference-data/administrative-units-statistical-units/urban-audit

Eggenberger, H., Frey, D., Pellissier, L., Ghazoul, J., Fontana, S., Moretti, M. (2019). Urban bumblebees are smaller and more phenotypically diverse than their rural counterparts. Journal of Animal Ecology 88, 1522–1533. https://doi.org/10.1111/1365-2656.13051

Eigenbrod, F., Bell, V.A., Davies, H.N., Heinemeyer, A., Armsworth, P.R., Gaston, K.J. (2011). The impact of projected increases in urbanization on ecosystem services. Proceedings of the Royal Society B: Biological Sciences 278, 3201-3208.

Elmqvist T., Andersson E., Frantzeskaki N., et al. (2019). Sustainability and resilience for transformation in the urban century. Nature Sustainability 2, 267-273.

[dataset]Euro+Med: Euro+Med PlantBase - the information resource for Euro-Mediterranean plant diversity. (2006-). Published on the Internet http://ww2.bgbm.org/EuroPlusMed/ [accessed February, 3-5 2021].

Faegri, K., van der Pijl, L. (1979). Structural Blossom Classes, Principles of Pollination Ecology, 88–95 .

Faeth, S.H., Saari, S., Bang, C. (2012). Urban Biodiversity: Patterns, Processes and Implications for Conservation. In: eLS. John Wiley & Sons, Ltd: Chichester. DOI: 10.1002/9780470015902.a0023572

Fagerli, H., Tsyro, S., Jonson, J.E., Nyíri, Á., Gauss, M., Simpson, D., Wind, P., Benetictow, A., Klein, H., Mortier, A., et al. (2019). Transboundary particulate matter, photo-oxidants, acidifying and eutrophying components. 15046109 (ISSN). Meteorologisk institutt Norwegian Meteorological Institute, EMEP Status Report 2019.

Foley, J.A., De Fries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N., Snyder, P.K. (2005). Global consequences of land use. Science 309, 570-574.

Fong KC, Hart JE, James P. (2018). A review of epidemiologic studies on greenness and health: updated literature through 2017. Current Environmental Health Reports 5, 77-87.

Forrester, D.I., Tachauer, I.H.H., Annigohoefer, P., Barbeito, I., Pretzsch, H., Ruiz-Peinado, R., Stark, H., Vacchiano, G., Zlatanov, T., Chakraborty, T., Saha, S., & Sileshi, G.W. (2017). Generalized biomass and leaf area allometric equations for European tree species incorporating stand structure, tree age and climate. Forest Ecology and Management, 369, 160-175. http://dx.doi.org/10.1016/j.foreco.2017.04.011

Fournier, B., Frey, D., Moretti, M. (2020). The origin of urban communities: From the regional species pool to community assemblages in city. Journal of Biogeography 47, 615–629. https://doi.org/10.1111/jbi.13772

Funk, J.L., Cleland, E.E., Suding, K.N., Zavaleta, E.S. (2008). Restoration through reassembly: plant traits and invasion resistance. Trends in Ecology and Evolution 23, 695–703. https://doi.org/10.1016/j.tree.2008.07.013

Funk, J.L., Larson, J.E., Ames, G.M., Butterfield, B.J., Cavender-Bares, J., Firn, J., Laughlin, D.C., Sutton-Grier, A.E., Williams, L., Wright, J. (2017). Revisiting the Holy Grail: using plant functional traits to understand ecological processes. Biological reviews of the Cambridge Philosophical Society 92, 1156–1173.

Gascon, M., Triguero-Mas, M., Martínez, D., Dadvand, P., Rojas-Rueda, D., Plasència, A., Nieuwenhuijsen, M.J. (2016). Residential green spaces and mortality: a systematic review. Environment International 86, 60-67.

Gaston, K. (Ed.). (2010). Urban Ecology. Cambridge: Cambridge University Press. doi: 10.1017/CBO9780511778483

Gillner, S., Vogt, J., Tharang, A., Dettmann, S., Roloff, A. (2015). Role of street trees in mitigating effects of heat and drought at highly sealed urban sites. Landscape and Urban Planning 143, 33-42.

Giordani, P., Malaspina, P. (2017). Do tree-related factors mediate the response of lichen functional groups to eutrophication? Plant Biosystems-An International Journal Dealing with all Aspects of Plant Biology 151, 1062-1072.

Goulson, D. (1999). Foraging strategies of insects for gathering nectar and pollen, and implications for plant ecology and evolution. Perspectives in Plant Ecology, Evolution and Systematics 2, 185–209. https://doi.org/10.1078/1433-8319-00070

Grimm, N.B., Faeth, S.H., Golubiewski, N.E., Redman, C.L., Wu, J.G., Bai, X.M., Briggs, J.M. (2008). Global change and the ecology of cities. Science 319, 756-760.

Gustafson, E.J., Parker, G.R. (1992). Relationship between landcover proportion and indices of landscape spatial pattern. Landscape Ecology 7, 101-110

Haider, M., Dorn, S., Sedivy, C., Müller, A. (2014). Phylogeny and floral hosts of a predominantly pollen generalist group of mason bees (*Megachilidae: Osmiini*). Biological Journal of the Linnean Society 111, 78–91. https://doi.org/10.1111/bij.12186

Hand, K.L., Freeman, C., Seddon, P.J., Recio, M.R., Stein, A., van Heezik, Y. (2017). The importance of urban gardens in sup- porting children's biophilia. Proceedings of the National Acad- emy of Sciences of the United States of America 114, 274–279.

Harrell, F.E. (2020). Hmisc: Harrell Miscellaneous. R package version 4.4-1. https://CRAN.R-project.org/package=Hmisc

Hartig, T., Mitchell, R., de Vries, S., Frumkin, H. (2014). Nature and health. Annual Review of Public Health 35, 207-228.

Hector, A., Bagchi, R. (2007) Biodiversity and ecosystem multifunctionality. Nature 448, 188–190. https://doi.org/10.1038/nature05947

Higgs, E.S. (2017). Novel and designed ecosystems. Restoration Ecology 25, 8–13.

Hobbs, R.J., Arico, S., Aronson, J. et al. (2006). Novel ecosystems: theoretical and management aspects of the new ecological world order. Global Ecology and Biogeography 15, 1–7.

Hofman, J., Bartholomeus, H., Janssen, S., Calders, K., Wuyts, K., Van Wittenberghe, S., Samson, R. (2016). Influence of tree crown characteristics on the local PM10 distribution inside an urban street canyon in Antwerp (Belgium): A model and experimental approach. Urban Forestry & Urban Greening 20, 265-276.

Hurtado, P., Matos, P., Aragón, G., Branquinho, C., Prieto, M., Martínez, I. (2020). How much matching there is in functional, phylogenetic and taxonomic optima of epiphytic macrolichen communities along a European climatic gradient? Science of The Total Environment 712, 136533, doi:https://doi.org/10.1016/j.scitotenv.2020.136533.

Hurtado, P., Prieto, M., De Bello, F., Aragón, G., López-Angulo, J., Giordani, P., Díaz-Peña, E.M., Vicente, R., Merinero, S., Košuthová, A. et al. (2020). Contrasting Environmental Drivers Determine Biodiversity Patterns in Epiphytic Lichen Communities along a European Gradient. Microorganisms 8, 1913, doi:10.3390/microorganisms8121913.

IPBES. (2019): Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. E. S. Brondizio, J. Settele, S. Díaz, and H. T. Ngo (editors). IPBES secretariat, Bonn, Germany. 1148 pages. https://doi.org/10.5281/zenodo.3831673

Isbell, F., Calcagno, V., Hector, A., Connolly, J., Harpole, W. S., Reich, P. B., et al. (2011). High plant diversity is needed to maintain ecosystem services. Nature 477, 199–202.

James, P., Banay, R.F., Hart, J.E., Laden, F. (2015). A review of the health benefits of greenness. Current Epidemiology Reports 2, 131-142.

Jeanjean, A., Monks, P., Leigh, R. (2016). Modelling the effectiveness of urban trees and grass on PM2.5 reduction via dispersion and deposition at a city scale. Atmospheric Environment, 147, 1-10.

Jin, Y., Qian, H. (2019). V.PhyloMaker: an R package that can generate very large phylogenies for vascular plants. Ecography 42, 1353–1359. doi: 10.1111/ecog.04434

Kabisch, N. (2015). Ecosystem service implementation and governance challenges in urban green space planning: The case of Berlin, Germany. Land Use Policy 42, 557–567.

Kanduth, L., Chartier, M., Schönenberger, J., Dellinger, A.S. (2021). Red and white clover provide food resources for honeybees and wild bees in urban environments. Nordic Journal of Botany 39, 1–11. https://doi.org/10.1111/njb.03005

Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Zimmermann, N.E., Linder, H.P., Kessler, M. (2017). Climatologies at high resolution for the earth's land surface areas. Scientific Data 4, 170122, doi:10.1038/sdata.2017.122.

Karger D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Zimmermann, N.E., Linder, H.P., Kessler, M. (2018). Data from: Climatologies at high resolution for the earth's land surface areas. Dryad Digital Repository.

Kassambara, A., Mundt, F. (2020). Factoextra: Extract and Visualize the Results of Multivariate Data Analyses. R package version 1.0.7. https://CRAN.R-project.org/package=factoextra

Kaye, J.P., Groffman, P.M., Grimm,. NB., Baker, L.A., Pouyat, R.V. (2006). A distinct urban biogeochemistry? Trends in Ecology & Evolution 21, 192-199.

Klingberg, J., Broberg, M., Strandberg, B., Thorsson, P., Pleijel, H. (2017). Influence of urban vegetation on air pollution and noise exposure - a case study in Gothenburg, Sweden. Science of the Total Environment 599–600, 1728-1739.

Koch, N.M., Matos, P., Branquinho, C., Pinho, P., Lucheta, F., Martins, S.M.d.A., Vargas, V.M.F., (2019). Selecting lichen functional traits as ecological indicators of the effects of urban environment. Science of The Total Environment 654, 705-713. https://doi.org/10.1016/j.scitotenv.2018.11.107

Kondratyeva, A., Knapp, S., Durka, W., Kühn, I., Vallet, J., Machon, N., Martin, G., Motard, E., Grandcolas, P. Pavoine, S. (2020). Urbanization Effectson Biodiversity Revealed by aTwo-Scale

Analysis of SpeciesFunctional Uniqueness vs. Redundancy. Frontiers in Ecology and Evolution 8:73.

Kowarik, I. (2011). Novel urban ecosystems, biodiversity, and conservation. Environmental Pollution 159, 1974–1983.

Kremen, C., Williams, N.E., Aizen, M.A., Gemmill-Herren, B., LeBuhn, G., Minckley, R. et al. (2007). Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. Ecology Letters 10, 299–314

Kurucz, K., Purger, J.J., Batáry, P. (2021). Urbanization shapes bird communities and nest survival, but not their food quantity. Global Ecology and Conservation 26, e01475.

Kühn, I., Klotz, S. (2006). Urbanization and homogenization – Comparing the floras of urban and rural areas in Germany. Biological Conservation 127, 292–300. https://doi.org/10.1016/j.biocon.2005.06.033

Laliberté, E., Legendre, P., Shipley, B. (2014). FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-12.

LaPoint, S., Balkenhol, N., Hale, J., Sadler, J., van der Ree, R. (2015). Ecological connectivity research in urban areas. Functional Ecology 29, 868-878.

Larsen, R.S., Bell, J.N.B., James, P.W., Chimonides, P.J., Rumsey, F.J., Tremper, A., Purvis, O.W., (2007). Lichen and bryophyte distribution on oak in London in relation to air pollution and bark acidity. Environmental Pollution 146, 332-340.

Larson, J.L., Kesheimer, A.J., Potter, D.A. (2014). Pollinator assemblages on dandelions and white clover in urban and suburban lawns. Journal of Insect Conservation 18, 863–873. https://doi. org/10.1007/s10841-014-9694-9

Laughlin, D.C. (2014). Applying trait-based models to achieve functional targets for theory-driven ecological restoration. Ecology Letters 17, 771–784.

Lauwaet, D., De Ridder, K., Saeed, S., Brisson, E., Chatterjee, F., Van Lipzig, N.P.M., ... & Hooyberghs, H. (2016). Assessing the current and future urban heat island of Brussels. Urban Climate 15, 1-15

Lawler, J.J., Lewis, D.J., Nelson, E., Plantinga, A.J., Polasky, S., Withey, J.C., Helmers, D.P., Martinuzzi, S., Pennington, D., Radeloff, V.C. (2014). Projected land-use change impacts on ecosystem services in the United States. Proceedings of the National Academy of Sciences of the United States of America 111, 7492-7497.

Leclère, D., Obersteiner, M., Barrett, M. et al. (2020). Bending the curve of terrestrial biodiversity needs an integrated strategy. Nature 585, 551–556

Lee, A.C., Maheswaran, R. (2011). The health benefits of urban green spaces: a review of the evidence. Journal of Public Health 33, 212-222.

Liaw, A., Wiener, M. (2002). Classification and Regression by randomForest. R News 2, 18-22. https://www.stat.berkeley.edu/~breiman/RandomForests/

Llop, E., Pinho, P., Matos, P., Pereira, M.J., Branquinho, C., 2012. The use of lichen functional groups as indicators of air quality in a Mediterranean urban environment. Ecological indicators 13, 215-221.

Llop, E., Pinho, P., Ribeiro, M.C., Pereira, M.J., Branquinho, C. (2017). Traffic represents the main source of pollution in small Mediterranean urban areas as seen by lichen functional groups. Environmental Science and Pollution Research 24, 12016-12025, doi:10.1007/s11356-017-8598-0.

Luederitz, C., Brink, E., Gralla, F., Hermelingmeier, V., Meyer, M., Niven, L., et al. (2015). A review of urban ecosystem services, six key challenges for future research. Ecosystem Services 14, 98–112.

Lundholm, J., MacIvor, J.S., MacDougall, Z., Ranalli, M. (2010). Plant species and functional group combinations affect green roof ecosystem functions. PLoS One 5. http://dx.doi.org/10.1371/journal.pone.0009677.

Magle, S.B., Hunt, V.M., Vernon, M., Crooks, K.R. (2012). Urban wildlife research: Past, present, and future. Biological Conservation 155, 23–32. doi:10.1016/j.biocon.2012.06.018

Manes, F., Incerti, G., Salvatori, E., Vitale, M., Ricotta, C., Costanza, R. (2012). Urban ecosystem services: tree diversity and stability of tropospheric ozone removal. Ecological Applications 22, 349-360.

Martin, G., Devictor, V., Motard, E., Machon, N., Porcher, E. (2019). Short-term climate-induced change in French plant communities. Biology Letters 15, 20190280.

Mason, N.W.H., de Bello, F., Doležal, J., Lepš, J. (2011). Niche overlap reveals the effects of competition, disturbance and contrasting assembly processes in experimental grassland communities. Journal of Ecology 99, 788–796.

Matos, P., Pinho, P., Aragon, G., Martínez, I., Nunes, A., Soares, A.M., Branquinho, C., (2015). Lichen traits responding to aridity. Journal of Ecology 103, 451-458.

Matos, P., Vieira, J., Rocha, B., Branquinho, C., Pinho, P. (2019). Modeling the provision of air-quality regulation ecosystem service provided by urban green spaces using lichens as ecological indicators. Science of the Total Environment 705-713, doi:https://doi.org/10.1016/j.scitotenv.2019.02.023.

McCarthy, M.P., Best, M.J., Betts, R.A. (2010). Climate change in cities due to global warming and urban effects. Geophysical research letters 37(9).

McGarigal, K., Cushman, S.A., Ene, E. (2012). FRAGSTATS v4: spatial pattern analysis program for categorical and continuous maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. Retrieved from http://www.umass.edu/landeco/research/fragstats/fragstats.html

McKinney, M.L. (2008). Effects of urbanization on species richness: A review of plants and animals. Urban Ecosystems 11, 161-176.

McPhearson, T., Hamstead, Z.A., Kremer, P. (2014). Urban ecosystem services for resilience planning and management in New York City. Ambio 43, 502–515.

Mexia, T., Vieira, J., Principe, A., Anjos, A., Silva, P., Lopes, N., et al. (2018). Ecosystem services, Urban parks under a magnifying glass. Environmental Research 160, 469–478.

MEA, Millennium Ecosystem Assessment. 2005. Ecosystems and Human Well-being: Desertification Synthesis. A Report of the Millennium Ecosystem Assessment World Resources Institute, Washington, DC.

Morgenroth, J., Östberg, J., Konijnendijk van den Bosch, C., Nielsen, A.B., Hauer, R., Sjöman, H., Chen, W., Jansson, M. (2016). Urban tree diversity—Taking stock and looking ahead. Urban Forestry & Urban Greening, 15, 1–5. https://doi.org/10.1016/j.ufug.2015.11.003

Moudrý, V., Moudrá, L., Barták, V., Bejček, V., Gdulová, K., Hendrychová, M., ... Šálek, M. (2021). The role of the vegetation structure, primary productivity and senescence derived from airborne LiDAR and hyperspectral data for birds diversity and rarity on a restored site. Landscape and Urban Planning, 210, 104064. https://doi.org/10.1016/j.landurbplan.2021.104064

Mouratidis, K. (2019). The impact of urban tree cover on perceived safety. Urban Forestry & Urban Greening 44, 126434. doi:126434. 10.1016/j.ufug.2019.126434

Munzi, S., Correia, O., Silva, P., Lopes, N., Freitas, C., Branquinho, C., Pinho, P. (2014). Lichens as ecological indicators in urban areas: beyond the effects of pollutants. Journal of Applied Ecology 51, 1750-1757.

Munzi, S., Ravera, S., Caneva, G. (2007). Epiphytic lichens as indicators of environmental quality in Rome. Environmental Pollution 146, 350-358.

Nilon, C.H., Aronson, M.F.J., Cilliers, S.S., Dobbs, C., Frazee, L.J., Goddard M.A., O'Neill K.M., Roberts, D., Stander, E.K., Werner, P., Winter, M., Yocom, K.P. (2017). Planning for the Future of Urban Biodiversity: A Global Review of City-Scale Initiatives, BioScience 67, 332–342, https://doi.org/10.1093/biosci/bix012

Nimis, P.L., Martellos, S., (2021). ITALIC - The Information System on Italian Lichens. Version 5.0. University of Trieste, Dept. of Biology, (http://dryades.units.it/italic).

Nitoslawski, S.A., Galle, N.J., Van Den Bosch, C.K., Steenberg, J.W.N. (2019). Smarter ecosystems for smarter cities? A review of trends, technologies, and turning points for smart urban forestry. Sustainable Cities and Society 51, 101770.

Nuissl, H., Siedentop, S. (2021) Urbanisation and Land Use Change. In: Weith T., Barkmann T., Gaasch N., Rogga S., Strauß C., Zscheischler J. (eds) Sustainable Land Management in a European Context. Human-Environment Interactions, vol 8. Springer, Cham. https://doi.org/10.1007/978-3-030-50841-8_5

Ogle, D.H., Wheeler, P., Dinno, A. (2021). FSA: Fisheries Stock Analysis. R package version 0.8.32. https://github.com/droglenc/FSA.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'hara, R., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H. (2011). Vegan: Community ecology package. R package version 2011, 117-118.

Ortiz, A.G., Guerreiro, C., Soares, J. (2020). Air quality in Europe — 2020 report; European Environment Agency, p. 164.

Ossola, A., Hoeppner, M.J., Burley, H.M., Gallagher, R. V., Beaumont, L.J., Leishman, M.R. (2020). The global urban tree inventory: A database of the diverse tree flora that inhabits the world's cities. Global Ecology and Biogeography 29, 1907–1914. https://doi.org/10.1111/geb.13169

Pataki, D.E., Carreiro, M.M., Cherrier, J., Grulke, N.E., Jennings, V., Pincetl, S., Pouyat, R.V., Whitlow, T.H., Zipperer, W.C. (2011). Coupling biogeochemical cycles in urban environments: ecosystem services, green solutions, and misconceptions. Frontiers in Ecology and the Environment 9, 27-36.

Pataki, D.E., McCarthy, H.R., Litvak, E., Pincetl, S. (2011). Transpiration of urban forests in the Los Angeles metropolitan area. Ecological Applications 21, 661–677. https://doi.org/10.1890/09-1717.1

Pauleit, S., Jones, N., García-Martín, G., García-Valdecantos, J.L., Marie Rivière, L., Vidal-Beaudet, ... Randurp, T.B. (2002). Tree establishment practice in towns and cities – Results from a European survey. Urban Forestry & Urban Greening 1, 83-96. https://doi.org/10.1078/1618-8667-00009

Paź-Dyderska, S., Ladach-Zajdler, A., Jagodziński, A.M., Dyderski, M.K. (2020). Landscape and parental tree availability drive spread of Ailanthus altissima in the urban ecosystem of Poznań, Poland. Urban Forestry & Urban Greening 56, 126868. https://doi.org/10.1016/j.ufug.2020.126868

Pickett, S.T.A., Cadenasso, M.L., Grove, J.M., Nilon, C.H., Pouyat, R.V.,. Zipperer, W.C, Costanza, R. (2001). Urban Ecological Systems: Linking Terrestrial Ecological, Physical, and Socioeconomic Components of Metropolitan Area. Annual Review of Ecology and Systematics 32, 127-157, doi: 10.1146/annurev.ecolsys.32.081501.114012

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. (2021). nlme: Linear and Nonlinear Mixed Effects Models_. R package version 3.1-152. https://CRAN.R-project.org/package=nlme>.

Pinho, P., Casanelles-Abella, J., Luz, A. C., Kubicka, A. M., Branquinho, C., Laanisto, L., Neuenkamp, L., Alós Ortí, M., Obrist, M. K., Deguines, N., Tryjanowski, P., Samson, R., Niinemets, L., Moretti, M. (2021). Research agenda on biodiversity and ecosystem functions and services in European cities. Basic and Applied Ecology 53, 124–133.

Pinho, P., Correia, O., Lecoq, M., Munzi, S., Vasconcelos, S., Gonçalves, P., ... Branquinho, C. (2016). Evaluating green infrastructure in urban environments using a multi-taxa and functional diversity approach. Environmental Research 147, 601-610.

Pinho, P., Dias, T., Cruz, C., Sim Tang, Y., Sutton, M.A., Martins-Loução, M.A., Máguas, C., Branquinho, C. (2011). Using lichen functional diversity to assess the effects of atmospheric ammonia in Mediterranean woodlands. Journal of Applied Ecology 48, 1107-1116.

Potgieter, L.J., Gaertner, M., O'Farrell, P.J., Richardson, D.M. (2019). Perceptions of impact: Invasive alien plants in the urban environment. Journal of Environmental Management 229, 76–87.

Prendergast, K.S., Tomlinson, S., Dixon, K.W., Bateman, P.W., Menz, M.H.M., (2022). Urban native vegetation remnants support more diverse native bee communities than residential gardens in Australia's southwest biodiversity hotspot. Biological Conservation 265, 109408. DOI 10.1016/j.biocon.2021.109408.

Pretzsch, H., Biber, P., Uhl, E., Dahlhausen, J., Schütze, G., Perkins, D., ... Lefer, B. (2017). Climate change accelerates growth of urban trees in metropolises worldwide. Scientific Reports 7, 15403. https://doi.org/10.1038/s41598-017-14831-w

Proietti, C., Anav, A., De Marco, A., Sicard, P., Vitale, M. (2016). A multi-sites analysis on the ozone effects on Gross Primary Production of European forests. Science of the Total Environment 556, 1-11.

Puchałka, R., Dyderski, M.K., Vítková, M., Sádlo, J., Klisz, M., Netsvetov, M., Prokopuk, Y., Matisons, R., Mionskowski, M., Wojda, T., Koprowski, M., Jagodziński, A.M. (2021), Black locust (*Robinia pseudoacacia* L.) range contraction and expansion in Europe under changing climate. Global Change Biology 27, 1587-1600. https://doi.org/10.1111/gcb.15486

Pyšek, P. (1998). Alien and native species in central European urban floras: a quantitative comparison. Journal of Biogeography 25, 155–163. https://doi.org/10.1046/j.1365-2699.1998.251177.x

R Core Team. (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Retrieved from https://www.R-project.org/

R Core Team. (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Retrieved from https://www.R-project.org/

R Core Team. (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Radchuk, V., Reed, T., Teplitsky, C. et al. (2019). Adaptive responses of animals to climate change are most likely insufficient. Nature Communications 10, 3109. https://doi.org/10.1038/s41467-019-10924-4

Rahman, M.A., Moser, A., Rötzer, T., & Pauleit, S. (2019). Comparing the transpirational and shading effects of two contrasting urban tree species. Urban Ecosystems 22, 683-697. https://doi.org/10.1007/s11252-019-00853-x

Remme, R. P., Frumkin, H., Guerry, A.D., King, A. C., Mandle, L., Sarabu, C., ... Daily, G.C. (2021). An ecosystem service perspective on urban nature, physical activity, and health. Proceedings of the National Academy of Sciences 118(22).

Rocha, B., Pinho, P., Vieira, J., Branquinho, C., Matos, P., (2019). Testing the Poleotolerance Lichen Response Trait as an Indicator of Anthropic Disturbance in an Urban Environment. Diversity 11, 55.

Sack, C. (2013). Landscape architecture and novel ecosystems: ecological restoration in an expanded field. Ecological Process 2, 35. https://doi.org/10.1186/2192-1709-2-35

Salinitro, M., Alessandrini, A., Zappi, A., Melucci, D., & Tassoni, A. (2018). Floristic diversity in different urban ecological niches of a southern European city. Scientific Reports 8, 15110. https://doi.org/10.1038/s41598-018-33346-6

Salisbury, A., Armitage, J., Bostock, H., Perry, J., Tatchell, M., Thompson, K. (2015). Enhancing gardens as habitats for flower- visiting aerial insects (pollinators): Should we plant native or exotic species? Journal of Applied Ecology 52, 1156–1164. https://doi. org/10.1111/1365-2664.12499

Santini, L., González-Suárez, M., Russo, D., Gonzalez-Voyer, A., von Hardenberg, A., Ancillotto, L. (2019). One strategy does not fit all: determinants of urban adaptation in mammals. Ecology Letters 22, 365-376.

Savage, A.M., Hackett, B., Guénard, B., Youngsteadt, E.K., Dunn, R.R. (2015). Fine-scale heterogeneity across Manhattan's urban habitat mosaic is associated with variation in ant composition and richness. Insect Conservation and Diversity 8, 216-228.

Säumel, I., Kowarik, I. & Butenschön, S. (2010). Green traces from past to future: the interplay of culture and ecological processes in European historical parks. Acta Horticulturae 881, 933-938. https://doi.org/10.17660/ActaHortic.2010.881.156

Scholz, M., Uzomah, V.C., Al-Faraj, F.A.M. (2016). Potential tree species for use in urban areas in temperate and oceanic climates. Heliyon, 2, e00154. https://doi.org/10.1016/j.heliyon.2016.e00154

Schwarz, N., Moretti, M., Bugalho, M. N., Davies, Z. G., Haase, D., Hack, J., et al. (2017). Understanding biodiversity- ecosystem service relationships in urban areas, a comprehensive literature review. Ecosystem Services 27, 161–171.

Serret, H., Deguines, N., Jang, Y., Lois, G., Julliard, R. (2019). Data quality and participant engagement in citizen science, comparing two approaches for monitoring pollinators in France and South Korea. Citizen Science, Theory and Practice 4, 22.

Seto, K., Güneralp, B., Hutyra, L. (2012). Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. Proceedings of the National Academy of Sciences of the United States of America 109, 16083-16088.

Shaffer, H.B. (2018). Urban biodiversity arks. Nature Sustainability 1, 725–727. doi:10.1038/s41893-018-0193-y

Shanahan, D.F., Bush, R., Lin, B.B., Gaston, J.K., Barber, L., Dean, J., Fuller, R.A. (2015). Towards improved public health outcomes from urban nature. American Journal of Public Health 105, 470-477.

Shaw, B.J., van Vliet, J., Verburg, P.H. (2020). The peri-urbanization of Europe: A systematic review of a multifaceted process. Landscape and Urban Planning 196, 103733.

Sicard, P.,Agathokleous, E., De Marco, A., Paoletti, E., Calatayud, V. (2021). Urban population exposure to air pollution in Europe over the last decades. Environmental Sciences Europe 33. doi:10.1186/ s12302-020-00450-2.

Silvertown, J. (2009). A new dawn for citizen science. Trends in Ecology and Evolution 24, 467–471.

Siragusa, A., Vizcaino, M.P., Proietti, P. and Lavalle, C. (2020) European Handbook for SDG Voluntary Local Reviews, EUR 30067 EN, Publications Office of the European Union, Luxembourg, 2020, ISBN 978-92-76-15403-7, doi:10.2760/670387, JRC118682.

Smith, I.A., Dearborn, V.K., Hutyra, L.R. (2019). Live fast, die young: Accelerated growth, mortality, and turnover in street trees. PLoS ONE 14, e0215846. https://doi.org/10.1371/journal.pone.0215846

Somme, L., Moquet, L., Quinet, M., Vanderplanck, M., Michez, D., Lognay, G., Jacquemart, A. L. (2016). Food in a row: Urban trees offer valuable floral resources to pollinating insects. Urban Ecosystems, 19(3), 1149–1161. https://doi.org/10.1007/s11252-016-0555-z

Spasojevic, M.J., Catano, C.P., LaManna, J.A., Myers, J.A. (2018). Integrating species traits into species pools. Ecology 99, 1265-1276.

Stevens, C.J., Bell, J.N.B., Brimblecombe, P., Clark, C.M., Dise, N.B., Fowler, D., Lovett, G.M., Wolseley, P.A. (2020). The impact of air pollution on terrestrial managed and natural vegetation. Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences 378, 20190317, doi:10.1098/rsta.2019.0317.

Sutter, L., Jeanneret, P., Bartual, A. M., Bocci, G., Albrecht, M. (2017). Enhancing plant diversity in agricultural landscapes promotes both rare bees and dominant crop-pollinating bees through complementary increase in key floral resources. Journal of Applied Ecology 54, 1856–1864. https://doi.org/10.1111/1365-2664.12907

Swan, C.M., Pickett, S.T.A., Szlavecz, K., Waren, P., Willey, T. (2011). “Chapter 3.5: Urban ecology: patterns, processes, and applications,” in Biodiversity and Community Composition in Urban Ecosystems: Coupled Human, Spatial, and Metacommunity Processes, ed J.

Niemela (Oxford: Oxford University Press), 179–186. doi: 10.1093/acprof:oso/9780199563562.003.0021

Tabacchi, G., Di Cosmo, L., Gasparini, L., Morelli, S. (2011). Stima del volume e della fitomassa delle principali specie forestali italiane. Equazioni di previsione, tavole del volume e tavole della fitomassa arborea epigea (Estimation of the volume and phytomass of main Italian forest species. Equations and tables of volume and epigeal phytomass of trees). Consiglio per la Ricerca e la sperimentazione in Agricoltura, Unità di Ricerca per il Monitoraggio e la Pianificazione Forestale, 412 pp.

Teixeira, C.P., Fernandes, C.O. (2020). Novel ecosystems: a review of the concept in non-urban and urban contexts. Landscape Ecology 35, 23-39.

Tiwary, A., Williams, I.D., Heidrich, O., Namdeo, A., Bandaru, V., Calfapietra, C. (2016). Development of multi-functional streetscape green infrastructure using a performance index approach. Environmental Pollution 208, part A, 209-220. doi:10.1016/j.envpol.2015.09.003

Tran, T.J., Helmus, M.R., Behm, J.E. (2020). Green Infrastructure Space and Traits (GIST) Model: Integrating green infrastructure spatial placement and plant traits to maximize multifunctionality. Urban Forestry & Urban Greening 49, 126635. doi: https://doi.org/10.1016/j.ufug.2020.126635

Tremblay, M.A. St Clair, C.C. (2009) Factors affecting the permeability of transportation and riparian corridors to the movements of songbirds in an urban landscape. Journal of Applied Ecology 46, 1314–1322.

Tresch S., Frey D., Le Bayon R.C., Mader P., Stehle B., Fliessbach A., et al. (2019). Direct and indirect effects of urban gardening on aboveground and belowground diversity influencing soil multifunctionality. Scientific Reports 9, 9769

Tsay, J.S., Ko, P.H., Chang, P.T. (2015). Carbon storage potential of avenue trees: a comparison of Barringtonia racemosa, Cyclobalanopsis glauca, and Alnus formosana. Journal of Forest Research 26, 307-314.

Tutin, T.G., Heywood, V.H., Burges, N.A., Moore, D.M., Valentine, D.H., Walters, S.M. & Webb, D.A. (1964–1980). Flora Europaea. Cambridge University Press. 5 vols., 1. (1964), XXXII + 464 pp.,

2. (1968), XXVII + 455 pp., 3. (1972), XXIX + 370 pp., 4. (1976), XXIX + 505 pp. and 5. (1980), XXXVI + 452 pp.

Twohig-Bennett, C., Jones, A. (2018). The health benefits of the great outdoors: a systematic review and meta-analysis of greenspace exposure and health outcomes. Environmental Research 166, 628-637.

Uchida, K., Blakey, R. V., Burger, J. R., Cooper, D. S., Niesner, C. A., Blumstein, D. T. (2021). Urban biodiversity and the importance of scale. Trends in Ecology & Evolution 36, 123–131.

United Nations (UN). 2015. Transforming Our World: The 2030 Agenda for Sustainable Development. A/RES/70/1.

United Nations (UN). 2019. World Urbanization Prospects 2018: Highlights (ST/ESA/SER.A/421). Available online: https://population.un.org/wup/Publications/Files/WUP2018-Report.pdf

University of California - Santa Barbara. (2014, February 12). Cities support more native biodiversity than previously thought. ScienceDaily. Retrieved March 8, 2022 from www.sciencedaily.com/releases/2014/02/140212132950.htm

Van Cauwenberg, J., De Bourdeaudhuij, I., De Meester, F., Van Dyck, D., Salmon, J., Clarys, P., Deforche, B. (2011). Relationship between the physical environment and physical activity in older adults: a systematic review. Health Place 17, 458-469.

Van den Bosch, M., Sang, Å.O. (2017). Urban natural environments as nature-based solutions for improved public health–a systematic review of reviews. Environmental Research 158, 373-384.

Varela, Z.; López-Sánchez, G.; Yáñez, M.; Pérez, C.; Fernández, J.A.; Matos, P.; Branquinho, C.; Aboal, J.R. (2018). Changes in epiphytic lichen diversity are associated with air particulate matter levels: The case study of urban areas in Chile. Ecological Indicators 91, 307-314, doi:10.1016/j.ecolind.2018.04.023.

Vaudo, A. D., Tooker, J. F., Patch, H. M., Biddinger, D. J., Coccia, M., Crone, M. K., Fiely, M., Francis, J. S., Hines, H. M., Hodges, M., Jackson, S. W., Michez, D., Mu, J., Russo, L., Safari, M., Treanore, E. D., Vanderplanck, M., Yip, E., Leonard, A. S., Grozinger, C. M. (2020). Pollen protein: Lipid macronutrient ratios may guide broad patterns of bee species floral preferences. Insects 11, 132. https://doi.org/10.3390/insects11020132

Vergnes, A., Kerbiriou, C., Clergeau, P. (2013). Ecological corridors also operate in an urban matrix: a test case with garden shrews. Urban Ecosystems 16, 511-525.

Wei, T., Simko, V. (2017). R package "corrplot": Visualization of a Correlation Matrix (Version 0.84). Available from https://github.com/taiyun/corrplot

Wickham, H. (2016). ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag.

Wilkaniec, A., Borowiak-Sobkowiak, B., Irzykowska, L., Breś, W., Świerk, D., Pardela, Ł., ...Wielgus, K. (2021). Biotic and abiotic factors causing the collapse of *Robinia pseudoacacia* L. veteran trees in urban environments. PLoS ONE 16, e0245398.

Winfree, R., Reilly, J. R., Bartomeus, I., Cariveau, D. P., Williams, N. M., Gibbs, J. (2018). Species turnover promotes the importance of bee diversity for crop pollination at regional scales. Science 359, 791–793.

Wood, S.N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. In Journal of the Royal Statistical Society (B) 73, 3–36). https://cran.r-project.org/web/packages/mgcv/index.html

Wood, T. J., Ghisbain, G., Rasmont, P., Kleijn, D., Raemakers, I., Praz, C., Killewald, M., Gibbs, J., Bobiwash, K., Boustani, M., Martinet, B., Michez, D. (2021). Global patterns in bumble bee pollen collection show phylogenetic conservation of diet. Journal of Animal Ecology, 310(1365–2656), 13553. https://doi. org/10.1111/1365-2656.13553

Xie, W., Huang, Q., He, C., Zhao, X. (2018). Projecting the impacts of urban expansion on simultaneous losses of ecosystem services: A case study in Beijing, China. Ecological Indicators 84, 183-193.

Yow, D.M. (2007). Urban heat islands: Observations, impacts, and adaptation. Geography Compass 1, 1227-1251.

Zardo, L., Geneletti, D., Pérez-Soba, M., Van Eupen, M. (2017). Estimating the cooling capacity of green infrastructures to support urban planning. Ecosystem Services 26, 225-235. https://doi.org/10.1016/j.ecoser.2017.06.016

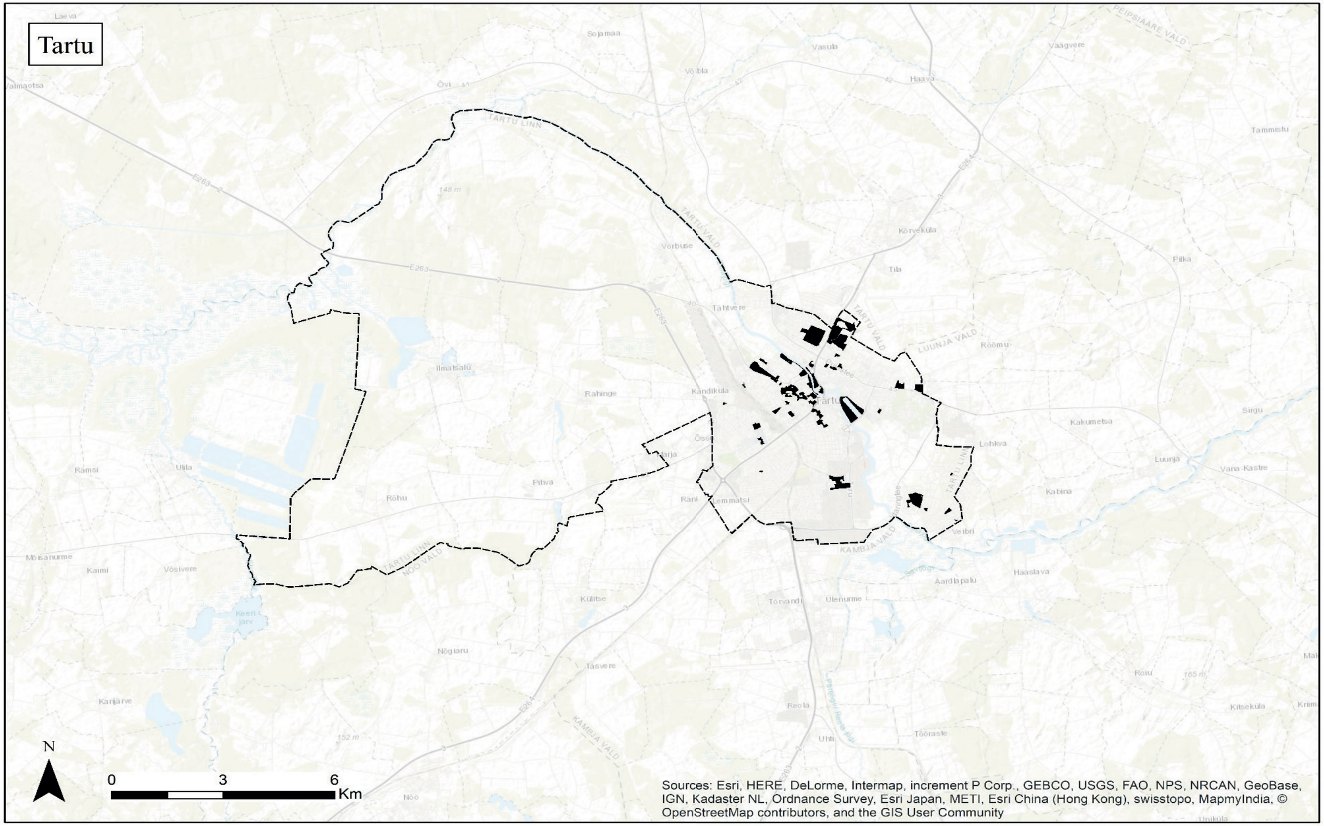
Zhang, C.L., Chen, F., Miao,. SG., Li, Q.C., Xia, X.A., Xuan, C.Y. (2009). Impacts of urban expansion and future green planting on summer precipitation in the Beijing metropolitan area. Journal of Geophysical Research 114, D02116.

Zianis, D., Muukkonen, P., Mäkipää, R., Mencuccini, M. (2005). Biomass and stem volume equations for tree species in Europe. Silva Fennica Monographs 4, Finnish Society of Forest Science/ Finnish Forest Research Institute, 63 pp.

Ziter, C., Pedersen, E., Kucharik, C., Turner, M. (2019). Scale-dependent interactions between tree canopy cover and impervious surfaces reduce daytime urban heat during summer. Proceedings of the National Academy of Sciences 116, 7575-7580, 10.1073/pnas.1817561116

Zobel, M., Davison, J., Edwards, M.E. et al. (2018). Ancient environmental DNA reveals shifts in dominant mutualisms during the late Quaternary. Nature Communications 9, 139.

APPENDIX



Sources: Esri, HERE, DeLorme, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, MapmyIndia, © OpenStreetMap contributors, and the GIS User Community

Figure A1. Distribution of the selected UGSs in Tartu (Estonia). Black polygons represent the different UGSs. Dotted line defines the city boundaries (Eurostat, 2020).

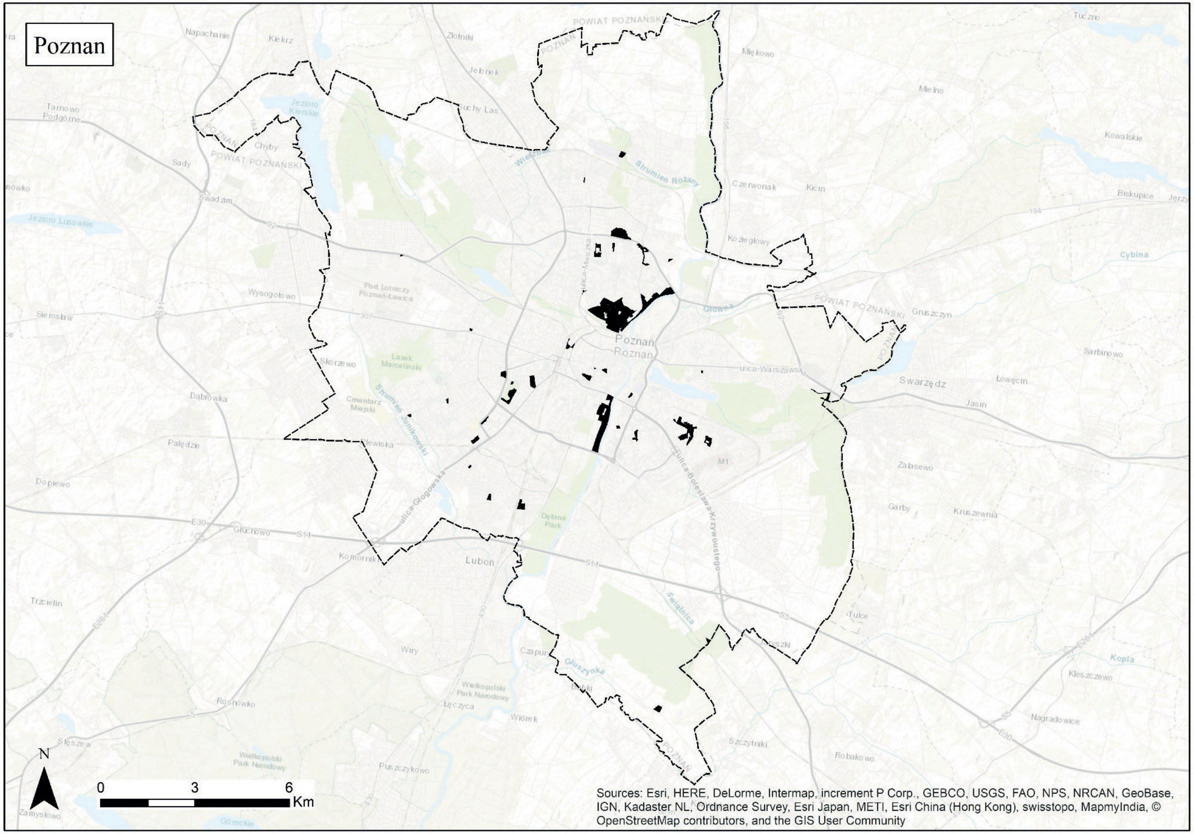


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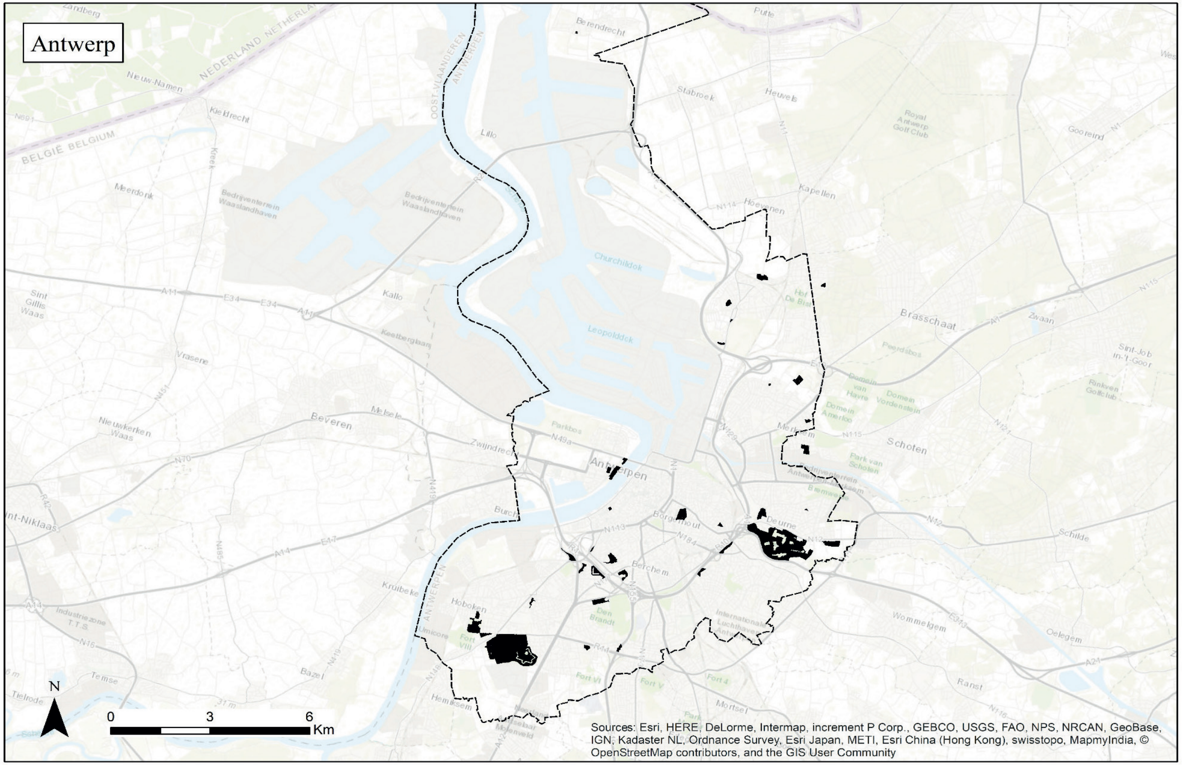
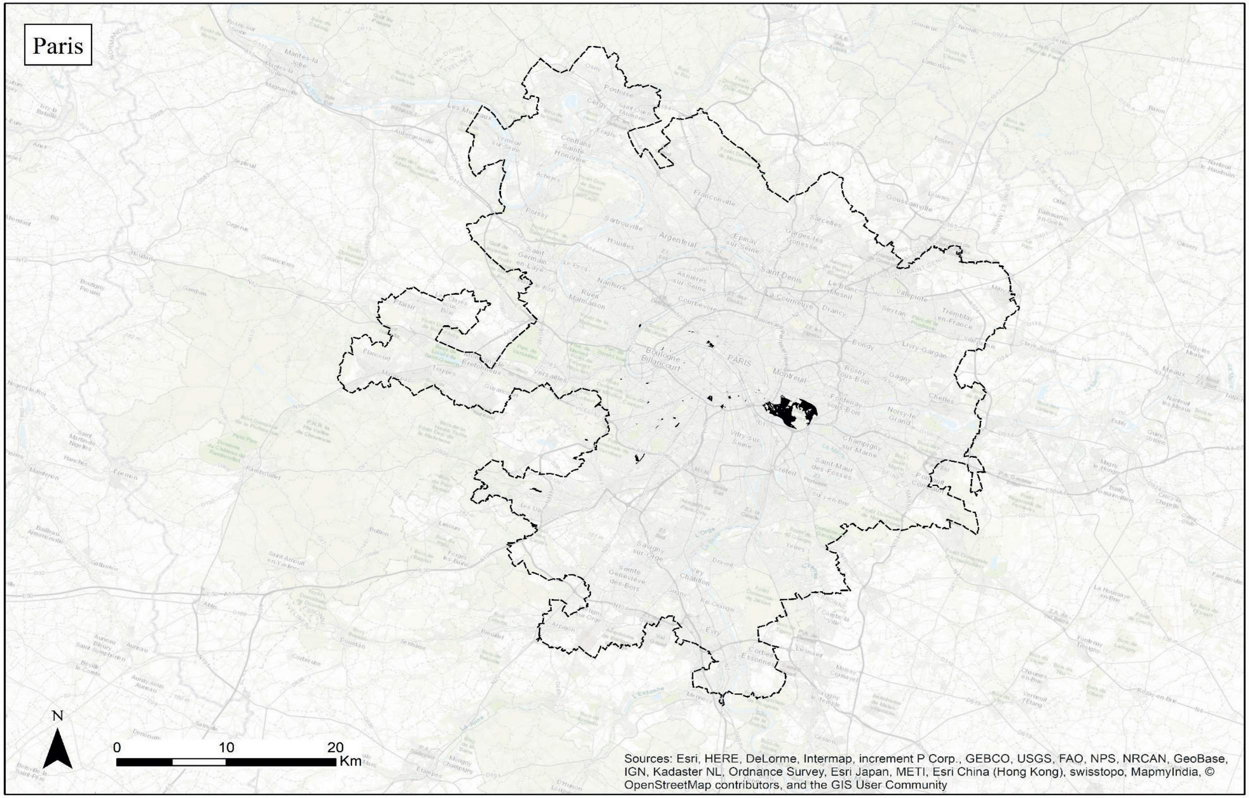
Figure A2. Distribution of the selected UGSs in Poznan (Poland). Black polygons represent the different UGSs. Dotted line defines the city boundaries (Eurostat, 2020).



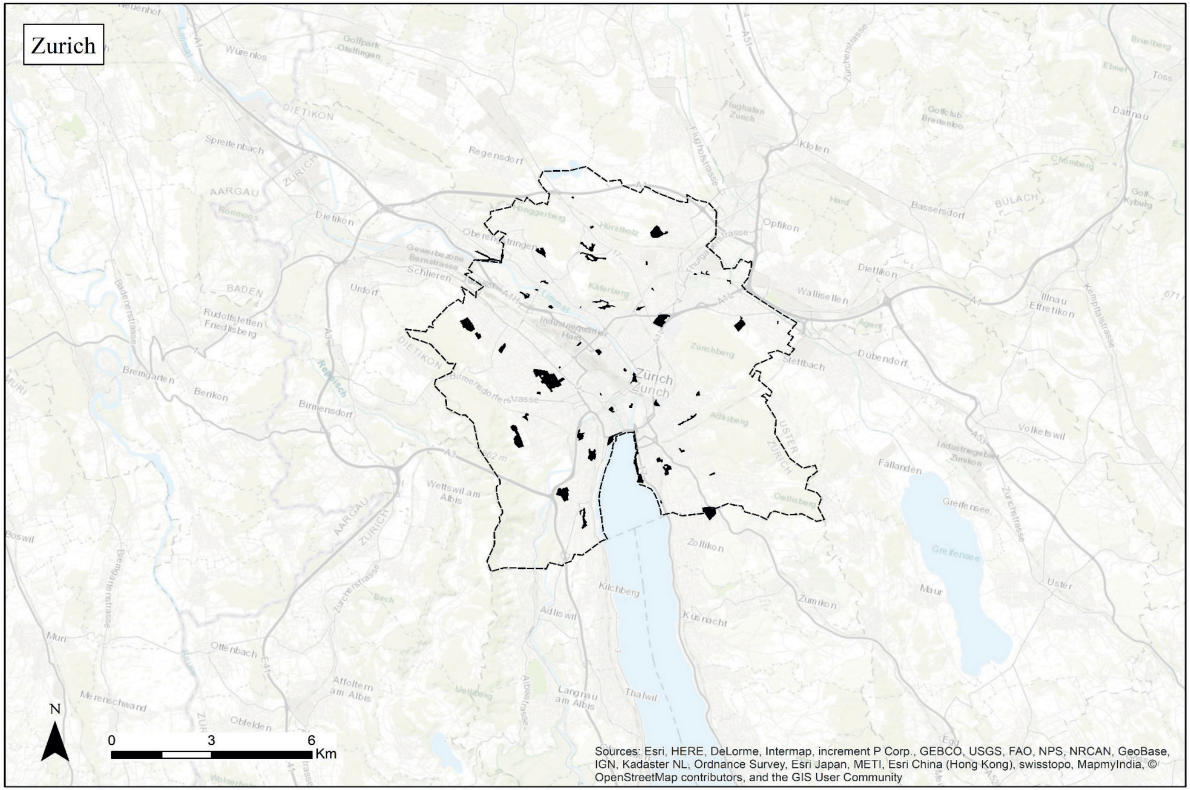
Sources: Esri, HERE, DeLorme, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, MapmyIndia, © OpenStreetMap contributors, and the GIS User Community

Figure A3. Distribution of the selected UGSs in Antwerp (Belgium). Black polygons represent the different UGSs. Dotted line defines the city boundaries (Eurostat, 2020).



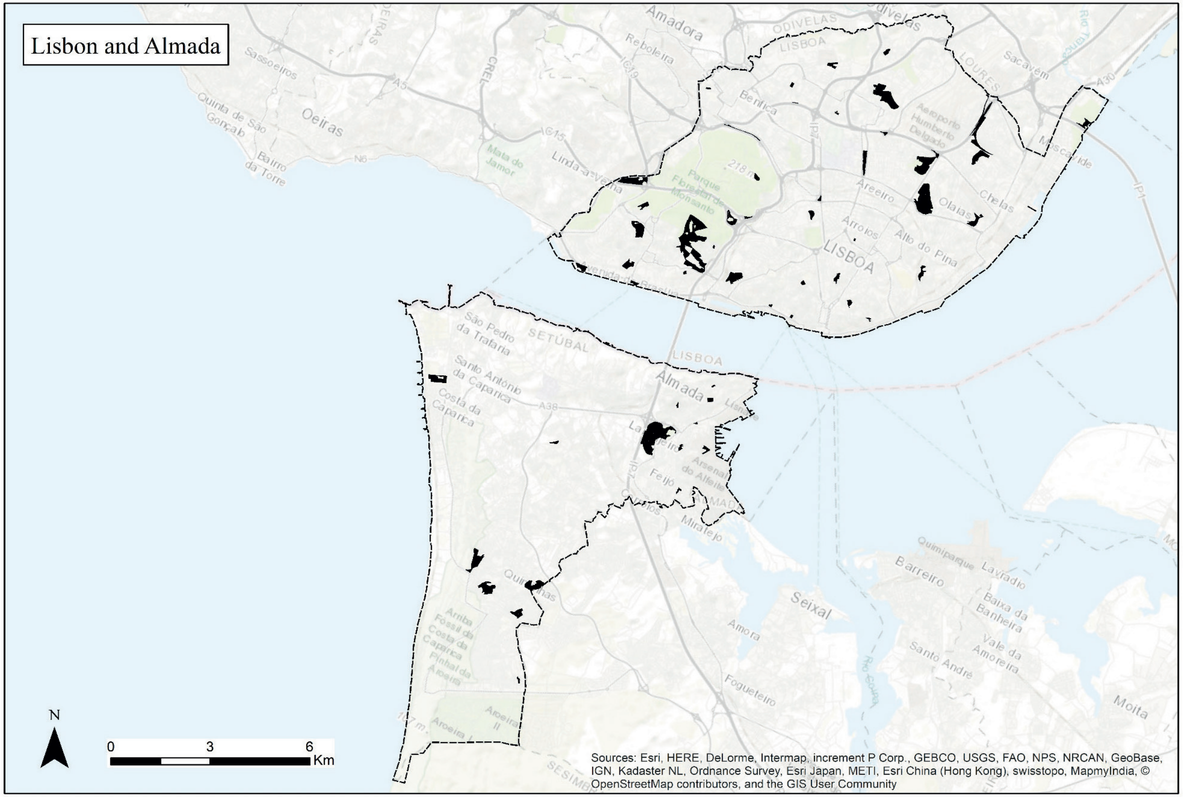
Sources: Esri, HERE, DeLorme, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, MapmyIndia, © OpenStreetMap contributors, and the GIS User Community

Figure A4. Distribution of the selected UGSs in Paris (France). Black polygons represent the different UGSs. Dotted line defines the Greater City of Paris boundaries (Eurostat, 2020).



Sources: Esri, HERE, DeLorme, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, MapmyIndia, © OpenStreetMap contributors, and the GIS User Community

Figure A5. Distribution of the selected UGSs in Zurich (Switzerland). Black polygons represent the different UGSs. Dotted line defines the city boundaries (Eurostat, 2020).



Sources: Esri, HERE, DeLorme, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, MapmyIndia, © OpenStreetMap contributors, and the GIS User Community

Figure A6. Distribution of the selected UGSs in Lisbon and Almada (Portugal). Black polygons represent the different UGSs. Dotted line defines the city boundaries (Eurostat, 2020).

Table A1. Plant and flower traits surveyed for bee species distribution modeling.

Trait	Description	Level
Growth form	*A trait related to the accessibility of the flowers considering the height where flowers occur*	Four broad categories were defined: tree, shrub, herb and climber. ● Trees included woody species typically classified as phanerophytes, including species described as small trees or tall shrubs. ● Shrubs included mostly chamerophytes. ● Herbs included all herbaceous plants regardless of their height or growth form. ● Climbers included woody and non-woody epiphytes such as lianas and vines.
Blossom class	*A trait related to accessibility of the flowers considering their morphology*	Six general blossom classes were defined according to the accessibility of the floral rewards (Faegri & van der Pijl, 1979): ● Dish-bowl ● Stalk-dish ● Bell-trumpet: for blossoms with deep corollas ● Brush: for blossom classes where the pollen exchange is generally external, such as catkins. ● Gullet ● Flag: For Papilionaceae species

Table A2. UGSs list and their associated landscape and vegetation features. UGS size from Urban Atlas (Copernicus, 2012), AGB from allometric models (Zianis et al., 2005; Tabacchi et al., 2011; Forrester et al., 2017) and land cover maps, woody species richness and density from vegetation survey and tree canopy cover in absolute and relative terms from land cover maps.

City	UGS code	Size (m2)	AGB (Kg)	Woody species richness (n)	Woody species density (n/ha)	Tree canopy cover (m2)	Tree canopy cover (%)
Almada	Al103	6494	8671	11	16.9	2494	38
Almada	Al115	19796	n.a.	7	3.5	3677	19
Almada	Al123	2965	472	8	27	3124	100
Almada	Al27	11071	106149	5	4.5	6710	61
Almada	Al39	51070	101747	13	2.5	11040	22
Almada	Al42	104557	492381	12	1.1	35608	34
Almada	Al46	95672	206333	12	1.3	57104	60
Almada	Al51	117097	110882	4	0.3	52438	45
Almada	Al62	8634	12587	9	10.4	2553	30
Almada	Al72	11060	45460	7	6.3	6490	59
Almada	Al83	11855	n.a.	4	3.4	2024	17
Almada	Al92	17946	5152	14	7.8	2055	11
Almada	Al94	82759	358164	9	1.1	16993	21
Almada	Al97	435559	264265	18	0.4	134013	31
Almada	Al98	4130	14324	10	24.2	2175	53
Antwerp	An100	22865	190668	12	5.2	12966	57
Antwerp	An102	52059	n.a.	14	2.7	7656	15
Antwerp	An103	13654	12001	9	6.6	6090	45
Antwerp	An11	1085854	n.a.	16	0.1	634943	58
Antwerp	An110	3849	12537	8	20.8	876	23
Antwerp	An12	20358	227276	5	2.5	12462	61
Antwerp	An15	128829	177136	9	0.7	110270	86
Antwerp	An16	12426	79306	12	9.7	13076	100
Antwerp	An17	27188	n.a.	8	2.9	18569	68
Antwerp	An20	20169	16205	9	4.5	14790	73
Antwerp	An26	58462	196210	8	1.4	50134	86
Antwerp	An33	63131	229128	18	2.9	19325	31
Antwerp	An34	25570	67086	9	3.5	9351	37
Antwerp	An35	48317	n.a.	10	2.1	39881	83
Antwerp	An38	40359	137402	7	1.7	28747	71
Antwerp	An42	69797	175975	9	1.3	58467	84
Antwerp	An43	26056	30250	6	2.3	12788	49
Antwerp	An45	7830	n.a.	1	1.3	60	1
Antwerp	An55	31154	141216	10	3.2	19519	63
Antwerp	An56	1054885	254953	10	0.1	747044	68
Antwerp	An57	6704	n.a.	5	7.5	3410	51
Antwerp	An62	11116	4529	5	4.5	4648	42

Antwerp	An65	82778	300748	10	1.2	19502	24
Antwerp	An68	93542	140374	8	0.9	34574	37
Antwerp	An69	67250	n.a.	10	1.5	10920	16
Antwerp	An71	5793	2966	3	5.2	573	10
Antwerp	An72	22520	64639	8	3.6	8670	38
Antwerp	An73	56928	n.a.	11	1.9	16425	29
Antwerp	An77	19127	137355	9	4.7	6992	37
Antwerp	An82	60943	230043	16	2.6	44196	73
Antwerp	An88	14401	202835	10	6.9	14287	99
Antwerp	An9	27703	196524	8	2.9	29080	100
Antwerp	An90	4025	4008	4	9.9	298	7
Antwerp	An92	56166	124426	12	2.1	8727	16
Antwerp	An94	15011	31867	10	6.7	4443	30
Antwerp	An97	4340	n.a.	2	4.6	1294	30
Lisbon	Lx132	21245	11269	4	1.9	2827	13
Lisbon	Lx134	6736	14074	8	11.9	2170	32
Lisbon	Lx135	51096	n.a.	3	0.6	11396	22
Lisbon	Lx138	5922	15895	7	11.8	6050	100
Lisbon	Lx143	8437	17213	6	7.1	5258	62
Lisbon	Lx148	6853	55518	6	8.8	5943	87
Lisbon	Lx149	600319	483441	14	0.2	240738	40
Lisbon	Lx154	22134	6103	8	3.6	4571	21
Lisbon	Lx156	102711	499791	19	1.8	75229	73
Lisbon	Lx164	13663	15056	11	8.1	9956	73
Lisbon	Lx178	5374	n.a.	6	11.2	2099	39
Lisbon	Lx179	30044	74815	9	3	13751	46
Lisbon	Lx186	121626	252035	10	0.8	21103	17
Lisbon	Lx199	27754	115398	8	2.9	19819	71
Lisbon	Lx201	40544	62160	16	3.9	25362	63
Lisbon	Lx211	3324	10620	6	18.1	2717	82
Lisbon	Lx217	136681	644774	9	0.7	95763	70
Lisbon	Lx228	11160	39637	6	5.4	5663	51
Lisbon	Lx233	18783	148125	6	3.2	19368	100
Lisbon	Lx237	60340	222394	11	1.8	26180	43
Lisbon	Lx240	308457	n.a.	4	0.1	52762	17
Lisbon	Lx241	10221	15127	6	5.9	3573	35
Lisbon	Lx246	61788	216124	8	1.3	40948	66
Lisbon	Lx252	193354	939276	8	0.4	121738	63
Lisbon	Lx264	10938	282	9	8.2	475	4
Lisbon	Lx267	6855	n.a.	5	7.3	3924	57
Lisbon	Lx270	266884	242911	11	0.4	135963	51
Lisbon	Lx273	5644	26734	3	5.3	914	16
Lisbon	Lx274	7658	23709	8	10.4	3181	42

Lisbon	Lx278	11688	85178	3	2.6	5540	47
Lisbon	Lx286	229523	2099495	10	0.4	166691	73
Lisbon	Lx290	31868	59243	10	3.1	12833	40
Lisbon	Lx293	46810	18894	14	3	9698	21
Lisbon	Lx299	20249	113754	8	4	10523	52
Paris	Pa13	126628	278083	29	2.3	123042	97
Paris	Pa154	6393	13944	22	34.4	2610	41
Paris	Pa160	13495	82931	17	12.6	12550	93
Paris	Pa172	4438	n.a.	17	38.3	1966	44
Paris	Pa174	3249	3043	28	86.2	2191	67
Paris	Pa176	47691	81342	28	5.9	39651	83
Paris	Pa179	17037	149752	17	10	14928	88
Paris	Pa191	24993	n.a.	14	5.6	19711	79
Paris	Pa216	15125	n.a.	27	17.9	12042	80
Paris	Pa230	8533	n.a.	12	14.1	3479	41
Paris	Pa238	5988	n.a.	15	25.1	3282	55
Paris	Pa245	5933064	9419081	58	0.1	4999176	84
Paris	Pa246	2973	n.a.	13	43.7	1816	61
Paris	Pa247	55143	114092	71	12.9	37237	68
Paris	Pa262	8984	n.a.	16	17.8	8032	89
Paris	Pa265	3553	4723	28	78.8	1444	41
Paris	Pa269	159611	n.a.	101	6.3	100750	63
Paris	Pa270	17531	169040	19	10.8	13056	74
Paris	Pa282	9890	n.a.	27	27.3	2647	27
Paris	Pa286	42949	n.a.	67	15.6	23882	56
Paris	Pa295	8339	14521	31	37.2	6787	81
Paris	Pa303	2626	n.a.	13	49.5	1478	56
Paris	Pa310	3233	n.a.	20	61.9	1543	48
Paris	Pa332	3292	n.a.	19	57.7	1781	54
Paris	Pa358	3351	21101	3	9	3467	100
Paris	Pa398	169327	n.a.	21	1.2	113411	67
Paris	Pa418	4630	n.a.	8	17.3	3391	73
Paris	Pa471	4142	n.a.	16	38.6	2912	70
Paris	Pa492	n.a.	29762	18	n.a.	11516	n.a.
Paris	Pa535	164101	166650	50	3	84753	52
Paris	Pa550	37949	226149	27	7.1	35173	93
Paris	Pa565	29210	n.a.	26	8.9	11149	38
Paris	Pa573	4607	12349	19	41.2	3372	73
Paris	Pa75	231303	468125	40	19.5	137263	59
Paris	Pa87	41969	n.a.	20	4.8	30551	73
Paris	Pa89	31382	58057	23	7.3	25334	81
Poznan	Po117	13574	42819	5	3.7	8978	66
Poznan	Po126	6082	14692	8	13.2	2260	37

Poznan	Po135	29400	57335	8	2.7	8970	31
Poznan	Po136	11309	7163	7	6.2	1418	13
Poznan	Po137	187103	n.a.	6	0.3	n.a.	n.a.
Poznan	Po138	194281	718288	7	0.4	58198	30
Poznan	Po141	391094	421475	6	0.2	102924	26
Poznan	Po145	43107	27471	6	1.4	8416	20
Poznan	Po156	83090	307225	4	0.5	32800	39
Poznan	Po167	8569	15615	3	3.5	1585	18
Poznan	Po178	30473	10763	5	1.6	29876	98
Poznan	Po179	56886	408149	9	1.6	36417	64
Poznan	Po183	10423	n.a.	10	9.6	n.a.	n.a.
Poznan	Po196	35939	40990	7	1.9	19391	54
Poznan	Po2	11983	31422	4	3.3	2484	21
Poznan	Po210	13222	n.a.	5	3.8	n.a.	n.a.
Poznan	Po227	8406	20747	5	5.9	4087	49
Poznan	Po232	4600	n.a.	11	23.9	n.a.	n.a.
Poznan	Po235	31345	267237	4	1.3	14251	45
Poznan	Po239	38721	196283	9	2.3	26337	68
Poznan	Po267	1059825	10900523	8	0.1	674103	64
Poznan	Po299	3423	n.a.	8	23.4	n.a.	n.a.
Poznan	Po301	6154	1294	4	6.5	503	8
Poznan	Po332	62262	109805	5	0.8	29330	47
Poznan	Po334	57356	59851	7	1.2	9412	16
Poznan	Po340	6943	397	7	10.1	3112	45
Poznan	Po348	18721	n.a.	5	2.7	7186	38
Poznan	Po35	18891	19200	5	2.6	4526	24
Poznan	Po37	48772	2049519	5	1	42755	88
Poznan	Po371	137914	762508	8	0.6	132734	96
Poznan	Po406	5624	36006	9	16	2745	49
Poznan	Po423	27974	24417	5	1.8	6072	22
Poznan	Po59	8200	6967	4	4.9	1646	20
Poznan	Po89	31263	545330	4	1.3	28143	90
Poznan	Po99	8658	89582	7	8.1	5480	63
Tartu	Ta10	133206	n.a.	14	1.1	107896	81
Tartu	Ta102	13236	289580	8	6	14477	100
Tartu	Ta104	37412	382155	27	7.2	18481	49
Tartu	Ta107	51184	n.a.	14	2.7	28595	56
Tartu	Ta108	7942	106994	5	6.3	10654	100
Tartu	Ta109	13409	105284	18	13.4	12634	94
Tartu	Ta11	3584	13881	13	36.3	2935	82
Tartu	Ta110	8623	4410	10	11.6	5653	66
Tartu	Ta112	8108	44271	7	8.6	6975	86
Tartu	Ta122	8629	179219	12	13.9	9055	100

Tartu	Ta124	309385	445078	29	0.9	112529	36
Tartu	Ta125	245706	4130241	4	0.2	233273	95
Tartu	Ta13	122857	n.a.	17	1.4	83409	68
Tartu	Ta21	15904	259930	15	9.4	14623	92
Tartu	Ta22	3435	n.a.	9	26.2	2034	59
Tartu	Ta25	33237	219118	17	5.1	25715	77
Tartu	Ta33	6225	56153	9	14.5	3270	53
Tartu	Ta36	17567	25744	7	4	12553	71
Tartu	Ta39	17304	19101	13	7.5	13215	76
Tartu	Ta40	36590	140882	28	7.7	27024	74
Tartu	Ta42	6283	n.a.	9	14.3	8176	100
Tartu	Ta45	20877	n.a.	18	8.6	7260	35
Tartu	Ta47	131100	1313364	20	1.5	128613	98
Tartu	Ta5	3079	15580	8	26.0	1003	33
Tartu	Ta57	5066	n.a.	13	25.7	4001	79
Tartu	Ta58	27560	n.a.	10	3.6	15628	57
Tartu	Ta64	183227	445130	18	1	45943	25
Tartu	Ta68	120132	n.a.	48	4	69185	58
Tartu	Ta73	3697	31681	17	46	2918	79
Tartu	Ta75	17614	n.a.	15	8.5	10205	58
Tartu	Ta77	124983	650330	22	1.8	102810	82
Tartu	Ta8	6338	19227	14	22.1	4594	72
Tartu	Ta9	15868	n.a.	17	10.7	11367	72
Tartu	Ta95	47334	n.a.	16	3.4	34017	72
Zurich	Zu105	9576	11182	8	8.4	4216	44
Zurich	Zu117	3886	93	10	25.7	889	23
Zurich	Zu124	12777	n.a.	7	5.5	6606	52
Zurich	Zu127	71558	n.a.	18	2.5	23175	32
Zurich	Zu133	3511	8202	14	39.9	2442	70
Zurich	Zu135	49392	842534	11	2.2	37472	76
Zurich	Zu15	39258	520993	27	6.9	27369	70
Zurich	Zu151	45145	n.a.	22	4.9	16739	37
Zurich	Zu155	4346	51329	13	29.9	2494	57
Zurich	Zu160	35074	n.a.	8	2.3	21241	61
Zurich	Zu173	5607	n.a.	10	17.8	4021	72
Zurich	Zu179	103083	n.a.	25	2.4	32728	32
Zurich	Zu18	57666	n.a.	10	1.7	32293	56
Zurich	Zu188	6110	n.a.	5	8.2	n.a.	n.a.
Zurich	Zu19	8599	19044	14	16.3	7876	92
Zurich	Zu21	19203	42055	11	5.7	11069	58
Zurich	Zu22	124650	1209163	6	0.5	47740	38
Zurich	Zu31	38669	n.a.	21	5.4	25557	66
Zurich	Zu33	10400	15281	23	22.1	6231	60

Zurich	Zu35	19439	n.a.	2	1	5339	27
Zurich	Zu43	89860	n.a.	12	1.3	43738	49
Zurich	Zu57	13040	n.a.	24	18.4	10505	81
Zurich	Zu58	9543	n.a.	6	6.3	2072	22
Zurich	Zu59	29734	66613	7	2.4	26056	88
Zurich	Zu6	104871	205890	14	1.3	50872	49
Zurich	Zu65	2679	n.a.	2	7.5	1740	65
Zurich	Zu66	19044	13659	7	3.7	11757	62
Zurich	Zu67	275320	n.a.	6	0.2	112277	41
Zurich	Zu7	3717	17784	13	35.0	2668	72
Zurich	Zu73	2871	n.a.	5	17.4	n.a.	n.a.
Zurich	Zu80	26855	n.a.	11	4.1	21311	79
Zurich	Zu81	7014	n.a.	5	7.1	5715	81
Zurich	Zu83	21605	42075	17	7.9	7196	33
Zurich	Zu87	22711	n.a.	4	1.8	8003	35
Zurich	Zu88	17450	n.a.	5	2.9	n.a.	n.a.

Table A3. Presence/absence and biogeographic status of woody species in UGSs from each of the studied cities. Letters “n” and “e” indicate if a species was native or exotic, respectively, in a given city. Absences are left blank. Letter “x” corresponds to species where the origin status could not be unambiguously attributed (Paper II).

Family	Species	Almada	Antwerp	Lisbon	Paris	Poznan	Tartu	Zurich
Adoxaceae	*Sambucus nigra*		n		n	n		n
	Sambucus racemosa						e	n
	Sambucus sp.					x		x
	Viburnum lantana				n		e	n
	Viburnum opulus		n		n		n	n
	Viburnum rhytidophyllum				e			
	Viburnum tinus	n		n	n			e
	Viburnum x pragense				e			
	Viburnum sp.				x	x		x
Altingiaceae	*Liquidambar orientalis*							e
	Liquidambar styraciflua		e		e			
Anacardiaceae	*Cotinus coggygria*				n		e	
	Pistacia lentiscus	n		n				
	Pistacia therebinthus			n				

Family	Species	Almada	Antwerp	Lisbon	Paris	Poznan	Tartu	Zurich
	Rhus typhina				e	e		
	Rhus sp.					x		
Annonaceae	*Asimina triloba*							e
Apocynaceae	*Nerium oleander*	n		n				
Aquifoliaceae	*Ilex aquifolium*		n		n			
	Ilex sp.				x			x
Araliaceae	*Aralia elata*							e
	Eleutherococcus sessiliflorus						e	
Araucariaceae	*Araucaria* sp.	e						
Arecaceae	*Brahea* sp.			e				
	Chamaerops humilis			n				
	Phoenix canariensis			e				
	Phoenix dactylifera			e				
	Trachycarpus fortunei			e	e			
Asparagaceae	*Cordyline australis*			e				
	Dracaena sp.				e			

Family	Species	Almada	Antwerp	Lisbon	Paris	Poznan	Tartu	Zurich
	Yucca elephantipes			e				
Asteraceae	*Albizia julibrissin*			e	e			
Berberidaceae	*Berberis julianae*		e		e			
	Berberis thunbergii	e						
	Berberis vulgaris	n			n		n	
	Berberis sp.	x			x			x
	Berberis aquifolium				e			
	Nandina domestica				e			
Betulaceae	*Alnus cordata*				e			
	Alnus glutinosa		n		n		n	n
	Alnus incana						n	n
	Alnus sp.					x		x
	Betula maximowicziana							e
	Betula papyrifera							e
	Betula pendula		n	n	n		n	n
	Betula pubescens				n		n	n

Family	Species	Almada	Antwerp	Lisbon	Paris	Poznan	Tartu	Zurich
	Betula sp.				x	x	x	x
	Carpinus betulus		n	e	n		e	n
	Corylus americana						e	
	Corylus avellana		n		n	n	n	n
	Corylus colurna				e		e	
	Corylus cornuta						e	
	Ostrya carpinifolia				n			n
Bignoniaceae	*Catalpa bignonioides*				e	e		
	Jacaranda mimosifolia	e		e				
Buxaceae	*Buxus sempervirens*		n	n	n			
Calycanthaceae	*Calycanthus floridus*							e
Cannabaceae	*Celtis australis*	n		n	n			
	Celtis occidentalis							e
Caprifoliaceae	*Kolkwitzia amabilis*				e			
	Kolkwitzia sp.				x			
	Lonicera caerulea						n	

Family	Species	Almada	Antwerp	Lisbon	Paris	Poznan	Tartu	Zurich
	Lonicera demissa						e	
	Lonicera fragrantissima							e
	Lonicera nitida				e			
	Lonicera periclymenum				n			
	Lonicera tatarica				e			
	Lonicera xylosteum				n		n	n
	Lonicera sp.				x			
	Symphoricarpos albus		e		e		e	e
	Symphoricarpos sp.					x		
	Weigela praecox							e
	Weigela sp.				e			
Casuarinaceae	*Casuarina cunninghamiana*			e				
Celastraceae	*Euonymus europaeus*	n	n	n			n	n
	Euonymus japonicus				e			
	Euonymus latifolius		n					
	Euonymus nanus						e	

Family	Species	Almada	Antwerp	Lisbon	Paris	Poznan	Tartu	Zurich
	Euonymus sp.				x			
Cephalotaxaceae	*Cephalotaxus fortunei*				e			
	Cephalotaxus harringtonia							e
Cerambycidae	*Howea forsteriana*			e				
Cercidiphyllaceae	*Cercidiphyllum japonicum*				e			
Cistaceae	*Cistus ladanifer*	n						
	Cistus salviifolius	n						
	Cistus sp.				x			
Cornaceae	*Cornus florida*							e
	Cornus kousa				e			
	Cornus mas		n		n			n
	Cornus sanguinea		n		n		n	
	Cornus suecica						n	
	Cornus sp.				x	x		x
Cupressaceae	*Calocedrus decurrens*				e			
	Chamaecyparis lawsoniana		e					

Family	Species	Almada	Antwerp	Lisbon	Paris	Poznan	Tartu	Zurich
	Chamaecyparis obtusa							e
	Chamaecyparis pisifera						e	
	Chamaecyparis sp.				e			x
	Cryptomeria japonica				e			
	Cunninghamia lanceolata							e
	Cupressus lusitanica			e				
	Cupressus macrocarpa			e				
	Cupressus nootkatensis							e
	Cupressus sempervirens	e		e	e			
	Cupressus sp.				x	x		
	Juniperus communis	n					n	
	Juniperus horizontalis			e				
	Juniperus sabina						e	n
	Juniperus sp.				x			x
	Metasequoia glyptostroboides		e		e			

Family	Species	Almada	Antwerp	Lisbon	Paris	Poznan	Tartu	Zurich
	Microbiota decussata				e			
	Sequoia sempervirens				e			
	Sequoiadendron giganteum				e			
	Taxodium distichum				e			e
	Thuja occidentalis	e	e				e	e
	Thuja plicata							e
	Thuja sp.			x		x	x	x
Elaeagnaceae	*Elaeagnus angustifolia*	e		e	e			
	Elaeagnus commutata				e			
	Elaeagnus pungens				e			
	Elaeagnus sp.				x			
	Hippophae rhamnoides				n	n		
	Hippophae sp.					x		
Ericaceae	*Arbutus* sp.				x			
	Arbutus unedo	n		n	n			
	Calluna vulgaris		n					

Family	Species	Almada	Antwerp	Lisbon	Paris	Poznan	Tartu	Zurich
	Rhododendron sp.		x	x	x			
Euphorbiaceae	*Euphorbia dendroides*							e
	Euphorbia sp.	x						
Fabaceae	*Acacia melanoxylon*			e				
	Acacia retinoides	e						
	Acacia saligna	e						
	Acacia sp.	x						
	Caragana arborescens				e		e	
	Caragana frutex						e	
	Ceratonia siliqua	e		e				
	Cercis siliquastrum	e		e	n			
	Coronilla glauca			n				
	Gleditsia triacanthos			e	e			
	Gymnocladus dioica				e			
	Indigofera tinctoria				e			

Family	Species	Almada	Antwerp	Lisbon	Paris	Poznan	Tartu	Zurich
	Laburnum alpinum				n			
	Robinia pseudoacacia	e	e	e	e	e	e	e
	Styphnolobium japonicum			e	e			e
	Spartium junceum				n			
	Tipuana tipu			e				
	Ulex australis	n						
	Ulex jussiaei	n						
	Wisteria sinensis				e			e
Fagaceae	*Castanea sativa*		e		e	e		
	Castanea sp.					x		
	Fagus sylvatica		n		n	n		n
	Fagus sp.					x		
	Quercus castaneifolia				e			
	Quercus dentata				e			
	Quercus faginea			n				

Family	Species	Almada	Antwerp	Lisbon	Paris	Poznan	Tartu	Zurich
	Quercus ilex				n			n
	Quercus palustris		e		e			
	Quercus petraea			e		n		
	Quercus phillyraeoides							e
	Quercus robur	n	n	n	n		n	n
	Quercus rotundifolia			n				
	Quercus rubra		e		e	e	e	e
	Quercus suber	n		n				
	Quercus sp.				x	x	x	x
Ficidae	*Ficus benjamina*			e				
	Ficus carica	n			e			
Garryaceae	*Aucuba japonica*				e			
Ginkgoaceae	*Ginkgo biloba*	e	e	e	e			e
Grossulariaceae	*Ribes alpinum*						n	
	Ribes nigrum				n		n	
	Ribes rubrum						n	

Family	Species	Almada	Antwerp	Lisbon	Paris	Poznan	Tartu	Zurich
	Ribes sp.							x
Hamamelidaceae	*Parrotia persica*				e			
Hydrangeaceae	*Deutzia* sp.				e			
	Forsythia sp.				x			
	Forsythia x intermedia		e					
	Philadelphus coronarius		e		e	e	e	e
	Philadelphus pubescens						e	
	Philadelphus sp.				x			
Hypericaceae	*Hypericum calycinum*				e			
	Hypericum sp.				x			
Juglandaceae	*Carya illinoinensis*				e			
	Juglans cinerea						e	
	Juglans mandshurica						e	e
	Juglans nigra				e			
	Juglans regia		e		e			
	Juglans sp.					x		x

Family	Species	Almada	Antwerp	Lisbon	Paris	Poznan	Tartu	Zurich
	Pterocarya fraxinifolia				e			
Lamiaceae	*Lavandula stoechas*	n						
	Rosmarinus officinalis			n				
	Vitex agnus-castus				n			
Lauraceae	*Laurus nobilis*							e
Lythraceae	*Punica granatum*	e		e	e			
Magnoliaceae	*Liriodendron tulipifera*				e			
	Magnolia grandiflora			e	e			e
	Magnolia sp.			x	x			x
	Magnolia stellata							e
Malvaceae	*Brachychiton populneus*	e		e				
	Brachychiton sp.	e						
	Hibiscus syriacus	e						
	Tilia cordata		n		n		n	n
	Tilia platyphyllos		n		n		e	n
	Tilia tomentosa	e	e	e	e		e	e

Family	Species	Almada	Antwerp	Lisbon	Paris	Poznan	Tartu	Zurich
	Tilia x europaea				n		e	
	Tilia sp.			x		x		x
Meliaceae	*Cedrus atlantica*		e		e			
	Cedrus deodara				e			
	Cedrus libani				e			
	Cedrus sp.				x			
	Melia azedarach				e			
Moraceae	*Broussonetia papyrifera*				e			
	Morus nigra			e	e			
Musaceae	*Musa balbisiana*			e				
Myrtaceae	*Eucalyptus* sp.	e		e				
	Myrtus communis	n						
Nyssaceae	*Nyssa sylvatica*				e			
Oleaceae	*Fraxinus angustifolia*	n		n	n			
	Fraxinus excelsior		n	e	n	n	n	n
	Fraxinus ornus				e			

Family	Species	Almada	Antwerp	Lisbon	Paris	Poznan	Tartu	Zurich
	Fraxinus sp.			x		x		x
	Ligustrum japonicum	e						
	Ligustrum lucidum			e	e			
	Ligustrum obtusifolium							e
	Ligustrum vulgare	n	n		n			
	Ligustrum sp.	x		x		x		x
	Olea europaea	n		n	n			
	Olea maroccana			e				
	Phillyrea angustifolia	n		n				
	Phillyrea latifolia			n				e
	Syringa josikaea						e	
	Syringa reticulata						e	
	Syringa vulgaris				e	e	e	e
	Syringa sp.			x	x		x	
Paulowniaceae	*Paulownia tomentosa*				e			
Pentaphylacaceae	*Camellia japonica*				e			

Family	Species	Almada	Antwerp	Lisbon	Paris	Poznan	Tartu	Zurich
	Camellia sp.				e			
Pinaceae	*Abies alba*						e	
	Abies balsamifera						e	
	Abies concolor						e	
	Abies pinsapo							e
	Abies sp.				x			x
	Larix decidua			e			e	n
	Larix gmelinii						e	
	Larix kaempferi							e
	Larix laricina							e
	Larix marschlinsii						e	
	Larix sibirica						e	
	Larix sp.			x		x	x	x
	Picea abies				n		n	n
	Picea canadensis						e	

Family	Species	Almada	Antwerp	Lisbon	Paris	Poznan	Tartu	Zurich
	Picea glauca				e		e	
	Picea obovata						e	
	Picea omorica							e
	Picea orientalis							e
	Picea pungens		e	e	e		e	
	Picea sp.					x		x
	Pinus aristata							e
	Pinus brutia							e
	Pinus cembra			e		n	e	n
	Pinus contorta				e			e
	Pinus halepensis	e						
	Pinus mugo				n		e	n
	Pinus nigra				e			e
	Pinus pinaster	n		n				
	Pinus pinea	n		n				

Family	Species	Almada	Antwerp	Lisbon	Paris	Poznan	Tartu	Zurich
	Pinus sibirica						e	
	Pinus sylvestris		e		n		n	n
	Pinus wallichiana				e			
	Pinus sp.	x		x	x	x		x
	Pseudotsuga menziesii				e			
	Tsuga canadensis							e
Pittosporaceae	*Pittosporum tobira*	e		e	e			
	Pittosporum undulatum			e				
	Pittosporum sp.				x			
Plantaginaceae	*Veronica salicifolia*				e			
Platanaceae	*Platanus orientalis*				e			
	Platanus x hispanica	e	e	e	e			
	Platanus sp.					x		
Poaceae	*Bambusa* sp.			x				
Polyporaceae	*Davidia involucrata*							e
Proteaceae	*Grevillea robusta*	e		e				

Family	Species	Almada	Antwerp	Lisbon	Paris	Poznan	Tartu	Zurich
Rhamnaceae	*Ceanothus* sp.				e			
	Ceanothus thyrsiflorus				e			
	Frangula alnus		n				n	
	Rhamnus alaternus			n				
	Rhamnus cathartica		n		n		n	
Rosaceae	*Amelanchier lamarckii*		e					
	Amelanchier sp.				x			x
	Amelanchier spicata						e	
	Aronia melanocarpa						e	e
	Chaenomeles japonica						e	
	Chaenomeles speciosa							e
	Cotoneaster horizontalis				e			
	Cotoneaster lacteus				e			
	Cotoneaster lucidus						e	e
	Cotoneaster sp.				x			
	Crataegus laevigata		n					

Family	Species	Almada	Antwerp	Lisbon	Paris	Poznan	Tartu	Zurich
	Crataegus monogyna		n	n				
	Crataegus pedicellata							e
	Crataegus rhipidophylla						n	
	Crataegus submollis						e	
	Crataegus sp.			x	x	x	x	x
	Eriobotrya japonica	e			e			
	Eucalyptus camaldulensis	e						
	Kerria japonica				e			
	Malus domestica			e	e	e	e	e
	Malus sylvestris		n				n	
	Malus sp.				x			
	Mespilus germanica				e			
	Physocarpus opulifolius				e		e	e
	Physocarpus sp.							x
	Potentilla fruticosa				n		n	e

Family	Species	Almada	Antwerp	Lisbon	Paris	Poznan	Tartu	Zurich
	Prunus avium		n		n	n	e	
	Prunus cerasifera	e			e	e		
	Prunus cerasus	e			e	e		e
	Prunus domestica					e	e	e
	Prunus dulcis					e		
	Prunus japonica				e			
	Prunus laurocerasus		e		e			
	Prunus lusitanica				n			
	Prunus nipponica						e	
	Prunus padus				n		n	n
	Prunus persica			e				
	Prunus serotina		e					
	Prunus serrulata							e
	Prunus spinosa					n	n	
	Prunus sp.				x			

Family	Species	Almada	Antwerp	Lisbon	Paris	Poznan	Tartu	Zurich
	Pyracantha coccinea		e		n			
	Pyrus communis	e		e		e	e	e
	Pyrus pyraster							n
	Pyrus salicifolia							e
	Pyrus sp.				x			x
	Rosa canina		n					n
	Rosa maximowicziana							e
	Rosa multiflora		e		e			
	Rosa rugosa				e			
	Rosa sp.			x	x	x	x	x
	Rubus fruticosus		n					
	Rubus ulmifolius	n						
	Ruscus aculeatus				n			
	Sorbaria sorbifolia				e			
	Sorbaria sp.		x					

Family	Species	Almada	Antwerp	Lisbon	Paris	Poznan	Tartu	Zurich
	Sorbus aria		n					
	Sorbus aucuparia		n		n		n	n
	Sorbus intermedia				e		n	
	Sorbus torminalis			n				
	Sorbus sp.				x	x		
	Spiraea cantoniensis			e				
	Spiraea chamaedryfolia				e		e	
	Spiraea japonica				e	e		
	Spiraea sp.			x	x			
Rubiaceae	*Fuchsia* sp.				e			
Rutaceae	*Choisya ternata*				e			
	Citrus limon	e		e				
	Citrus trifoliata				e			
	Phellodendron amurense			e			e	
	Phellodendron sachalinense						e	
	Phellodendron sp.				e			

Family	Species	Almada	Antwerp	Lisbon	Paris	Poznan	Tartu	Zurich
Salicaceae	*Populus alba*	n	n	n	n		e	n
	Populus balsamifera				e			
	Populus canadensis		e					
	Populus nigra	x	x	x	x			
	Populus tremula		n	n	n	n	n	n
	Populus x canescens		n		n			
	Populus sp.			x		x	x	x
	Salix alba		n		n		e	n
	Salix babylonica		e	e	e			
	Salix caprea		n		n		n	n
	Salix cinerea				n		n	e
	Salix fragilis		n	n	n		n	
	Salix pentandra				n		n	
	Salix phylicifolia						n	
	Salix purpurea				n			

Family	Species	Almada	Antwerp	Lisbon	Paris	Poznan	Tartu	Zurich
	Salix repens		n					
	Salix rosmarinifolia						n	
	Salix triandra						n	
	Salix viminalis				n		n	
	Salix x rubens				n			
	Salix sp.		x		x	x		x
Salticidae	*Cydonia oblonga*							e
	Erica sp.				x			
Sapindaceae	*Acer buergerianum*							x
	Acer campestre		n		n			n
	Acer cappadocium				e			
	Acer ginnala				e		e	
	Acer griseum				e			e
	Acer japonicum							e
	Acer negundo	e		e	e	e	e	

Family	Species	Almada	Antwerp	Lisbon	Paris	Poznan	Tartu	Zurich
	Acer opulus				n			
	Acer palmatum				e			
	Acer platanoides		n		n	n	n	n
	Acer pseudoplatanus	n	n		n	n	e	n
	Acer saccharinum		e		e		e	e
	Acer sempervirens				e			
	Acer tataricum						e	
	Acer sp.					x	x	x
	Aesculus carnea			e	e			
	Aesculus hippocastanum	e	e	e	e		e	e
	Aesculus pavia				e			e
	Aesculus sp.			e				e
	Koelreuteria paniculata				e			
Scrophulariaceae	*Buddleja davidii*				e			
	Myoporum tenuifolium			e				

Family	Species	Almada	Antwerp	Lisbon	Paris	Poznan	Tartu	Zurich
Simaroubaceae	*Ailanthus altissima*				e			
Sphingidae	*Amorpha fruticosa*				e			
Staphyleaceae	*Staphylea pinnata*				n			
Tamaricaceae	*Tamarix gallica*				n			
	Tamarix indica				e			
Taxaceae	*Taxus baccata*		n	n	n	n	n	n
Thymelaeaceae	*Daphne gnidium*	n						
Ulmaceae	*Ulmus glabra*		n		n		n	
	Ulmus laevis				n			
	Ulmus minor		n	n	n			
	Ulmus pumila				e			
	Ulmus sp.			x	x	x		x
	Zelkova serrata				e			
Verbenaceae	*Lantana camara*	e		e				
Vitaceae	*Parthenocissus quinquefolia*						e	e

SUMMARY IN ESTONIAN

LINNAÖKOLOOGIA: UUED ÖKOSÜSTEEMID, UUED VÄLJAKUTSED

Käesoleva doktoritöö fookuses oli linnaökosüsteemide taksonoomiline ja funktsionaalne mitmekesisus Euroopa skaalal. Doktoritöös esitatud tulemuste aluseks oli H2020 uurimisprojekt BioVeins (2017-2020), mille raames uuriti seitsme Euroopa linna rohealade ökosüsteemide funktsionaalsust ja liigirikkust erinevatel elustikurühmadel, alates taimedest, lõpetades putukatega.

Praegusel ajal elab juba ligikaudu kolmveerand Euroopa elanikest linnades, ning nende osakaal on lähiaastatel suurenemas (UN, 2019). Linnad on väga heterogeense ja fragmenteerunud maakasutusega piirkonnad, mis on valdavale osale elusloodusest elamiskõlbmatu (tööstus- ja suurelamurajoonid), ent samas leidub linnades erineva suuruse ja ühenduvusega alasid (pargid, surnuaiad), mis võivad olla küllaltki elurikkamad (Faeth et al. 2012). Linnastumise käigus leiavad ühest küljest aset maakasutuse muutused, elupaikade killustumine, ja muud elustikule stressi tekitavad protsessid, kuid teisest küljest võivad selle käigus tekkida ka täiesti uued ökosüsteemid, kus samas koosluses elavad liigid, kes looduses kunagi omavahel kokku ei satu (Gaston, 2010; Swan et al., 2011). Linnas leiduvaid rohealasid nähakse sageli linna ümbritsevate aladega võrreldes liigirikkamatena, kuna seal leidub nii looduslikult levinud liike kui ka tulnukliike (Derbi Lewis et al., 2016), olles sel moel ökoloogilisteks oaasideks üldjuhul läbitungimatute pindade ja tehisstruktuuridega kaetud linnaruumis.

Seega sõltub linnaökosüsteemide funktsionaalsus, mis pakub linnaelanikele väga erinevaid ökosüsteemiteenuseid ja -hüvesid, väga suuresti varieeruda võivatest abiootilistest ja biootilistest teguritest, millede mõju avaldub linnaplaneerimise ja selle kujunemise käigus (Spasojevic et al., 2018). Samuti mängib linnaökosüsteemides väga suurt rolli levimine, mis on oluliselt suuremas sõltuvuses maastikulisest mustritest, kui looduslikes tingimustes; ent olulised, ja looduslike ökosüsteemidega võrreldes nihestatutena, on ka hõlbustamine, konkurents ja kohastumine (Kondratyeva et al., 2020). Lisaks sellele on linnades leiduvad ökosüsteemid sageli suurel määral inimese kujundatud

– seal leiduvad liikide kogumid erinevad sageli suurel määral linna ümbritsevate looduslike ja agraarsete piirkondade kooslustest (Mason et al., 2011). Seega võib eeldada, et linnaloodus funktsioneerib paljuski teistmoodi, ja teistest rõhuasetustest lähtuvalt, kui linnasid ümbritsev loodus – kuid meie senised teadmised linnalooduse funktsioneerimisest on väga piiratud. Millised liigid, nende tunnused, ning liikide omavahelised interaktsioonid on linnalooduses olulised, ja kui suurel määral erinev see looduslikes keskkondadega võrreldes, ning millised on nende erinevuste geograafilised ulatused?

Käesolevas doktoritöös esitatakse esmalt linnalooduse ökoloogilise uurimise raamistik (I), kus arutletakse viie võimaliku uurimisfookuse üle, mille abil oleks võimalik suurel määral täiendada teadmisi linnalooduse elurikkuse, funktsionaalsuse ja ökosüsteemiteenuste kohta. Seejärel rakendame seda raamistikku uurides seitsme Euroopa linna rohealade taimkatte (II), samblike (III) ja mesilaste (IV) taksonoomilist ja funktsionaalset mitmekesisust, ning neid mõjutavaid inimasustustihedusest suunatud tegureid, nagu heterogeensus ja fragmentatsioon, õhusaaste, looduslike ressursside maht linnaruumis jms.

Uurimisaladeks olid erineva suuruse ja ühenduvusega rohealad seitsmes Euroopa linnas: Tartus (Eesti). Poznanis (Poola), Antwerpenis (Belgia), Pariisis (Prantsusmaa), Zürichis (Šveits), Lissabonis ja Almadas (Portugal). Igas mainitud linnas sai valitud Euroopa Linnaatlasest (European Urban Atlas; EEA, 2012) maakatte klassi “1.4.1 Green Urban Areas” kuuluvad rohealad. Nende seast valisime stratifitseeritud juhuvaliku alusel välja uurimisalad, kuni 36 ala igast linnast. Alade valikul lähtusime kahest parameetrist: roheala suurus ja selle ühenduvus teiste ümberkaudsete rohealadega. Viimase puhul arvutasime välja rohealade võrgustiku 5 km raadiuses iga uuritava roheala ümber. Kõik algsesse alade valikusse jõudnud rohealad jaotati kuude suuruse ja ühenduvuse klassi, ning nende põhjal valiti välja kuni 36 ala, mis jagunesid kõikide suuruse ja ühenduvuse klassi kombinatsioonidesse. (Kahes linnas, Tartus ja Almadas, oli valtud alade number pisut väiksem, kuna mõnesse kombinatsiooni kuuluvaid rohealasid linnas ei leidunud. Seejärel rakendasime iga linna kõikides sõelale jäänud rohealades sama metoodikat uurimaks taimede, samblike ja mesilaste taksonoomilist ja funktsionaalset mitmekesisust.

BioVeinsi projekti linnalooduse ökoloogilise uurimise raamistiku (I) käigus tuvastasime viis kõige olulisemat uurimisfookust, mille abil saaks kõige tõhusamalt täiendada teadmisi linnalooduse elurikkusest, funktsionaalsusest ja ökosüsteemiteenustest: i) rakendada linnalooduse uurimisel rohkem funktsionaalsete tunnuste põhist lähenemist: ii) parendada elupaikade kaardistamist linnades; iii) rakendada linnalooduse uurimisel rohkem kodanikuteadust ja hobiteadlasi; iv) kasutada analüüsides üheaegselt rohkem kui ühte gradient; ja v) kaasata linnalooduse ökoloogilisse uurimisse ka mahajäetud alad ja tühermaad, kus leidub omajagu spetsiifilisi nišše.

Ajavahemikul 2018 kuni 2020 toimunud välitööde käigus tuvastasime uuritud kokku 418 puittaimeliiki (7 linna 225 rohealal), 140 samblikuliiki (7 linna 219 rohealal) ja 135 taimeliigi õietolmu nelja mesilaseliigi vastse toiduvalikus (5 linna 80 rohealal). Linna rohealade taimkattes leidus väga suurel määral võõr- ja tulnukliike – 40% kuni 65% linnade liigifondist. Liigirikkus, maapealne taimne biomass ja puittaimede võra katvus olid enamikes linnades küll positiivselt seotud rohealade pindalaga, ent puittaimede liigitihedus oli tugevas negatiivses seoses rohealade pindalaga kõikides linnades (II).

Samblike elurikkuse ja ohtruse näitajad olid kõige kõrgemad Lissabonis, Antwerpenis ja Tartus (III). Kuid samblikukoosluste funktsionaalsus oli linnade võrdluses küllaltki sarnane. Näiteks kiirgustaluvuse poolest olid kõikides linnades väga sarnased samblikukooslused – igas linnas moodustasid kiirgust taluvad liigid rohkem kui 75% samblike ohtrusest; samuti olid kõikides linnades enim levinud samblikud valdavalt põuatundlikud. Siiski seletasid samblike taksonoomilist ja funktsionaalset varieeruvust peamiselt lokaalse tasandi faktorid (~85% varieeruvusest), ning regionaalse ja globaalse skaala faktorite (õhusaaste ja kliima suureskaalalised gradiendid) mõju oli pigem väike (~15%).

Linnades leiduvad rohttaimed, aga ka puittaimed, on toiduallikaks linnas elavatele mesilastele, eriti nende vastsetele. Uurides nelja Euroopas laialt levinud mesilase vastsete toitumist taimede õietolmust viies linnas (IV) leidsime, et nende toitumisstrateegiad on küllalt erinevad. Spetsialistidest mesilasliikide toidutaimede eelistused olid kõikides uuritud linnades palju sarnasemad kui generalistist mesilasliikidel. Kui spetsialistliikide vastsed toitusid kõikides uuritud linnades samade taimetaksonite õietolmust, siis generalistide toiduvalik oli palju mitmekesisem ja varieeruvam, ning tulnuk- ja võõrliikide õietolmu osakaal oli toiduvalikud oluliselt suurem kui spetsialistliikidel. Mida suurema asustustihedusega linn, seda väiksema tõenäosusega seal spetsialistidest mesilasliike leidus.

Ajal, mil elurikkus hävib pretsedenditu kiirusega (Leclère et al., 2020) ja linnastumine aina kiireneb kõikjal maailmas (UN, 2019) on viimane aeg hakata linnaplaneerimisel ja linnade toimimise analüüsimisel arvesse võtma elurikkust ja ökoloogiat. Tänu linnalooduse eripäradele – suurem killustatus ja väiksem ühenduvus, uued ökosüsteemid ja liikide komplektid – ei saa me rakendada olemasolevaid analoogseid teadmisi looduslikest süsteemidest, vaid peame neid spetsiifiliselt linnaökosüsteemides uurima, seejuures lähenedes linnaloodusele paljutahuliselt, hõlmates üheaegselt nii erinevaid elustikurühmi, nii nende liigilist kui funktsionaalset mitmekesisust arvesse võttes, kui ka nende pakutavaid ökosüsteemiteenuseid ja -hüvesid. Linnades leiduvad rohealad on enamasti küllalt mitmekesise taimestikuga ning väga heterogeensed, pakkudes seeläbi nii ressursse kui ka pelgupaika väga erinevatele elusolenditele, nii sessiilsetele kui mobiilsetele. Paraku moodustavad valdava osa sellest taimestiku mitmekesisusest võõrliigid, mis on haljastuse käigus sinna taotluslikult kasvama pandud, kusjuures istutatavate taimeliikide valikut ei määra liikide ökoloogilised ja bioloogilised omadused, vaid peaasjalikult sotsioökonoomilised faktorid (hind, ornamentaalsus jms).

Linna rohealadel kultiveeritavate taimeliikide valik ja neist moodustatavad taimekooslused mängivad väga suurt rolli teiste linnas elavate organismide elus. Käesoleva doktoritöö tulemustest selgub, et linna rohealade planeerimisel kasutatakse haljastuses küll erinevaid puittaimeliike, kuid seda vaid teatud piirini, kaugeltki rohealade ökoloogilisi potentsiaalse realiseerimata. Sestap mõjutavad linnade rohealade elurikkust ja funktsioneerimist peamiselt kohaliku tasandi antropogeensed tegurid (nt Matos et al., 2019; Munzi et al., 2007). Terviklikumat pilti looduslikest protsessides linnaökosüsteemides, linnalooduse lõimituses väga arvesse ei võeta, ning linna rohealade planeerimise läbimõelduse kohta annavad head aimu teised linnades elavad organismid ja nende funktsionaalsus – alates rohealade samblikekooslustest kuni linnas elavate mesilasliikide vastsete toiduvalikuni.

Uurides linna rohealasid üheaegselt paljude eri tüüpi organismide seisukohast, korraga paljudes erineva vanuse ja asustustihedusega linnades, on võimalik terviklikumalt mõista linnalooduse elurikkust, selle mustreid ja seoseid linnaökosüsteemide toimimise ja nende pakutavate ökosüsteemiteenustega. Käesolevas doktoritöös esitatud analüüsid eri organismirühmade taksonoomilisest ja funktsionaalsest mitmekesisusest seitsmes Euroopa linnas annab hea ülevaate linnalooduse ökoloogilisest seisundist kontinentaalsel skaalal. Esitatud analüüside põhjal on võimalik ka tõhusamalt suunata kohalikul tasandil aset leidvat linna rohealade planeerimist ja haldamist, nii et selle käigus arvestataks ja soodustataks elurikkust ja ökosüsteemiteenuseid linnaökosüsteemides. Loodust ja looduslikke protsesse ka linnaökosüsteemides rohkem arvestades ja arvesse võttes on võimalik muuta linnasid jätkusuutlikumateks elukeskkondadeks nii inimeste endi kui ka teiste linnades elevate elusorganismide jaoks.

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I

ORIGINAL PUBLICATIONS

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Research agenda on biodiversity and ecosystem functions and services in European cities

Pedro Pinho[a,*], Joan Casanelles-Abella[b,c], Ana Catarina Luz[d], Anna Maria Kubicka[e], Cristina Branquinho[a], Lauri Laanisto[f], Lena Neuenkamp[g], Marta Alós Ortí[f], Martin K. Obrist[b], Nicolas Deguines[h,k], Piotr Tryjanowski[e], Roeland Samson[i], Ülo Niinemets[f,j], Marco Moretti[b]

[a]*Centre for Ecology, Evolution and Environmental Changes, Faculdade de Ciências, Universidade de Lisboa, Lisbon, Portugal*
[b]*Biodiversity and Conservation Biology, Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland*
[c]*Landscape Ecology, Institute of Terrestrial Ecosystems, ETH Zürich, Zürich, Switzerland*
[d]*ISEG – Lisbon School of Economics & Management, Universidade de Lisboa, Portugal*
[e]*Institute of Zoology, Poznań University of Life Sciences, Poznan, Poland*
[f]*Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, Tartu, Estonia*
[g]*Institute of Plant Sciences, University of Bern, Bern, Switzerland*
[h]*Université Paris-Saclay, CNRS, AgroParisTech, Ecologie Systématique Evolution, Orsay, France*
[i]*Laboratory of Environmental and Urban Ecology, University of Antwerp, Antwerp, Belgium*
[j]*Estonian Academy of Sciences, Tallinn, Estonia*
[k]*Laboratoire Ecologie et Biologie des Interactions, Equipe Ecologie Evolution Symbiose, Université de Poitiers, UMR CNRS 7267, France*

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Abstract

Cities are challenging environments for human life, because of multiple environmental issues driven by urbanization. These can sometimes be mitigated through ecosystem services provided by different functions supported by biodiversity. However, biodiversity in cities is affected by numerous factors, namely habitat loss, degradation, and fragmentation, as well as pollution, altered climate, and new biotic challenges. To better understand the link between biodiversity and ecosystem functions and services, we need to improve our mechanistic knowledge of these relationships. Trait-based ecology is a promising approach for unravelling the causes and consequences of biodiversity filtering on ecosystem processes and underlying services, but large gaps remain unexplored.

Here, we present a series of research directions that are aimed at extending the current knowledge of the relationship between trait-based biodiversity and ecosystem functions and services in cities. These directions are based on: (1) improving urban habitat mapping; (2) considering often neglected urban habitats and ecological niches; (3) integrating multiple urban gradients; (4) using trait-based approaches to improve our mechanistic understanding of the relationships between biodiversity and ecosystem functions and services; and (5) extending the involvement of citizens.

Pursuing these research directions may support the sustainable management of urban ecosystems and the long-term provision of ecosystem services, ultimately enhancing the well-being of urban populations.

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[*] Corresponding author.
E-mail address: ppinho@fc.ul.pt (P. Pinho).

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Introduction

Humans and their activities have been transforming the Earth and its ecosystems in multiple ways, including alterations of the landscape, disturbance regimes, species distributions and interactions (Boivin et al., 2016). Urbanization is one such global trend within the Anthropocene, impacting people, biodiversity and consequently ecosystem functions (EF) and services (ES).

Cities are socio-ecological systems mostly dominated by the grey infrastructure (built-up area, including buildings and roads) and the green and blue infrastructure, which include all natural, semi-natural and artificial (i.e. entirely human-made) habitats within a city, such as parks, rivers and green-roofs. Despite their socio-economic benefits, urban areas are a challenging environment for city-dwellers (Engemann et al., 2019). For instance, cities typically have higher temperatures and more air pollution than rural areas (Munzi et al., 2014). To mitigate these urban problems, cities can rely on a mixture of technological and nature-based solutions to provide key services, including climate and water regulation, noise reduction, air filtration and recreational and aesthetic value (Capotorti et al., 2019; Diaz et al., 2018; IPBES, 2019). Recently, the added value of green spaces to ameliorate the multiple negative impacts of pandemic situations (such as the CoVid-19) on human well-being is being heightened by a sharp increase in visitation to such green areas (Grima et al., 2020). Nature-based solutions are intended to benefit both people and nature, with the added advantage of promoting biodiversity and fostering cities as socio-ecologically resilient systems (Elmqvist, Andersson & Frantzeskaki, 2019).

Biodiversity faces multiple challenges in cities, including habitat fragmentation and high spatio-temporal disturbances when compared to non-urban areas. Changes in biodiversity and species composition due to these stressors often cascade down to shifts in EF and ES provisioning, including the potential loss of key ES (e.g., (Tresch et al., 2019b)). These stressors can also impact species composition with knock-on effects on ES provisioning due to species-specific responses depending on species traits, for example causing a decline in pollination service (measured by flower visitation) through favouring Hymenoptera in cities compared to Diptera and Lepidoptera (Theodorou et al. 2020). The need for ES provisioning differs across cities, depending on cultural, political, socio-economical, and historical aspects, as well as topographic, climatic, and geological conditions (Ossola, Locke, Lin & Minor, 2019). Nonetheless, biodiversity is universally shaped by a set of factors that filter the regional species pool and select for adapted species that might result in functionally similar species assemblages (Fournier, Frey & Moretti, 2020). In this regard, research approaches based on traits, i.e. phenotypic features of organisms that affect their fitness (Violle et al. 2007), have been proposed. Still, the relative contribution of different components of biodiversity and the mechanisms behind the provision of ES remains understudied (Schwarz et al., 2017). Moreover, studies about urban ecology, as in other fields of ecology (Meyer, Weigelt & Kreft, 2016), have some major spatial and taxonomic biases. Many studies can only cover a subset of the existing ecological components (e.g. through targeting specific habitats or times of the day) and taxonomic groups, ultimately limiting the knowledge on the relationship between biodiversity and EF.

Since cities are socio-ecological systems driven by human perceptions and needs, citizen science programs can provide important contributions to biodiversity data and promote awareness among city residents. Citizen science programs could ultimately help fill gaps in the knowledge of species' distributions and their relationships to ES in cities (Serret, Deguines, Jang, Lois & Julliard, 2019). To overcome these knowledge gaps, a comprehensive overview on trait-based biodiversity EF and ES research in cities is needed as a solid basis for future research agendas including academic and citizen sciences approaches. Building on extensive literature research focussed on the relationships between biodiversity, EF and ES provision, and on the questions raised during the development of the European research project BioVeins (Connectivity of green and blue infrastructures: living veins for biodiverse and healthy cities, BiodivERsA3201510), we identified multiple knowledge gaps for biodiversity, EF and ES research in cities. Acknowledging that these gaps could be tackled using an approach based on the quantification of EF and ES and their relationships with biodiversity, and with the ultimate objective of promoting resilient cities, we present a series of research directions that point towards: (1) improving urban habitat mapping; (2) considering neglected urban habitats and ecological niches; (3) integrating multiple urban environmental gradients; (4) using trait-based approaches to improve our mechanistic understanding of biodiversity and its relationship with EF and ES; and (5) extending the involvement of citizens in biodiversity, EF and ES research. A conceptual scheme of the research agenda is presented in Fig. 1.

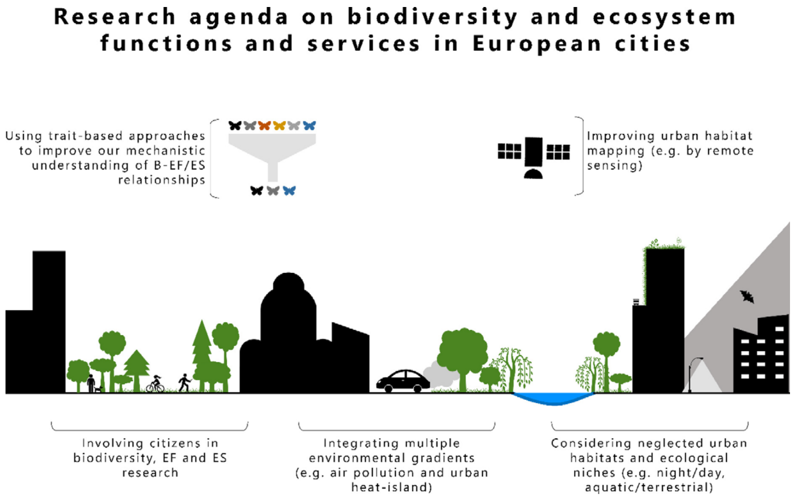

Fig. 1. Conceptual research agenda to improve our understanding of relationships between biodiversity and ecosystem functions and services (B-EF/ES) in cities. The five topics highlighted by text sections are discussed in detail in the main text.

Research agenda to assess biodiversity, EF and ES in cities

Improving urban habitat mapping

Urban biodiversity research needs detailed knowledge of the habitat types and their spatial distribution in cities. Habitat composition in the Natura 2000 network of protected areas is being characterized through a coordinated effort at the European level (EC, 2020), but this work remains limited to case studies and does not provide extensive mapping of urban areas. Some cities, such as Zurich or Paris, map their habitats at a very fine spatial resolution, and city-scale studies can make use of these resources. However, thematic and temporal resolutions are not compatible, and standard habitat mapping is currently not available at the European level (Kabisch, Strohbach, Haase & Kronenberg, 2016). Although the European Urban Atlas (EEA., European Environmental Agency, 2012) uses a consistent set of rules for mapping, its habitat definition is limited to only three classes: 'Green Urban Areas', 'Forest', and 'Herbaceous Vegetation Association', and it omits key attributes, such as vegetation structure and management, which are critical for linking them to biodiversity (Pinho et al., 2016) and ES provisioning (Mexia et al., 2018). Moreover, small habitat patches, such as green roofs and walls, flower beds and domestic gardens, as well as linear elements, such as green belts and ecotones, are often omitted even though they are novel urban habitats with critical features for biodiversity and ES provision (Hand et al., 2017).

Remote sensing data can be an important source for mapping urban land use. Unlike land-cover maps, remote sensing data is continuous over space, can be continuously updated, and has been used in urban areas to assess e.g. carbon stocks, urban heat island hotspots (Dobbs, Hernandez-Moreno, Reyes-Paecke & Miranda, 2018) and patterns of urban biodiversity (Pellissier, Mimet, Fontaine, Svenning & Couvet, 2017). An added value of remote sensing is that it enables rapid collection of data that can be used for monitoring and as part of an early warning system, i.e. signalling areas that are currently unchanged but that are likely to undergo changes in the future, such as drought-induced tree mortality, based on time-series analysis (Liu et al. 2019) . This area of research remains unexplored regarding biodiversity changes.

To avoid the pitfalls of using linear city-centre to peri-urban gradients to characterize polycentric cities (Ramalho & Hobbs, 2012), future studies should consider the characteristics of each habitat patch and its surroundings, irrespective of its geographical position and distance from the city centre. This can be done, for example, by stratifying sampling to the environmental factor of interest or to a proxy of environmental factors (e.g. dense urban landcover as a proxy for air pollution) (Pinho et al., 2016). Future work using spatially complete analyses (Pinho et al., 2008) could provide further insights into species-specific mechanisms (such as dispersion) or the spatial structure of underlying socio-ecological factors (such as management intensity, urban heat-island effect and equity in the distribution of ES).

Research directions - urban habitat mapping:

1. Create ecologically meaningful habitat-based maps of cities, including the full range of land uses, management strategies and habitat sizes.
2. Use remote sensing data series to create a spatially complete and temporally replicated sampling design, enabling better characterization of urban habitats and long-term processes.

Considering neglected urban habitats and ecological niches

Typically, urban areas contain three main land cover types: artificial built-up area, e.g. houses and roads (grey infrastructure), terrestrial and aquatic habitats (green and blue infrastructures, respectively). Although these land covers are intermingled in cities in space and time, they are often studied separately regarding: (1) their identity (green, blue, grey); (2) their vertical distribution (above vs. below the surface), (3) the time of day when the investigation occurs (day vs. night) and (4) typology (e.g. green roof vs. meadow). However, urban habitats are perceived and used by most animals as a continuum, since they often depend on more than one habitat to complete their life cycle or to perform important activities, such as reproduction, nesting, and foraging (Colding, 2007). Moreover, it is important not to minimize the importance of the below-ground habitat to many organisms, including bacteria, arthropods, fungi, and snails. Belowground biodiversity is tightly connected with the aboveground compartment through processes such as leaf litter decomposition, nutrient exchange, and soil formation. Participating in shaping primary productivity, the roles of belowground biodiversity thus cascades into the next trophic levels, ultimately determining other ES such as pest control, pollination, and food production (Tresch et al., 2019a). Such nutrient and energy transfers across neighbouring habitats are expected to be intense but remain largely unexplored.

Day and night provide two contrasting habitat spaces and ecological niches for nocturnal and diurnal organisms. Nocturnal habitats are key for species such as bats, ground-dwelling arthropods, moths and a myriad of other insects that carry out a range of under-studied ES in cities, such as pollination of night-flowering plants (Knop et al., 2017) and pest control. While other animals such as birds share the same space during the day, only by looking at both, nocturnal and diurnal organisms, we can have a complete perspective on the local food webs (Villarroya-Villalba et al., 2021).

To balance the impossibility of investigating all ecological niches and habitats during the whole life cycle of organisms, we can focus on traits related to daily and annual activity time, voltinism (number of generations an organism completes within a year), and ontogeny (the developmental history of an organism during its lifetime; see Moretti et al. (Moretti et al., 2017) for terrestrial invertebrates, Pérez-Harguindeguy et al. (2013) for plants, and Dawson et al. (Dawson et al., 2019) for fungi). Moreover, by investigating trait variation at the individual rather than species level, one could consider phenotypic plasticity and possible adaptations to the particular environmental conditions in cities, thereby shedding light on important eco-evolutionary mechanisms that need to be explored further at the genetic level (Uchida et al., 2021).

Research directions - neglected habitats and niches:

1. Use trait-based approaches to understand species' responses to unexplored niches and to compare responses across taxa, cities and regions.
2. Investigate intraspecific trait variability to quantify phenotypic plasticity and adaptations to the urban environmental conditions.

Integrating multiple environmental gradients

The processes related to urbanization are associated with a multitude of socio-ecological drivers, such as the management intensity of green areas, air, light, and noise pollution, and climatic conditions (temperature, humidity). Because these drivers act simultaneously with different spatio-temporal dynamics, it is increasingly important to study their effects jointly to identify potential non-additive effects on EF and trade-offs on ES.

Urban green space management (e.g. plant and vegetation composition, configuration, structure, and management) affects biodiversity and EF, and can cause trade-offs on ES provision. For example, slow-growing, open-crowned trees such as oaks and maples can increase the aesthetic value and microclimate regulation more than fast-growing narrow-crowned trees (de Abreu-Harbich, Labak & Matzarakis, 2015), but these effects can be limited during the cold season due to leaf loss, in comparison with evergreen species. Differences among vegetation traits and species composition also affect leaf litter (de)composition, which, in turn, affects environmental conditions for ground-dwelling organisms and their associated ES, such as protection against soil erosion, habitat provision for biodiversity (Smith, Broyles, Larzleer & Fellowes, 2014), organic matter decomposition, and nutrient cycling (Tresch et al., 2019a).

Choices of plant species featuring specific traits by both home gardeners and by managers of public green spaces, has major impacts on biodiversity and multi-trophic interactions. For instance, replacing intensively managed lawns with extensively managed meadows has been shown to enhance pollinator diversity (Baldock et al., 2019) and cultural services (Home et al., 2019), but meadows are less suitable for other recreational activities and may increase a sense of insecurity in people (Fischer, Neuenkamp, Lampinen, . . . & Klaus, 2020; Home et al., 2019). An unintended consequence of plant selection by gardeners and managers of public green spaces is the introduction of exotic and potentially invasive species, and the associated animals (such as herbivore insects) and pathogens (such as fungi and bacteria). While cultivar and exotic species provide ES and may benefit native biodiversity, especially under extensive management and appropriate densities and distributions (Ramírez-Cruz, Solano-Zavaleta, Mendoza-Hernández, Méndez-Janovitz & Suárez-Rodríguez, 2019), the risk of species becoming invasive must not be minimized, even if these species are particularly appreciated by people, e.g. for their aesthetic value (Marija et al. 2020). Consequences of invasive species may include e.g. being diseases vectors and homogenizing the biotic communities (see (Gaertner et al., 2017)). One important open question is whether exotic and invasive species traits ranges fall within the native species ranges (Finerty et al., 2016) and what are the consequences to Es and EF.

Vegetation can mitigate the effects of urban pollution (e.g. air pollution, (Grote et al., 2016; Matos, Vieira, Rocha, Branquinho & Pinho, 2019)) but is simultaneously affected by it. For instance, tree morphological, physiological and phenological traits influence the removal of tropospheric ozone (Manes et al., 2012), while volatile-emitting species can contribute to air pollution, providing an ecosystem disservice (Yuan et al., 2020). At the same time, reduced air pollution in European cities (EEA., European Environmental Agency, 2018) has positively influenced sensitive taxa, such as lichens, and nitrogen-tolerant species have recolonized cities after the decline in SO_2 (Van Dobben & Ter Braak, 1998). Nonetheless, water, noise and light pollution are still high in many urban areas (Gaston & Holt, 2018), impacting biodiversity by adding additional environmental filters (Aronson et al., 2016). However, we have limited knowledge of how changing pollution levels can affect the assembly of urban species (by modifying extinction and colonization rates) and subsequently the ES provided. For example, the shift towards electric vehicles will likely decrease the emissions of NOx in cities. This in turn could potentially reduce acidification and eutrophication, boost the biodiversity of plant communities, and increase the associated ES (Jones et al., 2014).

The urban heat-island effect, i.e. the higher temperature observed in cities than in surrounding rural areas, selects for heat- and drought-tolerant species (Fournier et al., 2020; Piano et al., 2017) and increases primary productivity (Shochat, Warren, Faeth, McIntyre & Hope, 2006), with possible effects on biotic interactions, leaf litter decomposition (Jochner & Menzel, 2015; Tresch et al., 2019a) and tree transpiration (Zölch, Maderspacher, Wamsler & Pauleit, 2016). There are several open questions regarding the effects of climate change superimposed on local urban heat-island effects (Grilo et al., 2020), with birds and plants showing contrasting responses between species (Wohlfahrt, Tomelleri & Hammerle, 2019).

All the environmental factors listed above act simultaneously on urban biodiversity and associated EF and ES. Their joint effects remain understudied but could be effectively explored by using both an adequate sampling design (de Keyzer, Rafferty, Inouye & Thomson, 2017) and a trait-based approach. The latter may allow us to identify and predict which socio-ecological filtering mechanisms drive species assembly and key ES in urban areas.

Research directions - multiple environmental gradients:

1. Quantify the multiple environmental drivers of biodiversity and EF, and the trade-offs on ES, considering the ecological, cultural, social, and economic dimensions.
2. Assess the new species assemblages, including exotic species, and individual adaptations resulting from changing environmental conditions, including ongoing climate change superimposed on the urban heat-island effect, and its consequences for ES.

Using trait-based approaches to improve our mechanistic understanding of biodiversity relationships with EF and ES

Trait-based approaches make it possible to identify biotic, abiotic and socio-cultural control mechanisms acting on community assemblages and the resulting consequences for EF within and across trophic levels (Diaz et al., 2007), as well as synergies and trade-offs among ES associated with the traits involved (Lavorel & Grigulis, 2012). Syntheses of empirical studies conducted in non-urban systems have shown that both trait dominance and trait complementarity, although not mutually exclusive (Dias et al., 2013), can be important drivers of EF and ES. As socio-ecological systems, cities challenge our traditional understanding of how species assemblages are filtered and how this, in turn, influences ecosystem functioning, stability and service delivery (Aronson et al., 2016). Which traits and functional components of biodiversity drive EF and ES, and how these can be translated into planning and management guidelines that can be implemented in restoration or conservation activities remains unknown (Luederitz et al., 2015; Schwarz et al., 2017). For example, what type of socio-ecological filters are working during a pandemic situation and that lead people to visit more a given green space than other (Grima et al., 2020) remains unexplored. Investigation of the types of filters, traits and functional components (including those related to socio-economic factors) could therefore unravel the mechanisms linking biodiversity with EF and ES in cities. By understanding these mechanisms, predictions of ES under global change and restoration strategies could be improved, e.g. by promoting species assemblages that are able to provide the desired ES (Laughlin, 2014).

Recent studies have highlighted the importance of long-term research (Weisser et al., 2017). While species composition is temporally variable (e.g. due to stochastic processes), functionally redundant species may be abundant in different years, thereby contributing to the overall stability of EF and ES (Isbell et al., 2011; Winfree et al., 2018). Thus, research conducted over long timescales and multi-service provision is an important research direction, due to their paramount importance to understand ecosystem resilience in ES provisioning.

Research directions - trait-based approaches:

1. Identify relevant socio-environmental filters, species traits and functional components to unravel the mechanisms linking biodiversity and EF with ES.
2. Identify traits that will become important given future global changes and include them in studies and restoration and conservation guidelines.

Involving citizens in biodiversity, EF and ES research

Public participation is the involvement of stakeholders (mostly citizens) in public consultations or scientific inquiries and ranges from information exchanges to active decision-making processes (Ambrose-Oji et al., 2017). Citizen scientists can become involved in management and conservation and often improve their urban ecology knowledge in doing so (Deguines, de Flores, Loïs, Julliard & Fontaine, 2018; Deguines, Princé, Prévot and Fontaine, 2020). Citizen science projects target a broad range of taxa (vertebrates, invertebrates, plants, bacteria, fungi, and protozoa) in many marine and terrestrial ecosystems, many of which are normally inaccessible, such as private gardens. Citizen scientists can also investigate and map the (spatio-temporal dynamics of) urban filters such as air pollution and air temperature (Sauermann et al., 2020). Cities encompass most of the world's human population; consequently, enhancing the collection of data on urban biodiversity in future projects using citizen science will improve the ability of citizens and policy-makers to respond to a wide range of ecological and environmental questions related to e.g. air quality, climate change, invasive species, conservation biology, population ecology, ecosystem functioning, and ecosystem service delivery by increasing the number and size of datasets (Martin, Devictor, Motard, Machon & Porcher, 2019; Silvertown, 2009). Thus, the involvement of citizens in observing and sampling biodiversity has expanded to the fields of urban governance and planning (Buijs et al., 2016), often driven by global and national policy agendas (e.g. EC 2013, UN—HABITAT 2016).

The usefulness of citizen science projects in science is, however, dependent on the quality of the collected data (Serret et al., 2019) and can be limited by the non-random distribution of sampling effort and poorly classified species (Crall et al., 2011). Future studies in citizen science must ensure that standard protocols developed with statisticians are used (Bird et al., 2014). Another open question regarding citizen science is related to error propagation through complex chains of data collection, because data is collected in very different conditions, by multiple people, and in multiple events. Future research should attempt to identify the main steps of data collection while validating each step along the chain (Snyder, Whitney, Dam, Jacobs and Baumann, 2019).

One way to boost the participation of citizens in future studies is to promote bottom-up initiatives that engage citizens with local green spaces. It is important to ground such initiatives using a combination of social and environmental objectives, rooted in environmental stewardship that goes beyond immediate personal benefit and incorporates wider cultural values (Buijs et al., 2016), thus contributing to science and helping fulfil the aim of monitoring through indicators, as set out in the Sustainable Development Goals (SDG). A powerful tool available to do so is the public participation geographic information system (PPGIS), a method combining spatially explicit data with local knowledge, perceptions and values of individuals or groups of people (Brown & Fagerholm, 2015). This method should be used in future studies to map ES (Burkhard, Maes, Burkhard & Maes, 2017), identify cultural and meaningful green spaces (Rall, Bieling, Zytynska & Haase, 2017), model residents' visits to green spaces (Luz et al., 2019), and identify potential land use conflicts (Brown & Raymond, 2014) and environmental justice issues (Raymond, Gottwald, Kuoppa & Kyttä, 2016), amongst many other uses (Rall et al. 2019).

Research directions - involving citizens:

1. Use standard sampling protocols, include error reporting and analysis, and frame future work within international initiatives, such as the Sustainable Development Goals.
2. Support bottom-up initiatives of citizen science.

Conclusions

Here, we identified five major research gaps in urban ecology research and put forth suggestions for future research directions, including habitat mapping, neglected habitats and ecological niches, multiple urban gradients, trait-based approaches, and citizens engagement. Overall, trait-based approaches emerged as a common ground to integrate all research directions, from remote sensing detection, measuring impacts of disturbance to targets of citizen science. In fact, trait-based metrics are expected to provide the link of biodiversity with ecosystem functions (EF) and thus ecosystem services (ES). Since these approaches remain poorly investigated in urban environments, especially within the identified research directions, focussing on those directions can help overcome the current knowledge gaps and enable us to make cities more resilient for both nature and human life.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

Ambrose-Oji, B., Buijs, A., Gerőházi, E., Mattijssen, T., Száraz, L., Van der Jagt, A., et al. (2017). *Innovative governance for urban green infrastructure, a guide for practitioners*. Copenhagen, Denmark: University of Copenhagen GREEN SURGE project Deliverable 6.3.

Aronson, M. F. J., Nilon, C. H., Lepczyk, C. A., Parker, T. S., Warren, P. S., Cilliers, S. S., et al. (2016). Hierarchical filters determine community assembly of urban species pools. *Ecology*, *97*, 2952–s063.

Baldock, K. C. R., Goddard, M. A., Hicks, D. M., Kunin, W. E., Mitschunas, N. M., Morse, H., . . . Memmott, J., et al. (2019). A systems approach reveals urban pollinator hotspots and conservation opportunities. *Nature Ecology & Evolution*, *3*, 363–373.

Bird, T. J., Bates, A. E., Lefcheck, J. S., Hill, N. A., Thomson, R. J., Edgar, G. J., et al. (2014). Statistical solutions for error and bias in global citizen science datasets. *Biological Conservation*, *173*, 144–154.

Boivin, N. L., Zeder, M. A., Fuller, D. Q., Crowther, A., Larson, G., Erlandson, J. M., et al. (2016). Ecological consequences of human niche construction, examining long-term anthropogenic shaping of global species distributions. *Proceedings of the National Academy of Sciences of the United States of America*, *113*, 6388–6396.

Brown, G., & Fagerholm, N. (2015). Empirical PPGIS/PGIS mapping of ecosystem services, a review and evaluation. (2015). *Ecosystem Services*, *13*, 119–133.

Brown, G., & Raymond, C. M. (2014). Methods for identifying land use conflict potential using participatory mapping. *Landscape and Urban Planning*, *122*, 196–208.

Buijs, A. E., Mattijssen, T. J. M., Van der Jagt, A. P. N., Ambrose-Oji, B., Andersson, E., Elands, B. H. M., et al. (2016). Active citizenship for urban green infrastructure, fostering the diversity and dynamics of citizen contributions through mosaic governance. *Current Opinion in Environmental Sustainability*, *22*, 1–6.

Burkhard, B., & Maes, J (Eds.). (2017). *Mapping ecosystem services* (p. 374). Sofia: Pensoft Publishers.

Capotorti, G., Alós Ortí, M. M., Copiz, R., Fusaro, L., Mollo, B., Salvatori, E., et al. (2019). Biodiversity and ecosystem services in urban green infrastructure planning, a case study from the metropolitan area of Rome (Italy). *Urban Forestry & Urban Greening*, *37*, 87–96.

Colding, J. (2007). 'Ecological land-use complementation' for building resilience in urban ecosystems. *Landscape and Urban Planning*, *81*, 46–55.

Crall, A. W., Newman, G. J., Stohlgren, T. J., Holfelder, K. A., Graham, J., & Waller, D. M. (2011). Assessing citizen science data quality, an invasive species case study. *Conservation Letters*, *4*, 433–442.

Dawson, S. K., Boddy, L., Halbwachs, H., et al. (2019). Handbook for the measurement of macrofungal functional traits, a start with basidiomycete wood fungi. *Fuctional Ecology*, *33*, 372–387.

de Abreu-Harbich, V., Labak, L., & Matzarakis, A. (2015). Effect of tree planting design and tree species on human thermal comfort in the tropics. *Landscape and Urban Planning*, *138*, 99–109.

de Keyzer, C. W., Rafferty, N. E., Inouye, D. W., & Thomson, J. D. (2017). Confounding effects of spatial variation on shifts in phenology. *Global Change Biology*, *23*, 1783–1791.

Deguines, N., de Flores, M., Loïs, G., Julliard, R., & Fontaine, C. (2018). Fostering close encounters of the entomological kind. *Frontiers in Ecology and the Environment*, *16*, 202–203.

Deguines, N., Princé, K., Prévot, A.-. C., & Fontaine, B. (2020). Assessing the emergence of pro-biodiversity practices in citizen scientists of a backyard butterfly survey. *Science of The Total Environment 136842*.

Dias, A. T. C., Berg, M. P., de Bello, . F., Van Oosten, A. R., Bila, . K., & Moretti, . M. (2013). An experimental framework to identify community functional components driving ecosystem processes and services delivery. *Journal of Ecology*, *101*, 29–37.

Diaz, S., Lavorel, S., de Bello, F., Quétier, F., Grigulis, K., & Robson, T. (2007). Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences*, *104*, 20684–20689.

Diaz, S., Pascual, U., Stenseke, M., Martín-López, B., Watson, R. T., Molnár, Z., et al. (2018). Assessing nature's contributions to people. *Science*, *359*, 270–272.

Dobbs, C., Hernandez-Moreno, A., Reyes-Paecke, S., & Miranda, M. D. (2018). Exploring temporal dynamics of urban ecosystem services in Latin America, The case of Bogota (Colombia) and Santiago (Chile). *Ecological Indicators*, *85*, 1068–1080.

EC. (2020). *NATURA 2000 in cities*. Luxembourg: Publications Office of the European Union. 2020 https://ec.europa.eu/environment/nature/natura2000.

EEA., European Environmental Agency (2012). European urban atlas. EC., Copenhagen, Denmark.

EEA., European Environmental Agency (2018). Air quality in Europe — 2018 report. EC., Copenhagen, Denmark.

Elmqvist, T., Andersson, E., Frantzeskaki, N., et al. (2019). Sustainability and resilience for transformation in the urban century. *Nature Sustainability*, *2*, 267–273.

Engemann, K., Pedersen, C. B., Arge, L., Tsirogiannis, C., Mortensen, P. B., & Svenning, J. C. (2019). Residential green space in childhood is associated with lower risk of psychiatric disorders from adolescence into adulthood. *Proceedings of the National Academy of Sciences of the United States of America*, *116*, 5188–5193.

Finerty, G. E., de Bello, F., Bílá, K., Berg, M. P., Dias, A. T., Pezzatti, G. B., et al. (2016). Exotic or not, leaf trait dissimilarity modulates the effect of dominant species on mixed litter decomposition. *Journal of Ecology*, *104*, 1400–1409.

Fischer, L. K., Neuenkamp, L., Lampinen, J., . . . Klaus, V. H. (2020). Public attitudes toward biodiversity-friendly greenspace management in Europe. *Conservation Letters*, *13*(13), E12718.

Fournier, B., Frey, D., & Moretti, M. (2020). The origin of urban communities, from the regional species pool to community assemblages in city. *Journal of biogeography*, *47*, 615–629.

Gaertner, M., Wilson, J. R. U., Cadotte, M. W., MacIvor, J. S., Zenni, R. D., & Richardson, D. M. (2017). Non-native species in urban environments: Patterns, processes, impacts and challenges. *Biological Invasions*, *19*, 3461–3469.

Gaston, K. J., & Holt, L. A. (2018). Nature, extent and ecological implications of night-time light from road vehicles. *Journal of Applied Ecology*, *55*, 2296–2307.

Grilo, F., Pinh.o, P., Aleixo, C., Catita, C., Silva, P., Lopes, N., et al. (2020). Using green to cool the grey: Modelling the cooling effect of green spaces with a high spatial resolution. *Science of the Total Environment*, *724*, 138182.

Grima, N., Corcoran, W., Hill-James, C., Langton, B., Sommer, H., & Fisher, B. (2020). The importance of urban natural areas and urban ecosystem services during the COVID-19 pandemic. *PloS one*, *15*, E0243344.

Grote, R., Samson, R., Alonso, R., Amorim, J. H., Cariñanos, P., Churkina, G., et al. (2016). Functional traits of urban trees: Air pollution mitigation potential. *Frontiers in Ecology and Environment*, *14*, 543–550.

Hand, K. L., Freeman, C., Seddon, P. J., Recio, M. R., Stein, A., & van Heezik, Y. (2017). The importance of urban gardens in supporting children's biophilia. *Proceedings of the National Academy of Sciences of the United States of America*, *114*, 274–279.

Home, R., Lewis, O., Bauer, N., Fliessbach, A., Frey, D., Lichtsteiner, S., et al. (2019). Effects of garden management practices, by different types of gardeners, on human wellbeing and ecological and soil sustainability in Swiss cities. *Urban Ecosystems*, *22*, 189–199.

IPBES. (2019). *The global assessment report on summary on policymakers of the IPBES global assessment report on biodiversity and ecosystem services*. Retrieved from https://ipbes.net/system/tdf/ipbes_global_assessment_report_summary_for_policymakers.pdf?file=1&type=node&id=35329

Isbell, F., Calcagno, V., Hector, A., Connolly, J., Harpole, W. S., Reich, P. B., et al. (2011). High plant diversity is needed to maintain ecosystem services. *Nature*, *477*, 199–202.

Jochner, S., & Menzel, A. (2015). Urban phenological studies−past, present, future. *Environmental Pollution*, *203*, 250–261.

Jones, L., Provins, . A., Holland, . M., Mills, . G., Hayes, . F., Emmett, . B., et al. (2014). A review and application of the evidence for nitrogen impacts on ecosystem services. *Ecosystem Services*, *7*, 76–88.

Kabisch, N., Strohbach, M., Haase, D., & Kronenberg, J. (2016). Urban green space availability in European cities. *Ecological Indicators*, *70*, 586–596.

Knop, E., Zoller, L., Ryser, R., Erpe, C. G., Horler, M., & Fontaine, C. (2017). Artificial light at night as a new threat to pollination. *Nature*, *548*, 7666. doi:10.1038/nature23288.

Laughlin, D. C. (2014). Applying trait-based models to achieve functional targets for theory-driven ecological restoration. *Ecology Letters*, *17*, 771–784.

Lavorel, S., & Grigulis, K. (2012). How fundamental plant functional trait relationships scale-up to trade-offs and synergies in ecosystem services. *Journal of Ecology*, *100*, 128–140.

Luederitz, C., Brink, E., Gralla, F., Hermelingmeier, V., Meyer, M., Niven, L., et al. (2015). A review of urban ecosystem services, six key challenges for future research. *Ecosystem Services*, *14*, 98–112.

Luz, A. C., Buijs, M., Aleixo, C., Metelo, I., Grilo, F., Branquinho, C., et al. (2019). Should I stay or should I go? Modelling the fluxes of urban residents to visit green spaces. *Urban Forestry and Urban Greening*, *40*, 195–203.

Manes, F., Incerti, G., Salvatori, E., Vitale, M., Ricotta, C., & Costanza, R. (2012). Urban ecosystem services, tree diversity and stability of tropospheric ozone removal. *Ecological Applications*, *22*, 349–360.

Martin, G., Devictor, V., Motard, E., Machon, N., & Porcher, E. (2019). Short-term climate-induced change in French plant communities. *Biology Letters*, *15*, 20190280.

Matos, P., Vieira, J., Rocha, B., Branquinho, C., & Pinho, P. (2019). Modeling the provision of air-quality regulation ecosystem service provided by urban green spaces using lichens as ecological indicators. *Science of the Total Environment*, *654*, 705–713.

Mexia, T., Vieira, J., Principe, A., Anjos, A., Silva, P., Lopes, N., et al. (2018). Ecosystem services, Urban parks under a magnifying glass. *Environmental Research*, *160*, 469–478.

Meyer, C., Weigelt, P., & Kreft, H. (2016). Multidimensional biases, gaps and uncertainties in global plant occurrence information. *Ecology Letters*, *19*, 992–1006.

Moretti, M., Dias, A., De Bello, F., et al. (2017). Handbook of protocols for standardized measurements of terrestrial invertebrate functional traits. *Functional Ecology*, *31*, 558–567.

Munzi, S., Correia, O., Silva, P., Lopes, N., Freitas, C., Branquinho, C., et al. (2014). Lichens as ecological indicators in urban areas, beyond the effects of pollutants. *Journal of Applied Ecology*, *51*, 1750–1757.

Ossola, A., Locke, D., Lin, B., & Minor, E. (2019). Greening in style, urban form, architecture and the structure of front and backyard vegetation. *Landscape and Urban Planning*, *185*, 141–157.

Pellissier, V., Mimet, A., Fontaine, C., Svenning, J. C., & Couvet, D. (2017). Relative importance of the land-use composition and intensity for the bird community composition in anthropogenic landscapes. *Ecology and Evolution*, *7*, 10513–10535.

Piano, E., De Wolf, K., Bona, F., Bonte, D., Bowler, D. E., Isaia, M., et al. (2017). Urbanization drives community shifts towards thermophilic and dispersive species at local and landscape scales. *Global Change Biology*, *23*, 2554–2564.

Pinho, P., Augusto, S., Martins-Loucao, M. A., Pereira, M. J., Soares, A., Maguas, C., et al. (2008). Causes of change in nitrophytic and oligotrophic lichen species in a Mediterranean climate, Impact of land cover and atmospheric pollutants. *Environmental Pollution*, *154*, 380–389.

Pinho, P., Correia, O., Lecoq, M., Munzi, S., Vasconcelos, S., Goncalves, P., et al. (2016). Evaluating green infrastructure in urban environments using a multi-taxa and functional diversity approach. *Environmental Research*, *147*, 601–610.

Rall, E., Bieling, C., Zytynska, S., & Haase, D. (2017). Exploring city-wide patterns of cultural ecosystem service perceptions and use. *Ecological Indicators*, *77*, 80–95.

Ramalho, C. E., & Hobbs, R. J. (2012). Time for a change, dynamic urban ecology. *Trends in Ecology & Evolution*, *27*, 179–188.

Ramírez-Cruz, G. A., Solano-Zavaleta, I., Mendoza-Hernández, P. E., Méndez-Janovitz, M., Suárez-Rodríguez, M., et al. (2019). This town ain't big enough for both of us…or is it? Spatial co-occurrence between exotic and native species in an urban reserve. *PloS one*, *14*, e0211050.

Raymond, C. M., Gottwald, S., Kuoppa, J., & Kyttä, M. (2016). Integrating multiple elements of environmental justice into urban blue space planning using public participation geographic information systems. *Landscape and Urban Planning*, *153*, 198–208.

Sauermann, H., Vohland, K., Antoniou, V., Balázs, B., Göbel, C., Karatzas, K., et al. (2020). Citizen science and sustainability transitions. *Research Policy*, *49*, 103978.

Schwarz, N., Moretti, M., Bugalho, M. N., Davies, Z. G., Haase, D., Hack, J., et al. (2017). Understanding biodiversity-ecosystem service relationships in urban areas, a comprehensive literature review. *Ecosystem Services*, *27*, 161–171.

Serret, H., Deguines, N., Jang, Y., Lois, G., & Julliard, R. (2019). Data quality and participant engagement in citizen science, comparing two approaches for monitoring pollinators in France and South Korea. *Citizen Science, Theory and Practice*, *4*, 22.

Shochat, E., Warren, P. S., Faeth, S. H., McIntyre, N. E., & Hope, D. (2006). From patterns to emerging processes in mechanistic urban ecology. *Trends in Ecology & Evolution*, *21*, 186–191.

Silvertown, J. (2009). A new dawn for citizen science. *Trends in Ecology and Evolution*, *24*, 467–471.

Smith, L. S., Broyles, M. E. J., Larzleer, H. K., & Fellowes, M. D. E. (2014). Adding ecological value to the urban lawnscape. Insect abundance and diversity in grass-free lawns. *Biodiversity and Conservation*, *24*, 47–62.

Snyder, J. T., Whitney, M. M., Dam, H. G., Jacobs, M. W., & Baumann, H. (2019). Citizen science observations reveal rapid, multi-decadal ecosystem changes in eastern Long Island Sound. *Marine Environmental Research*, *146*, 80–88.

Tresch, S., Frey, D., Le Bayon, R. C., Mader, P., Stehle, B., Fliessbach, A., et al. (2019b). Direct and indirect effects of urban gardening on aboveground and belowground diversity influencing soil multifunctionality. *Scientific Reports*, *9*, 9769.

Tresch, S., Frey, D., Le Bayon, R. C., Zanetta, A., Rasche, F., Fliessbach, A., et al. (2019a). Litter decomposition driven by soil fauna, plant diversity and soil management in urban gardens. *Science of the Total Environment*, *658*, 1614–1629.

Uchida, K., Blakey, R. V., Burger, J. R., Cooper, D. S., Niesner, C. A., & Blumstein, D. T. (2021). Urban biodiversity and the importance of scale. *Trends in Ecology & Evolution*, *36*, 123–131.

Van Dobben, H. F., & Ter Braak, C. J. F. (1998). Effects of atmospheric NH3 on epiphytic lichens in the Netherlands, the pitfalls of biological monitoring. *Atmospheric Environment*, *32*, 551–557.

Villarroya-Villalba, L., Casanelles-Abella, J., Moretti, M., Pinho, P., van Mensel, A., Chiron, F., et al. (2021). Response of bats and nocturnal insects to urban green areas in Central Europe. *Basic and Applied Ecology*, *51*, 59–70.

Weisser, W. W., Roscher, C., Meyer, S. T., Ebeling, A., Luo, G., Allan, E., et al. (2017). Biodiversity effects on ecosystem functioning in a 15-year grassland experiment, Patterns, mechanisms, and open questions. *Basic and Applied Ecology*, *23*, 1–73.

Winfree, R., Reilly, J. R., Bartomeus, I., Cariveau, D. P., Williams, N. M., & Gibbs, J. (2018). Species turnover promotes the importance of bee diversity for crop pollination at regional scales. *Science*, *359*, 791–793.

Wohlfahrt, G., Tomelleri, E., & Hammerle, A. (2019). The urban imprint on plant phenology. *Nature Ecology & Evolution*, *3*, 1668–1674.

Yuan, Y., Sun, Z., Kännaste, A., Guo, M., Zhou, G., & Niinemets, U. (2020). Isoprenoid and aromatic compound emissions in relation to leaf structure, plant growth form and species ecology in 45 East-Asian urban subtropical woody species. *Urban Forestry & Urban Greening*, *53*, 126705.

Zölch, T., Maderspacher, J., Wamsler, C., & Pauleit, S. (2016). Using green infrastructure for urban climate-proofing: An evaluation of heat mitigation measures at the micro-scale. *Urban Forestry & Urban Greening*, *20*, 305–316.

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummer, I., Garnier, E., et al. (2007). Let the concept of trait be functional!. *Oikos*, *116*, 882–892. doi:10.1111/j.0030-1299.2007.15559.x.

Theodorou, P, Radzevičiūtė, R, Lentendu, G, et al. (2020). Urban areas as hotspots for bees and pollination but not a panacea for all insects. *Nat Commun*, *11*, 576.

Liu, Y, Katul, G, et al. (2019). Reduced resilience as an early warning signal of forest mortality. *Nat. Clim. Chang.*, *9*, 880–885. doi:10.1038/s41558-019-0583-9.

Pérez-Harguindeguy, N, Díaz, S, Vendramini, F, et al. (2013). Leaf traits and herbivore selection in the field and in cafeteria experiments. *Austral Ecology*, *28*, 642–650.

Milanović, Marija, Knapp, Sonja, Pyšek, Petr, et al. (2020). Linking traits of invasive plants with ecosystem services and disservices. *Ecosystem Services*, *42*, 101072.

Rall, E, Hansen, R, & Stephan, P (2019). The added value of public participation GIS (PPGIS) for urban green infrastructure planning. *Urban Forestry & Urban Greening*, *40*, 264–274.

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Alós Ortí, M., Casanelles J, Chiron F, Deguines N, Hallikma T, Jaksi P, Kwiatkowska P, Moretti M, Muyshdont B, Niinemets Ü, Pinho P, Pinto MM, Saar P, Samson R, Tryjanowski P, Van Mensel A, Laanisto L. (2022). Negative relationship between woody species density and urban green spaces in seven European cities. Urban Forestry & Urban Greening. https://doi.org/10.1016/j.ufug.2022.127650

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Negative relationship between woody species density and size of urban green spaces in seven European cities

Marta Alós Ortí[a,*], Joan Casanelles-Abella[b,c], François Chiron[d], Nicolas Deguines[d,e], Tiit Hallikma[a], Piia Jaksi[a], Patrycja K. Kwiatkowska[f], Marco Moretti[b], Babette Muyshondt[g], Ülo Niinemets[a], Pedro Pinho[h], Manuel João Pinto[i], Peedu Saar[a], Roeland Samson[g], Piotr Tryjanowski[f], Anskje Van Mensel[g], Lauri Laanisto[a]

[a] *Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, Tartu, Estonia*
[b] *Biodiversity and Conservation Biology, Swiss Federal Research Institute WSL, Birmensdorf, Switzerland*
[c] *Landscape Ecology, Institute of Terrestrial Ecosystems, ETH Zurich, Zurich, Switzerland*
[d] *Université Paris-Saclay, CNRS, AgroParisTech, Ecologie Systématique Evolution, Orsay, France*
[e] *Université de Poitiers, CNRS, EBI, F-86000 Poitiers, France*
[f] *Department of Zoology, Poznań University of Life Sciences, Poznan, Poland*
[g] *Laboratory of Environmental and Urban Ecology, Department of Bioscience Engineering, University of Antwerp, Antwerp, Belgium*
[h] *Centre for Ecology, Evolution and Environmental Changes, Faculdade de Ciências, Universidade de Lisboa, Lisbon, Portugal*
[i] *Departments of Plant Biology and Geology, Faculty of Sciences University of Lisbon, Lisbon, Portugal*

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ABSTRACT

Urban green spaces (UGSs) are important elements of urban landscapes. Woody vegetation is a key component of UGSs, providing many socio-ecological benefits such as habitat provision and human well-being. Knowing plant diversity and vegetation configuration that underpin urban ecosystem processes and functions is critical to maximize nature contributions to city dwellers. Here, we present a well-replicated multi-city study showing a detailed description of taxonomic and structural diversity of woody vegetation in 225 UGSs distributed across seven European cities along a NE-SW gradient. Our aim was to understand how UGSs attributes, including size and fragmentation, influence woody vegetation features. A total of 418 woody species belonging to 76 families were identified. UGS size displayed weak positive correlations with woody species richness, but a strong negative correlation with woody species density. Alien woody species were abundant in all cities (from 40% of all species recorded in Antwerp to 64% in Lisbon and Zurich). Among the native tree species we found a predominance of *Pinus* spp. in southern cities and *Acer* spp. in cooler climates. On average, tree canopies extent was 56% of UGSs. This paper provides insights on the plant diversity and woody vegetation composition in UGSs of different size, climate and urban planning history. Our results encourage and contribute to future urban ecology studies involving different taxa and ecosystem services as well as support effective urban planning and management practices.

1. Introduction

Plants constitute the vast majority of biomass in terrestrial ecosystems including highly anthropogenic ecosystems, and support directly and indirectly biodiversity (Bar-On et al., 2018). Particularly, plants provide food, shelter and create microenvironmental conditions for other taxa in most ecological systems. Humans have been and are still transforming natural ecosystems into human-dominated biomes (Ellis and Ramankutty, 2008). Therefore, plant species richness in urban ecosystems mainly depends on human practices (Kühn et al., 2004) and on the type of built-up area (Godefroid and Koedam, 2007) and not only on natural processes related to dispersal, filtering and interactions (Nielsen et al., 2014).

Planting non-native species highly contribute to more diverse woody vegetation communities in urban areas – almost half of the non-native woody species in urban ecosystems are deliberately planted (Aronson

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[*] Correspondence to: Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, Kreutzwaldi 5, 51006 Tartu, Estonia.
E-mail address: marta.alos@emu.ee (M. Alós Ortí).

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et al., 2014; Kowarik, 2011). Around 40% of plant species in European cities are non-native (Pyšek, 1998), although lower (30%; Salinitro et al., 2018) and higher (66%; Säumel et al., 2010) proportions have also been reported (Kowarik et al., 2013; Tsiotsiou and Christodoulakis, 2010). Plant diversity provides various ecological niches for a wide variety of birds, insects, cryptogams and other biota (e.g. Grote et al., 2016; Grove et al., 2013). Also composition and structure of vegetation and landscape attributes contribute to the overall biodiversity (Threlfall et al., 2016). Higher vegetation biomass can provide greater resources for many different organisms (e.g. Großmann et al., 2020), which consequently allows for larger and thereby more viable and stable populations. A global meta-analysis on biodiversity in cities (Beninde et al., 2015) concluded that in addition to patch size, vegetation structure together with species richness, tree cover and vegetative biomass play significant roles in providing better habitat for other organism groups that inhabit urban green spaces.

The role of woody vegetation in urban areas is especially crucial in providing habitat for other organisms (Baruch et al., 2020), and ecosystem services (Capotorti et al., 2019). Vegetation of UGSs provides regulating ecosystem services (ESs) such as local climate regulation and air pollution removal (Grote et al., 2016; Locosselli et al., 2019), supporting and provisioning ESs (e.g. primary production and food, respectively) as well as cultural ESs (e.g. recreation activities, Bjerke et al., 2006). Therefore, municipalities have the opportunity and responsibility to implement ecosystem-based management and planning strategies for providing a higher quality environment for both humans and other organisms (Beery et al., 2016).

European cities share common standards in the planning of green spaces based on transforming densely built-up cities -with a scarce consideration of ecological factors in the urban design process- into more sustainable living environments (Kohout et al., 2020). As part of the new EU Biodiversity Strategy 2030, cities with a minimum population of 20,000 were requested to elaborate Urban Greening Plans by the end of 2021 with a special focus on increasing biodiversity among green infrastructure elements such as UGSs (EC, 2020). Therefore, knowing the current plant diversity and functioning in UGSs is a key tool for stakeholders involved in the urban planning process.

Many urban ecology studies focus on urbanization effects on biodiversity across urban-rural gradients (e.g. McKinney, 2002). Other studies have typically focused on single cities or locations, mainly assessing specific applied research goals using intra-urban transects, and meta-analysis conducted at broader scale commonly use existing data from different sources (Beninde et al., 2015). Systematically sampled comparable data on woody vegetation in UGSs is relatively scarce, especially on large scales and at high resolution level that would comprise data from urban settlements in different countries (Beninde et al., 2015). Thus, there is a knowledge gap on the taxonomic and structural diversity of woody vegetation stemming from common standardized surveys and at fine-grained detail comprising different urban spaces at the continental scale (Yang et al., 2015) which we aim to fulfill. Here we also follow research directions highlighted by Pinho et al. (2021) aimed at enhancing our understanding on urban biodiversity and ecosystem functions and services, particularly by including several key plant traits in our study and providing high resolution urban habitat maps.

Several studies in urban areas have found positive correlation between species richness and patch area (Cornelis and Hermy, 2004; Shwartz et al., 2013). Nonetheless, different patterns of diversity in urban parks and other green spaces have been found (Talal et al., 2019), suggesting that the increase in the number of woody species is not always proportional to the increase of UGS size, but other factors play a role in shaping urban biodiversity (e.g. urbanization degree, McKinney, 2008). UGSs tend to have lower diversity than expected from their size. Woody species density (i.e., number of species per unit area) is thus expected to be negatively correlated with UGS size. However, such analyses for urban vegetation are so far missing from the literature.

We studied 225 UGSs in 7 European cities along a SW-NE latitudinal gradient, from Portugal to Estonia. We systematically sampled and mapped woody vegetation in UGSs with different degrees of size and fragmentation, as both landscape metrics have an effect on ecological processes (e.g. Shanahan et al., 2011). Our main aim was to understand the influence of UGSs size on woody vegetation features. We tested this looking at i) species richness (expecting a relatively weak positive relationship), ii) species density (expecting an overall negative relationship), and iii) tree cover and biomass (expecting a non-significant effect).

2. Methods

2.1. Sampling sites selection

We selected 225 UGSs belonging to 7 European cities from Lisbon (38º N) to Tartu (58º N), covering most of the climatic variability in mainland Europe (Fig. 1). Selection was based on patches classified as ‘Green urban areas’ category (code 1.4.1. of the Urban Atlas) in the Pan-European Urban Atlas (2012), providing high-resolution land use and land cover maps for urban areas across Europe. To avoid major management differences between sites, we also manually excluded patches that were predominantly occupied by cemeteries and zoos, which are included in the ‘Green urban areas’ class. Other vegetated areas such as ’Forest’ class (code 3.1. of the Urban Atlas, included in natural and semi-natural areas category) and private UGSs with no public access were left out in order to minimize heterogeneity due to type and intensity of management practices. Site selection was conducted based on two independent gradients: i) size of UGSs, and ii) their structural connectivity with other green elements embedded in the urban matrix (i.e., discontinuous low density urban fabric (10-30%), discontinuous very low density urban fabric (<10%) and forests), as landscape configuration plays a role in shaping several urban taxa diversity and distribution (e.g. insects and birds). Thus considering both size and connectivity degree in our sites selection allows cities and taxa comparison. The degree of connectivity was calculated using the Proximity Index in Fragstats software within a 5 km radius from every patch.

2.2. Vegetation survey

Vegetation survey was conducted between June 2018 and June 2020. The survey consisted of a field assessment in each selected UGS, and subsequent analysis based on land cover maps of UGSs. All woody species throughout the UGSs were identified (i.e., woody species richness, Table 1) and separated by provenance into native and non-native species (see Supplementary Table S1 for source information). Species-specific mean height was recorded for each woody species (i.e., mean height of woody layer, Table 1). Then, a more detailed vegetation survey was carried out in the centroid of each selected UGS (Fig. 2a). If the geometric centroid was not available for sampling (e.g. inaccessible area, water bodies, area without trees), then the closest available area was chosen. The new sampling centroid had to accomplish two criteria: i) include woody vegetation that was representative of the UGS, and ii) occur as close as possible to the original centroid. Sampling in centroids was used in order to minimize the effects of surrounding urban non-green areas. From the five 5 m x 5 m plots in the sampling centroid all woody species were identified, the height, diameter at breast height (i.e., diameter of the trunk at 1.3 m from the ground, only for trees, DBH, Table 1) and crown or hedge size were measured on each woody individual in each plot (Fig. 2b). Woody species richness, both at the centroid and at the site scale were compared to UGS size to determine if the same relationship among total richness and patch size was also found at the plot level (i.e., if the patch size had an effect on species richness at every level, as expected in natural systems, or it rather depends on UGS design and management). When we refer to the percentages of native and non-native species, we mean the whole woody species pool in each

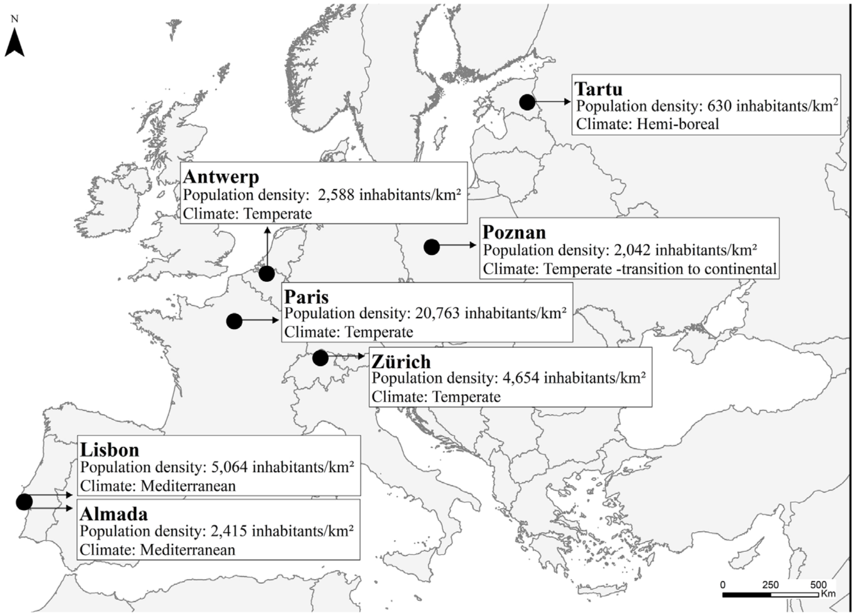

Fig. 1. Location of the selected cities, with information on demography and climate provided.

Table 1
Description of the variables included in the analysis, their units, type of variable, scale of measure and data source.

Variable	Description	Units	Scale	Source
UGS size	Urban Green area extent	m^2	UGS	Urban Atlas 2012
AGB	Tree above-ground biomass derived from allometric models	kg	Tree	(see Supplementary Table S1 for source information)
Canopy cover	Absolute coverage of tree canopies	m^2	UGS	Photo-interpretation
Canopypercentage	Relative coverage of tree canopies	%	UGS	Photo-interpretation
Mean height woody layer	Species-specific mean height of the woody layer	m	UGS	Vegetation survey
DBH	Diameter at breast height (~1.3 m)	cm	Tree	Vegetation survey
Woody species richness	Woody species richness	–	UGS centroid	Vegetation survey
Species density	Amount of woody species per unit of UGA	nr. of spp./ m^2	UGS	Vegetation survey

city (i.e., all the species recorded across the UGSs of a given city) not to its predominance among UGSs.

2.3. Land cover maps

A land cover map of each sampled UGS was made by photo-interpretation of the high resolution (i.e., 0.5 m) World Imagery basemap from 2015 using ESRI ArcMap 10.4. Photo-interpretation was done at a scale of 1:600 which allowed to distinguish between the different land cover types within the UGS (Fig. 2c). Tree species types (i.e., coniferous, broadleaf deciduous and broadleaf evergreen trees) were separated by checking images provided by Google Earth Pro v.7.3.2.5776 and street view in Google Maps from different phenological stages. The resulting vegetation maps were validated during the vegetation survey. Satellite imagery does not allow to precisely classify the extent of all land cover types due to overlapping vertical layers. Therefore, our land cover maps provided accurate information about the upper layer (i.e., tree canopy cover and canopy percentage, Table 1). Tree canopy cover was used to extend the aboveground biomass results of measured trees to the entire tree cover of each UGS.

2.4. Aboveground biomass calculation

Above-ground biomass (AGB, Table 1) of trees was calculated by using species-, genus- or plant functional type-specific allometric equations (see Supplementary Table S1 for source information). Species-specific allometric equations were used, but if not available, then genus-specific models were used, or generalized equations for either broad-

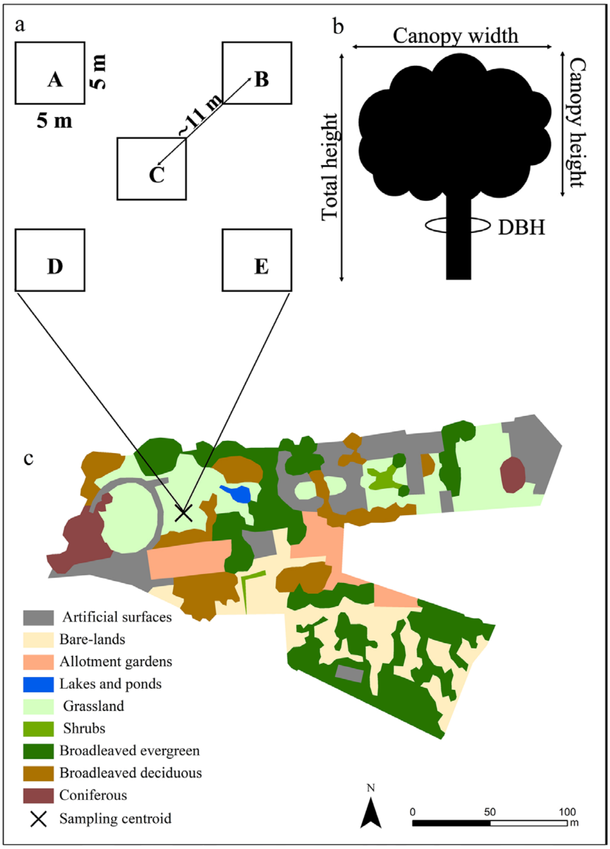

Fig. 2. Sampling design (a), quadrat C is located in the sampling centroid of the urban green space (UGS). Plant traits measured for tree plants (b). Example of one of the studied UGSs in Lisbon (size=31868.26 m^2), land cover map and location of the sampling centroid (38°46'13.7"N, 9°10'33.9"W) (c).

leaved and coniferous trees were applied. The allometric models used were based on combinations of the measured plant traits, specifically DBH and plant height and calibrated across specific ranges of these plant traits. Therefore, we considered the trees whose traits fitted such ranges. This avoided possible under- and over-estimations of AGB, but restrained the AGB results to 154 UGSs from which 139 were used for analysis (i.e., 15 UGSs were outliers, see *Statistical analysis* section). When more than one equation was available, the mean was used.

2.5. *Statistical analysis*

All analyses were conducted in R v. 3.6.1 (R Core Team, 2019) (see Supplementary Table S1 for packages source information). In order to avoid distortions in descriptive metrics and statistical tests, AGB outliers highlighted in boxplots were removed from the dataset prior to analysis. The overall variables are described in Table 1, namely: UGS size, AGB, canopy cover (both in absolute and relative terms), mean height of the woody layer, woody species richness and species density.

Linear regression models for all cities together and separately were made for exploring the response of woody species richness, woody species density (number of woody species per unit area of UGS), canopy cover and AGB (i.e., response variables) to UGS size (i.e., explanatory variable). Logarithmic transformations were applied to both response and explanatory variables to better fit linearity. Coefficients of determination are shown as R^2. Then, we performed linear mixed effects models (LMM) of those above mentioned relationships including cities as a random factor in order to account for variation of woody vegetation features in the studied cities. P-values for model comparison were obtained by likelihood ratio tests of the full model with the city effect against the model without the city effect.

3. Results

3.1. An overview of European UGSs vegetation

A total of 418 woody plant species from 76 families were identified across 225 European UGSs (Table 2 and Supplementary Table S2). Each UGS had a mean of 13 ± 0.8 species of woody plants with big differences among cities (i.e., from 6.1 in Poznan to 27.2 in Paris) and 9.3 species per hectare ($9.3\cdot10^{-4}$ spp./m^2). The most commonly found plants were deciduous broadleaved trees. Among them, the most widely represented species were *Acer platanoides* L. (occurring in 79 UGSs, 35% of the total, in five cities) and *Quercus robur* L. (60 UGSs, six cities). The most common conifer was *Taxus baccata* L. (60 UGSs, six cities) (Supplementary Table S2). *Populus alba* L. and *Populus tremula* L., also native in Europe, were very commonly found across the studied cities but presented a low abundance within city boundaries (i.e., they occurred in six cities in a total of 21 and 16 UGSs, respectively). In addition, the North American species *Robinia pseudoacacia* L., that is currently a widely-spread invasive species in Europe, was found in 55 UGSs from all the sampled cities.

At city level, more than 50% of the species recorded were non-native, except in Antwerp (Table 2). More than 60% of woody species in UGSs from Lisbon, Zurich, Paris and Tartu were non-native. The woody layer (i.e., trees and shrubs) had a mean height of 8.7 ± 0.2 m (ranging from 6.5 m in Almada to 11.3 m in Antwerp) and trees covered around 56% of the UGSs, ranging from 40% of UGSs in Almada and 74% in Tartu. Mean woody species density (number of species per unit area) in UGSs per city was distributed as follows: Antwerp 4 spp./ha, Lisbon 4.7, Poznan 4.7, Almada 6.5, Zurich: 9.5, Tartu 10.6, Paris 23.2. Distribution patterns of woody species richness and density, coefficient of variation of woody plants height, mean height of the woody layer, relative canopy cover and AGB across all the studied cities are displayed in Fig. S2. The response variables (i.e., woody species richness and density, coefficient of variation of woody plants height (CV), canopy cover and AGB) accounted for 68.4% of the overall dataset variation (Fig. S3). A main trend was formed by tree cover and AGB, while CV, woody species richness and density displayed a different trend.

3.2. Woody species richness and UGS size

We found clear latitudinal differences in the predominance of species with different species being the most common in different cities (Table 2). Highest woody species richness in a single UGS was found in Paris and Tartu (i.e., 101 and 48 woody species, respectively) (Table 2). Mean woody species richness per UGS in Paris was 27.2 ± 3.3 and, in the rest of the cities, it ranged from 6.1 ± 0.3 in Poznan to 15.3 ± 1.4 in Tartu.

Overall, large green spaces hosted slightly more woody species (Fig. 3a). At the city level, this correlation was significant in Antwerp, Lisbon, Paris and Tartu (Fig. 3a and Supplementary Table S3). In the other cities (i.e., Poznan, Zurich and Almada), UGS size did not show significant effect on woody species richness (Fig. 3a). Centroid woody species richness was not related to the size of the UGS ($p > 0.05$) (Supplementary Fig. S1).

Woody species richness of the whole UGS was positively related to UGS size and city had a significant effect ($\beta = 0.16$, SE=0.02, $t = 6.7$, $p < 0.0001$). Woody species density was negatively correlated with the size of UGSs across all cities ($R^2 = 0.77$) (Fig. 3b) with city having a significant effect ($\beta = 0.98$, SE=0.08, $t = 11.9$, $p = 0.08$). Within individual cities, the correlation coefficient varied from 0.72 in Zurich to 0.95 in Poznan (Fig. S3).

3.2.1. Tree cover and aboveground biomass

Bigger UGSs had generally more AGB and wider tree canopy cover (Fig. 4). Both correlations were significant in all the studied cities (Supplementary Table S3). The relationship between UGS size and canopy cover varied among cities ($\beta = 1.03$, SE=0.03, $t = 34$, $p < 0.0001$) (Fig. 4a), while UGS size and AGB relationship (Fig. 4b) was independent of the city ($\beta = 0.98$, SE=0.08, $t = 11.9$, $p > 0.05$). Not surprisingly, these two variables were highly correlated among them (Fig. S3), implying that wider canopies -normally belonging to bigger trees- inherently harbors more vegetative biomass. The strongest associations were observed between size and tree canopy cover, especially in Paris and Tartu (i.e., $R^2 > 0.90$), indicating that tree cover in these cities was generally more correlated with the size of UGS than in other cities (e.g. Antwerp, $R^2 = 0.76$). Size had also a strong effect on the amount of AGB contained in tree structure, especially in Paris ($R^2 = 0.76$) and Almada ($R^2 = 0.66$) compared to Lisbon ($R^2 = 0.43$).

Table 3 displays the distribution of tree cover and AGB in the seven cities. Despite Almada displayed the lowest tree cover percentages, it had the highest mean tree biomass per UGS after Tartu. Heights of trees (i.e., woody plants higher than 3 m) ranged from 8.2 ± 0.4 m in Almada to 11.3 ± 0.4 m in Antwerp, on average (Table 3). Tree DBH varied considerably between cities, with a mean ranging from 20 ± 2.3 cm in Zurich to 35 ± 3.3 and 36 ± 2.1 cm in Almada and Tartu, respectively.

4. Discussion

We aimed to understand how different woody vegetation is in differently sized urban green spaces of seven European cities by testing species richness and density on UGSs size gradient. Analyses confirmed our expectations - while the relationship between UGS size and woody species richness was overall positive, the relationship was weak and appeared only in certain cities (Fig. 3a), while the species density had a strong negative relationship with UGS size in every studied city (Fig. 3b). Bigger UGSs had more biomass and canopy only in absolute terms (Fig. 4). Thus, woody vegetation that dominates in urban green spaces is currently managed in a way that the potential of these valuable urban areas is not by far fully realized, neither for humans nor other organisms living and visiting urban areas.

Table 2
Woody species richness per city: total woody species (n species), mean and range (minimum and maximum) of species richness; percentage of non-native species; most predominant woody plant taxa per city; and number of UGSs investigated.

	Woody species richness					
City	n	Mean	Range	Non-native species (%)	Most common genus and species (n UGSs)	UGSs (n)
Almada	65	9.5 ± 1	4–18	54	*Pinus* spp. (13), *Olea europaea* (12)	15
Antwerp	74	8.9 ± 0.6	1–18	40	*Acer* spp. (25), *Quercus robur* (17),	35
Lisbon	102	8.2 ± 0.6	3–19	65	*Pinus* spp. (18), *Olea europaea* (17)	34
Paris	231	27.2 ± 3.3	3–101	65	*Acer* spp. (27), *Taxus baccata* (24)	36
Poznan	56	6.1 ± 0.3	3–11	54	*Acer* spp. (27), *Acer platanoides* (21)	36
Tartu	116	15.3 ± 1.4	4–48	61	*Acer* spp. (28), *Betula pendula* and *Quercus robur* (23)	34
Zurich	137	12 ± 1.2	2–27	64	*Acer* spp. (26), *Carpinus betulus* (19)	35

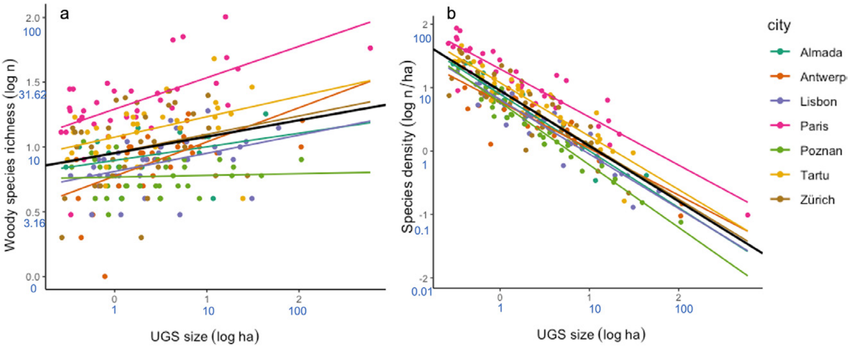

Fig. 3. The relationship of UGS size with woody species richness (a) and woody species density (b) per city. Both plots are on log-scale (black numbers) and absolute scale (blue numbers). Each dot is one UGS. The species richness data comprises all the woody species found in each urban green space. The overall relationships are described by the black regression lines. Estimates of the linear mixed effect model a: $\beta = 0.16$, SE= 0.02, $t = 6.7$, $p < 0.0001$; b: $\beta = -0.84$, SE= 0.02, $t = -34.8$, $p < 0.0001$. Regression coefficients and significances of simple linear models are displayed in Supplementary Table S3 for each city. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

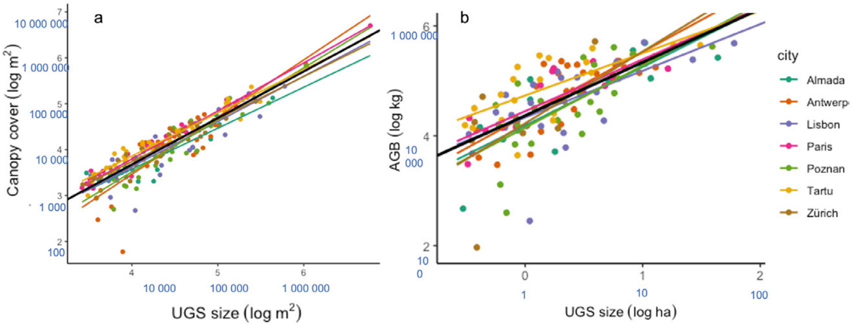

Fig. 4. The relationship of UGS size with canopy cover (a) and AGB (b) per city. Both plots are on log-scale (black numbers) and absolute scale (blue numbers). Each dot represents an UGS. The overall relationships are described by the black regression lines. Estimates of the linear mixed effect model a: $\beta = 1.03$, SE= 0.03, $t = 34$, $p < 0.0001$; b: $\beta = 0.98$, SE= 0.08, $t = 11.9$, $p = 0.08$). Regression coefficients and significances of simple linear models are displayed in Supplementary Table S3 for each city. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3
Percentage of tree canopy cover, mean above-ground biomass, mean height of the woody layer and diameter at breast height (DBH) of tree plants in the seven cities.

City	Canopy cover (%)	Mean AGB (tons)	Mean height (m)	DBH (cm)
Almada	40	133	8.2 ± 0.4	35 ± 3.3
Antwerp	50	120	11.3 ± 0.4	23 ± 2.5
Lisbon	50	105	9.3 ± 0.2	31 ± 1.5
Paris	67	111	9.8 ± 0.2	24 ± 2.6
Poznan	45	92	10.7 ± 0.5	26 ± 1.5
Tartu	74	148	9.8 ± 0.2	36 ± 2.1
Zurich	56	78	10.5 ± 0.3	20 ± 2.3

4.1. *An overview of European UGSs woody vegetation*

While cities tend to be more diverse in terms of plant species than the surrounding natural ecosystems (e.g. Kühn et al., 2006), a big proportion of that diversity in case of woody species is due to planting non-native species – on average 59% in our sampled UGSs (Supplementary Table S2). The proportion of native and non-native species and predominance of the abundance of native species in our sample are in line with previous research from other urban areas (Crosby et al., 2021; Pauleit et al., 2002).

Planting woody individuals is a common practice in urban areas, but the species selection always comprises a trade-off between environmental, social and economic features. For instance, *A. platanoides*, the most commonly found species in our European UGSs, has been shown to be effective in removing particulate matter (PM) and O_3 and storing CO_2

as part of its biomass (Baraldi et al., 2019). Nevertheless, it can also cause damage in urban structures, mainly on kerbs and other impervious surfaces (Scholz et al., 2016). Another example, *R. pseudoacacia*, is also a widespread species among the studied UGSs. It has been planted in cities in the last decades in part due to its resistance to harsh environmental conditions and diseases, even if it is considered an invasive species, especially in Central and Southern Europe (Puchałka et al., 2020). However, it has been shown to be less efficient than native species (*Tilia cordata*) in lowering temperature in cities (Rahman et al., 2019), and it is suffering the negative consequences of climate change and urban air pollution (Wilkaniec et al., 2021). In contrast to the high abundance of *R. pseudoacacia*, *Ailanthus altissima* was only found in four UGSs in Paris. This is surprising given that *A. altissima* is a fast-growing N_2-fixing tree adapted to urban conditions (i.e., it tolerates well high temperatures, drought and poor soil conditions). This species is a widespread invasive species in Europe and an important component of many urban areas across Europe (e.g. Casella et al., 2013). Our results show that its within-city distribution may be restricted to other land cover types rather than to UGSs; for example, Paź-Dyderska et al. (2020) recorded the species in Poznan recently, but only in paved and ruderal areas, claiming that management practices limit their ecological success.

Woody community composition will determine the resilience and effectiveness of UGSs in maintaining urban biodiversity and providing ESs. Our results contribute to knowing the actual species composition in UGSs. This is especially important in the context of global change that will raise temperatures affecting urban ecosystems (e.g. increased climate stress, pathogen threats) and, consequently, their functions and processes that influence the health and well-being of urban residents.

4.2. *Woody species richness and UGS size*

The positive relationship among area and species richness in natural areas has been demonstrated for vascular plants and other taxa also within city boundaries (e.g. Cornelis and Hermy, 2004). According to our results, this correlation is weak and city-dependent suggesting that other local factors may play an important role on shaping urban biodiversity. Since both mean and median woody species richness in the centroid were four and the minimum species recorded in UGSs varied between three and four (with few exceptions), we can say that this is the minimum species richness threshold that the municipalities apply when designing and maintaining UGSs. By testing the relationship between size of UGS and species richness at two different scales (i.e., whole UGS and centroid) we confirmed that the positive relationship between species richness and UGS size did not happen at the centroid level (Supplementary Fig. S1) as expected in natural ecosystems.

Our results suggest rather similar management practices at European scale, especially in the mean height of planted trees (between 8 and 11 m height) and a preference for large trees (DBH>20 cm). This is especially true for southern and northern cities (i.e., Lisbon, Almada and Tartu) where larger and older trees (i.e. mean DBH= 31–36 cm) are maintained. Conserving old trees is important for ESs provision, natural heritage and cultural identity as well as for biodiversity (e.g. urban tree microhabitats, Großmann et al., 2020). Trees in Tartu displayed the biggest diameters (i.e., mean DBH = 36 cm). This could be due to the increase in temperatures during the last decades (especially in urban areas, better known as urban heat island effect) that, combined with management practices that counteract some growth limiting factors, has overstimulated tree growth (Chmielewski et a, 2001). Also, urban trees in high latitudes are known to grow faster than their counterparts in rural areas or in warmer cities (Smith et al., 2019). Higher rain frequency in high latitudes, together with the urban environment (e.g. high CO_2 concentrations), might further foster tree growth rates in northern cities compared to meridional ones (Pretzsch et al., 2017). In warmer latitudes, climate may be a greater stressor for urban vegetation and act as a filter for plant species distribution and growth that is lessened by management.

4.3. *Woody species density and UGS size*

As expected, species density steeply decreased along the size gradient in all the sampled cities (Fig. 3b, Table S3), meaning that the current management policies do not use the full potential of urban parks in increasing biodiversity. Since the minimum amount of woody species used when designing and managing urban green spaces is ~4 woody species, park managers plant more species when more space is available, but only up to a certain limit that depends on the city (e.g. the maximum species richness in a UGS was 11 in Poznan and 101 in Paris - even though the UGSs in this study were selected based on comparable size classes).

Using species density in urban ecosystems is so far an unexplored practice that can be used as an efficient indicator of how policy instruments have been incorporating biodiversity in UGSs. In our study we included all woody species, i.e., also shrubs when accounting for species richness and density, since they can contribute significantly to the overall diversity and also provide ESs (e.g. noise reduction) (Moudrý et al., 2021).

4.4. *Tree cover and aboveground biomass*

Several studies have focused on how tree canopy properties in urban areas benefit city dwellers (Gillner et al., 2015; Pataki et al., 2011) and increase species richness of other organisms inhabiting urban ecosystems (Moudrý et al., 2021). Mouratidis (2019) found that urban tree cover increased people's feeling of safety. One of the most studied ESs derived from urban trees is their capacity to cool the urban environment by means of evapotranspiration, canopy shadow and reflection of the solar radiation (Venter et al., 2020; Zardo et al., 2017). This cooling effect increases with tree species richness (Wang et al., 2021).

The positive correlation among UGS size and tree canopy cover in absolute terms (i.e., total extent of tree crowns) was not found when relative canopy cover (i.e., percentage of UGS covered by trees) was considered. We argue that analyzing the relative amount of canopy cover in UGSs (usually expressed in %) is misleading in case of smaller UGSs - only a few tree individuals are necessary to provide nearly 100% canopy cover in small UGSs. However it is not sufficient amount of canopy to provide habitat for diverse biota, as the other species are often specialized to certain evolutionary lineages, or woody species types (conifers vs. broadleaf trees) and more specific traits (e.g. ridged bark). In addition, animals often tend to be highly territorial, which means that the high canopy cover percentage in an UGS does not ensure diverse biota inhabiting these UGSs. Which is why we used absolute, and not relative amount of canopy cover in our analysis (Fig. 4). However, relative canopy cover (Table 3) indicated that park designers promote non-tree land cover types (e.g. open lawns, paved surfaces) when planning and designing UGSs. All the studied cities had at least some UGSs that were fully covered by tree canopy (>90% of UGS extent), with 50 of them covering more than 75% of the entire UGS. Percentage of tree canopy cover and vegetation structure have been proven to strongly and directly influence temperature in cities (Chen et al., 2020). Therefore, local planning strategies should consider both horizontal and vertical components of the woody layer when designing management instruments in order to create a better urban environment.

Although large areas are slightly more biodiverse than smaller ones (Fig. 3a), increasing the size of a UGS is most probably not feasible in an already densely urbanized landscape, like in European cities. However, the strong negative relationship between species density and UGS size implicates that the existing UGSs could harbor much more species per unit area than they currently do. Planting more woody plant species that are suitable for the urban environmental condition is a cost-effective way to fulfill the demand for ESs in urban environments. Future policy regarding urban green planning should shift the focus more on community and ecosystem level functioning of UGSs, and woody vegetation is the fundamental foundation for enhancing the functionality and persistence of urban ecosystems (Hirons et al., 2019).

The differences found among the general trends and correlations at city level indicate that other parameters not considered in the study could be influential. For instance, woody species richness displayed a positive relationship with canopy cover when considering all the UGSs together. However, at the city scale, this correlation was only significant in Antwerp. This and other city-specific effects can be overcome if key local factors are known (e.g. socio-economic preferences). Another possible hidden trend is that an underlying mechanism to explain the role of size in multiple vegetation parameters could rely on the influence of UGS management option, i.e., management options of the largest UGSs tend to be similar when compared to smaller sites. Moreover, the selection of the Urban Atlas as an homogeneous basis of LULC information for studied sites selection influences the type of green spaces considered in the study, as they consider different types of urban vegetated surfaces into 'Green urban areas' class. However, since this happens in all the selected cities in comparable proportions, it probably does not imply any bias in our results. Still, we highlight that creating a continental scale comparable cartography with higher thematic classification is necessary to provide more details that allow future studies to separate the 'Green urban areas' class into sub-classes differing on the management practices or type of use.

5. Conclusion

Urban green spaces are multifunctional elements of the urban matrix, providing several social, environmental and economic benefits. Woody vegetation constitutes the main component of UGSs, providing valuable ecosystem services for humans, but also food and shelter for other organisms. However, there is very little comparable ecological data about vegetation in UGSs. This topic is of great interest not only for ecological research but also for urban planners and urban landscape designers.

Our extensive field survey in 225 UGSs with different sizes in seven European cities showed at all levels of analysis that: 1) species richness of UGS was only weakly related with UGS size; while 2) the species density had a strong negative relationship with UGS size. Moreover, we provide a complete list of the most common species among the seven European cities. There seems to be a certain threshold of how much effort is put into management of urban green spaces in the context of woody diversity. Thus, there seems to be a so far unseized opportunity to increase species density in the largest parks by management change only. This could create more heterogeneity and thus improve conditions for both other organisms living in UGSs, but also enhance ecosystem services beneficial for humans.

The outcomes of this research will assist urban planners and policy makers through the current biodiversity in urban green spaces and their unused potential. This is especially useful in the frame of the EU Biodiversity Strategy to 2030 which calls on cities to develop Urban Greening Plans by the end of 2021, putting special attention on urban biodiversity. In addition, our findings can also be used in urban ecology research involving a variety of taxa and ecosystem services.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.ufug.2022.127650.

References

Aronson, M.F.J., La Sorte, F.A., Nilon, C.H., Katti, M., Goddard, M.A., Lepczyk, C.A., Winter, M., 2014. A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. Proc. Biol. Sci. 281 (1780), 20133330 https://doi.org/10.1098/rspb.2013.3330pmid:24523278.

Bar-On, Y.M., Phillips, R., Milo, R., 2018. The biomass distribution on Earth. Proc. Natl. Acad. Sci. U.S.A. 115 (25), 6506–6511. https://doi.org/10.1073/pnas.1711842115.

Baraldi, R., Chieco, C., Facini, N.O., Rapparini, F., Morrone, L., Rotondi, A., Carierò, G., 2019. An integrated study on air mitigation potential of urban vegetation: from a multi-trait approach to modeling. Urban For. Urban Green. 41, 127–138. https://doi.org/10.1016/j.ufug.2019.03.020.

Baruch, Z., Liddicoat, C., Cando-Dumancela, C., Laws, M., Morelli, H., Weinstein, P., Breed, M.F., 2020. Increased plant species richness associates with greater soil bacterial diversity in urban green spaces. Environ. Res., 110425 https://doi.org/10.1016/j.envres.2020.110425.

Beery, T., Stålhammar, S., Jönsson, K.I., Wamsler, C., Bramryd, T., Brink, E., Schubert, P., 2016. Perceptions of the ecosystem services concept: opportunities and challenges in the Swedish municipal context. Ecosyst. Serv. 17, 123–130. https://doi.org/10.1016/j.ecoser.2015.12.002.

Beninde, J., Veith, M., Hochkirch, A., 2015. Biodiversity in cities needs space: a meta-analysis of factors determining intra-urban biodiversity variation. Ecol. Lett. 18 (6), 581–592. https://doi.org/10.1111/ele.12427.

Bjerke, T., Østdahl, T., Thrane, C., Strumse, E., 2006. Vegetation density of urban parks and perceived appropriateness for recreation. Urban For. Urban Green. 5 (1), 35–44. https://doi.org/10.1016/j.ufug.2006.01.006.

Casella, F., Burro, M., 2013. Ailanthus altissima (tree of heaven): spread and harmfulness in a case-study urban area. Arboric. J. 35 (3), 172–181. https://doi.org/10.1080/03071375.2013.852352.

Capotorti, G., Alós Ortí, M., Copiz, R., Fusaro, L., Mollo, B., Salvatori, E., Zavattero, L., 2019. Biodiversity and ecosystem services in urban green infrastructure planning: A case study from the metropolitan area of Rome (Italy). Urban For. Urban Green. 37, 87–96. https://doi.org/10.1016/j.ufug.2017.12.014.

Chen, J., Jin, S., Du, P., 2020. Roles of horizontal and vertical tree canopy structure in mitigating daytime and nighttime urban heat island effects. Int. J. Appl. Earth Obs. Geoinf. 89, 102060 https://doi.org/10.1016/j.jag.2020.102060.

Chmielewski, F.-M., Rötzer, T., 2001. Response of tree phenology to climate change across Europe. Agric. For. Meteorol. 108 (2), 101–112. https://doi.org/10.1016/S0168-1923(01)00233-7.

Cornelis, J., Hermy, M., 2004. Biodiversity relationships in urban and suburban parks in Flanders. Landsc. Urban Plan. 69 (4), 385–401. https://doi.org/10.1016/j.landurbplan.2003.10.038.

Crosby, M.K., McConnell, T.E., Holderieath, J.J., Kjartasson, B.Þ, Traustason, B., Jónsson, ÞH., Oddsdóttir, E.S., 2021. Urban street tree characteristics and benefits in city centre, Reykjavik, Iceland. Trees For. People 4, 100066. https://doi.org/10.1016/j.tfp.2021.100066.

Ellis, E.C., Ramankutty, N., 2008. Putting people in the map: anthropogenic biomes of the world. Front. Ecol. Environ. 6 (8), 439–447. https://doi.org/10.1890/070062.

Urban Atlas (2012). Available online: ⟨https://land.copernicus.eu/local/urban-atlas/urban-atlas-2012?tab=download⟩.

EC, (European Commission). (2020). EU Biodiversity Strategy for 2030: bringing nature back into our lives. COM(2020) 380 final. ⟨https://eur-lex.europa.eu/resource.html?uri=cellar:a3c806a6–9ab3–11ea-9d2d-01aa75ed71a1.0001.02/DOC_1&format=PDF⟩.

Gillner, S., Vogt, J., Tharang, A., Dettmann, S., Roloff, A., 2015. Role of street trees in mitigating effects of heat and drought at highly sealed urban sites. Landsc. Urban Plan. 143 (November 2015), 33–42.

Godefroid, S., Koedam, N., 2007. Urban plant species patterns are highly driven by density and function of built-up areas. Landsc. Ecol. 22 (1227–1239), 2007. https://doi.org/10.1007/s10980-007-9102-x.

Großmann, J., Pyttel, P., Bauhus, J., Lecigne, B., Messier, C., 2020. The benefits of tree wounds: microhabitat development in urban trees as affected by intensive tree maintenance. Urban For. Urban Green. 55, 126817 https://doi.org/10.1016/j.ufug.2020.126817.

Grote, R., Samson, R., Alonso, R., Amorim, J.H., Cariñanos, P., Churkina, G., Calfapietra, C., 2016. Functional traits of urban trees: air pollution mitigation potential. Front. Ecol. Environ. 14 (10), 543–550. https://doi.org/10.1002/fee.1426.

Grove, J.M., Pickett, S.T.A., Whitmer, A., Cadenasso, M.L., 2013. Building an urban LTSER: the case of the Baltimore ecosystem study and the D.C./B.C. ULTRA-Ex Project. In: Singh, S.J., Haberl, H., Chertow, M., Mirtl, M., Schmid, M. (Eds.), Long Term Socio-ecological Research. Springer. https://doi.org/10.1007/978-94-007-1177-8.

Hirons, A., Sjöman, H., 2019. Tree species selection for green infrastructure - a guide for specifiers. Trees and Design Action Group Trust.

Kohout, M., Kopp, J., 2020. Green space ideas and practices in European cities. J. Environ. Plan. Manag. 63 (14), 1–20. https://doi.org/10.1080/09640568.2020.1716698.

Kowarik, I., 2011. Novel urban ecosystems, biodiversity, and conservation. Environ. Pollut. 159 (8–9), 1974–1983. https://doi.org/10.1016/j.envpol.2011.02.022.

Kowarik, I., von der Lippe, M., Cierjacks, A., 2013. Prevalence of alien versus native species of woody plants in Berlin differs between habitats and at different scales. Preslia 85, 113–132.

Kühn, I., Brandl, R., Klotz, S., 2004. The flora of German cities is naturally species rich. Evolut. Ecol. Res. 6, 749–764.

Kühn, I., Klotz, S., 2006. Urbanization and homogenization – comparing the floras of urban and rural areas in Germany. Biol. Conserv. 127 (3), 292–300. https://doi.org/10.1016/j.biocon.2005.06.033.

Locosselli, G.M., de Camargo, E.P., Moreira, T.C.L., Todesco, E., de Fátima Andrade, M., de André, C.D.S., Buckeridge, M.S., 2019. The role of air pollution and climate on the growth of urban trees. Science Total Environ. 666, 652–661. https://doi.org/10.1016/j.scitotenv.2019.02.291.

McKinney, M.L., 2002. Urbanization, biodiversity, and conservation. BioScience 52, 883–890. https://doi.org/10.1641/0006-3568(2002)052[0883:UBAC]2.0.CO;2.

McKinney, M.L., 2008. Effects of urbanization on species richness: a review of plants and animals. Urban Ecosyst. 11, 161–176. https://doi.org/10.1007/s11252-007-0045-4.

Moudrý, V., Moudrá, L., Barták, V., Bejček, V., Gdulová, K., Hendrychová, M., Šálek, M., 2021. The role of the vegetation structure, primary productivity and senescence derived from airborne LiDAR and hyperspectral data for birds diversity and rarity on a restored site. Landscape Urban Plan. 210, 104064 https://doi.org/10.1016/j.landurbplan.2021.104064.

Mouratidis, K., 2019. The impact of urban tree cover on perceived safety. Urban For. Urban Green. 44, 126434 https://doi.org/10.1016/j.ufug.2019.126434.

Nielsen, A.B., van den Bosch, M., Maruthaveeran, S., van den Bosch, C.K., 2014. Species richness in urban parks and its drivers: A review of empirical evidence. Urban Ecosyst. 17, 305–327. https://doi.org/10.1007/s11252-013-0316-1.

Pataki, D.E., McCarthy, H.R., Litvak, E., Pincetl, S., 2011. Transpiration of urban forests in the Los Angeles metropolitan area. Ecol. Appl. 21 (3), 661–677. https://doi.org/10.1890/09-1717.1.

Pauleit, S., Jones, N., García-Martín, G., García-Valdecantos, J.L., Marie Rivière, L., Vidal-Beaudet, Randurp, T.B., 2002. Tree establishment practice in towns and cities – results from a European survey. Urban For. Urban Green. 1, 83–96. https://doi.org/10.1078/1618-8667-00009.

Paź-Dyderska, S., Ladach-Zajdler, A., Jagodziński, A.M., Dyderski, M.K., 2020. Landscape and parental tree availability drive spread of Ailanthus altissima in the urban ecosystem of Poznań, Poland. Urban For. Urban Green. 56, 126868 https://doi.org/10.1016/j.ufug.2020.126868.

Pinho, P., Casanelles-Abella, J., Luz, A.C., Kubicka, A.M., Branquinho, C., Laanisto, L., Neuenkamp, L., Alós Ortí, M., Obrist, M.K., Deguines, N., Tryjanowski, P., Samson, R., Niinemets, L., Moretti, M., 2021. Research agenda on biodiversity and ecosystem functions and services in European cities. Basic Appl. Ecol. 53, 124–133. https://doi.org/10.1016/j.baae.2021.02.014.

Pretzsch, H., Biber, P., Uhl, E., Dahlhausen, J., Schütze, G., Perkins, D., Lefer, B., 2017. Climate change accelerates growth of urban trees in metropolises worldwide. Sci. Rep. 7, 15403. https://doi.org/10.1038/s41598-017-14831-w.

Puchałka, R., Dyderski, M.K., Vítková, M., Sádlo, J., Klisz, M., Netsvetov, M., Jagodziński, A.M., 2020. Black locust (*Robinia pseudoacacia* L.) range contraction and expansion in Europe under changing climate. Glob. Change Biol. 27 (8), 1587–1600. https://doi.org/10.1111/gcb.15486.

Pyšek, P., 1998. Alien and native species in central European urban floras: a quantitative comparison. J. Biogeogr. 25 (1), 155–163. https://doi.org/10.1046/j.1365-2699.1998.251177.x.

R Core Team, 2019. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria (URL). 〈https://www.R-project.org/〉.

Rahman, M.A., Moser, A., Rötzer, T., Pauleit, S., 2019. Comparing the transpirational and shading effects of two contrasting urban tree species. Urban Ecosyst. 22, 683–697. https://doi.org/10.1007/s11252-019-00853-x.

Säumel, I., Kowarik, I., Butenschön, S., 2010. Green traces from past to future: the interplay of culture and ecological processes in European historical parks. Acta Hortic. 881, 933–938. https://doi.org/10.17660/ActaHortic.2010.881.156.

Salinitro, M., Alessandrini, A., Zappi, A., Melucci, D., Tassoni, A., 2018. Floristic diversity in different urban ecological niches of a southern European city. Sci. Rep. 8, 15110. https://doi.org/10.1038/s41598-018-33346-6.

Scholz, M., Uzomah, V.C., Al-Faraj, F.A.M., 2016. Potential tree species for use in urban areas in temperate and oceanic climates. Heliyon 2 (9), e00154. https://doi.org/10.1016/j.heliyon.2016.e00154.

Shanahan, D.F., Miller, C., Possingham, H.P., Fuller, R.A., 2011. The influence of patch area and connectivity on avian communities in urban revegetation. Biol. Conserv. 144, 722–729. https://doi.org/10.1016/j.biocon.2010.10.014.

Shwartz, A., Muratet, A., Simon, L., Julliard, R., 2013. Local and management variables outweigh landscape effects in enhancing the diversity of different taxa in a big metropolis. Biol. Conserv. 157, 285–292. https://doi.org/10.1016/j.biocon.2012.09.009.

Smith, I.A., Dearborn, V.K., Hutyra, L.R., 2019. Live fast, die young: accelerated growth, mortality, and turnover in street trees. PLoS One 14 (5), e0215846. https://doi.org/10.1371/journal.pone.0215846.

Talal, M.L., Santelmann, M.V., 2019. Plant Community composition and biodiversity patterns in urban parks of Portland, Oregon. Front. Ecol. Evol. 7, 201. https://doi.org/10.3389/fevo.2019.00201.

Threlfall, C.G., Ossola, A., Hahs, A.K., Williams, N.S.G., Wilson, L., Livesley, S.J., 2016. Variation in vegetation structure and composition across urban green space types. Front. Ecol. Evol. 4, 66. https://doi.org/10.3389/fevo.2016.00066.

Tsiotsiou, V., Christodoulakis, D., 2010. Woody plants in urban biotopes: studies in Patras (Greece). Fresenius Environ. Bull. 19 (12a), 2958–2965.

Venter, Z.S., Krog, N.H., Barton, D.N., 2020. Linking green infrastructure to urban heat and human health risk mitigation in Oslo, Norway. Sci. Total Environ. 709, 136193 https://doi.org/10.1016/j.scitotenv.2019.136193.

Wang, X., Dallimer, M., Scott, C.E., Shi, W., Gao, J., 2021. Tree species richness and diversity predicts the magnitude of urban heat island mitigation effects of greenspaces. Sci. Total Environ. 770, 145211 https://doi.org/10.1016/j.scitotenv.2021.145211.

Wilkaniec, A., Borowiak-Sobkowiak, B., Irzykowska, L., Breś, W., Świerk, D., Pardela, Ł., Wielgus, K., 2021. Biotic and abiotic factors causing the collapse of Robinia pseudoacacia L. veteran trees in urban environments. PLoS One 16 (1), e0245398.

Yang, J., La Sorte, F., Pyšek, P., Yan, P., Nowak, D., McBride, J., 2015. The compositional similarity of urban forests among the world's cities is scale dependent. Glob. Ecol. Biogeogr. 24 (12), 1413–1423. https://doi.org/10.1111/geb.12376.

Zardo, L., Geneletti, D., Pérez-Soba, M., Van Eupen, M., 2017. Estimating the cooling capacity of green infrastructures to support urban planning. Ecosyst. Serv. 225–235. https://doi.org/10.1016/j.ecoser.2017.06.016.

Supplementary material

Table S1. References used to identify the origin of the woody species found in the 225 UGSs, to carry out the pertinent statistical analysis and to calculate the tree above-ground biomass.

Reference source	Purpose
[dataset]Euro+Med: Euro+Med PlantBase - the information resource for Euro-Mediterranean plant diversity. (2006-). Published on the Internet http://ww2.bgbm.org/EuroPlusMed/ [accessed February, 3-5 2021].	Species provenience
Tutin, T.G., Heywood, V.H., Burges, N.A., Moore, D.M., Valentine, D.H., Walters, S.M. & Webb, D.A. (1964–1980). Flora Europaea. Cambridge University Press. 5 vols., 1. (1964), XXXII + 464 pp., 2. (1968), XXVII + 455 pp., 3. (1972), XXIX + 370 pp., 4. (1976), XXIX + 505 pp. and 5. (1980), XXXVI + 452 pp.	Species provenience
Harrell Jr, F.E. (2020). Hmisc: Harrell Miscellaneous. R package version 4.4-1. https://CRAN.R-project.org/package=Hmisc	Spearman test
Wei, T., & Simko, V. (2017). R package "corrplot": Visualization of a Correlation Matrix (Version 0.84). Available from https://github.com/taiyun/corrplot	Spearman test visualization (correlograms)
Pinheiro, J., Bates, D., DebRoy, S., & Sarkar, D. (2021). nlme: Linear and Nonlinear Mixed Effects Models_. R package version 3.1-152. https://CRAN.R-project.org/package=nlme>.	Linear mixed effect models
Wickham, H. (2016). ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag	Linear models visualization
Kassambara, A., & Mundt, F. (2020). factoextra: Extract and Visualize the Results of Multivariate Data Analyses. R package version 1.0.7. https://CRAN.R-project.org/package=factoextra	Principal Component Analysis
Ogle, D.H., Wheeler, P., & Dinno, A. (2021). FSA: Fisheries Stock Analysis. R package version 0.8.32. https://github.com/droglenc/FSA.	Post-hoc Dunn test for multiple comparisons of groups
Forrester, D.I., Tachauer, I.H.H., Annigohoefer, P., Barbeito, I., Pretzsch, H., Ruiz-Peinado, R., Stark, H., Vacchiano, G., Zlatanov, T., Chakraborty, T., Saha, S., & Sileshi, G.W. (2017). Generalized biomass and leaf area allometric equations for European tree species incorporating stand structure, tree age and climate. *Forest Ecology and Management, 369*, 160-175. http://dx.doi.org/10.1016/j.foreco.2017.04.011	Aboveground biomass calculations
Tabacchi, G., Di Cosmo, L., Gasparini, L., & Morelli, S. (2011). *Stima del volume e della fitomassa delle principali specie forestali italiane. Equazioni di previsione, tavole del volume e tavole della fitomassa arborea epigea (Estimation of the volumen and phytomass of main Italian forest species. Equations and tables of volume and epigeal phytomass of trees)*. Consiglio per la Ricerca e la sperimentazione in Agricoltura, Unità di Ricerca per il Monitoraggio e la Pianificazione Forestale, 412 pp.	Aboveground biomass calculations
Zianis, D., Muukkonen, P., Mäkipää, R., & Mencuccini, M. (2005). *Biomass and stem volume equations for tree species in Europe*. Silva Fennica Monographs 4, Finnish Society of Forest Science/ Finnish Forest Research Institute, 63 pp.	Aboveground biomass calculations

Table S2. Presence/absence of woody species in UGSs from each of the studied cities. Presences are displayed as ‘x’, absences are left in blank. Green cells represent native species in a given city, while red cells represent non-native species occurrences. Non-colored cells correspond to species where the origin status could not be unambiguously attributed.

Family	Species	Almada	Antwerp	Lisbon	Paris	Poznan	Tartu	Zurich
Adoxaceae	*Sambucus nigra*		🟩 x		🟩 x	🟩 x		🟩 x
	Sambucus racemosa						🟥 x	🟩 x
	Sambucus sp.					x		x
	Viburnum lantana				🟩 x		🟥 x	🟩 x
	Viburnum opulus		🟩 x		🟩 x		🟩 x	🟩 x
	Viburnum rhytidophyllum				🟥 x			
	Viburnum tinus	🟩 x		🟩 x	🟩 x			🟥 x
	Viburnum x pragense				🟥 x			
	Viburnum sp.				x	x		x
Altingiaceae	*Liquidambar orientalis*							🟥 x
	Liquidambar styraciflua		🟥 x		🟥 x			
Anacardiaceae	*Cotinus coggygria*				🟩 x		🟥 x	
	Pistacia lentiscus	🟩 x		🟩 x				

	Pistacia terebinthus			🟩 x				
	Rhus typhina				🟥 x	🟥 x		
	Rhus sp.					x		
Annonaceae	*Asimina triloba*							🟥 x
Apocynaceae	*Nerium oleander*	🟩 x		🟩 x				
Aquifoliaceae	*Ilex aquifolium*		🟩 x		🟩 x			
	Ilex sp.				x			x
Araliaceae	*Aralia elata*							🟥 x
	Eleutherococcus sessiliflorus						🟥 x	
Araucariaceae	*Araucaria* sp.	🟥 x						
Arecaceae	*Brahea* sp.			🟥 x				
	Chamaerops humilis			🟩 x				
	Phoenix canariensis			🟥 x				
	Phoenix dactylifera			🟥 x				
	Trachycarpus fortunei			🟥 x	🟥 x			
Asparagaceae	*Cordyline australis*			🟥 x				

	Dracaena sp.				🟥 x			
	Yucca elephantipes			🟥 x				
Asteraceae	*Albizia julibrissin*			🟥 x	🟥 x			
Berberidaceae	*Berberis julianae*		🟥 x		🟥 x			
	Berberis thunbergii	🟥 x						
	Berberis vulgaris	🟩 x			🟩 x		🟩 x	
	Berberis sp.	x			x			x
	Berberis aquifolium				🟥 x			
	Nandina domestica				🟥 x			
Betulaceae	*Alnus cordata*				🟥 x			
	Alnus glutinosa		🟩 x		🟩 x		🟩 x	🟩 x
	Alnus incana						🟩 x	🟩 x
	Alnus sp.					x		x
	Betula maximowicziana							🟥 x
	Betula papyrifera							🟥 x
	Betula pendula		🟩 x	🟩 x	🟩 x		🟩 x	🟩 x

3

	Betula pubescens				🟩 x		🟩 x	🟩 x
	Betula sp.				x	x	x	x
	Carpinus betulus		🟩 x	🟥 x	🟩 x		🟥 x	🟩 x
	Corylus americana						🟥 x	
	Corylus avellana		🟩 x		🟩 x	🟩 x	🟩 x	🟩 x
	Corylus colurna				🟥 x		🟥 x	
	Corylus cornuta						🟥 x	
	Ostrya carpinifolia				🟩 x			🟩 x
Bignoniaceae	*Catalpa bignonioides*				🟥 x	🟥 x		
	Jacaranda mimosifolia	🟥 x		🟥 x				
Buxaceae	*Buxus sempervirens*		🟩 x	🟩 x	🟩 x			
Calycanthaceae	*Calycanthus floridus*							🟥 x
Cannabaceae	*Celtis australis*	🟩 x		🟩 x	🟩 x			
	Celtis occidentalis							🟥 x
Caprifoliaceae	*Kolkwitzia amabilis*				🟥 x			
	Kolkwitzia sp.				x			

4

	Lonicera caerulea						🟩 x	
	Lonicera demissa						🟥 x	
	Lonicera fragrantissima							🟥 x
	Lonicera nitida				🟥 x			
	Lonicera periclymenum				🟩 x			
	Lonicera tatarica				🟥 x			
	Lonicera xylosteum				🟩 x		🟩 x	🟩 x
	Lonicera sp.				x			
	Symphoricarpos albus		🟥 x		🟥 x		🟥 x	🟥 x
	Symphoricarpos sp.					x		
	Weigela praecox							🟥 x
	Weigela sp.				🟥 x			
Casuarinaceae	*Casuarina cunninghamiana*			🟥 x				
Celastraceae	*Euonymus europaeus*	🟩 x	🟩 x	🟩 x			🟩 x	🟩 x
	Euonymus japonicus				🟥 x			

	Euonymus latifolius		x					
	Euonymus nanus						x	
	Euonymus sp.				x			
Cephalotaxaceae	*Cephalotaxus fortunei*				x			
	Cephalotaxus harringtonia							x
Cerambycidae	*Howea forsteriana*			x				
Cercidiphyllaceae	*Cercidiphyllum japonicum*				x			
Cistaceae	*Cistus ladanifer*	x						
	Cistus salviifolius	x						
	Cistus sp.				x			
Cornaceae	*Cornus florida*							x
	Cornus kousa				x			
	Cornus mas		x		x			x
	Cornus sanguinea		x		x		x	
	Cornus suecica						x	
	Cornus sp.				x	x		x

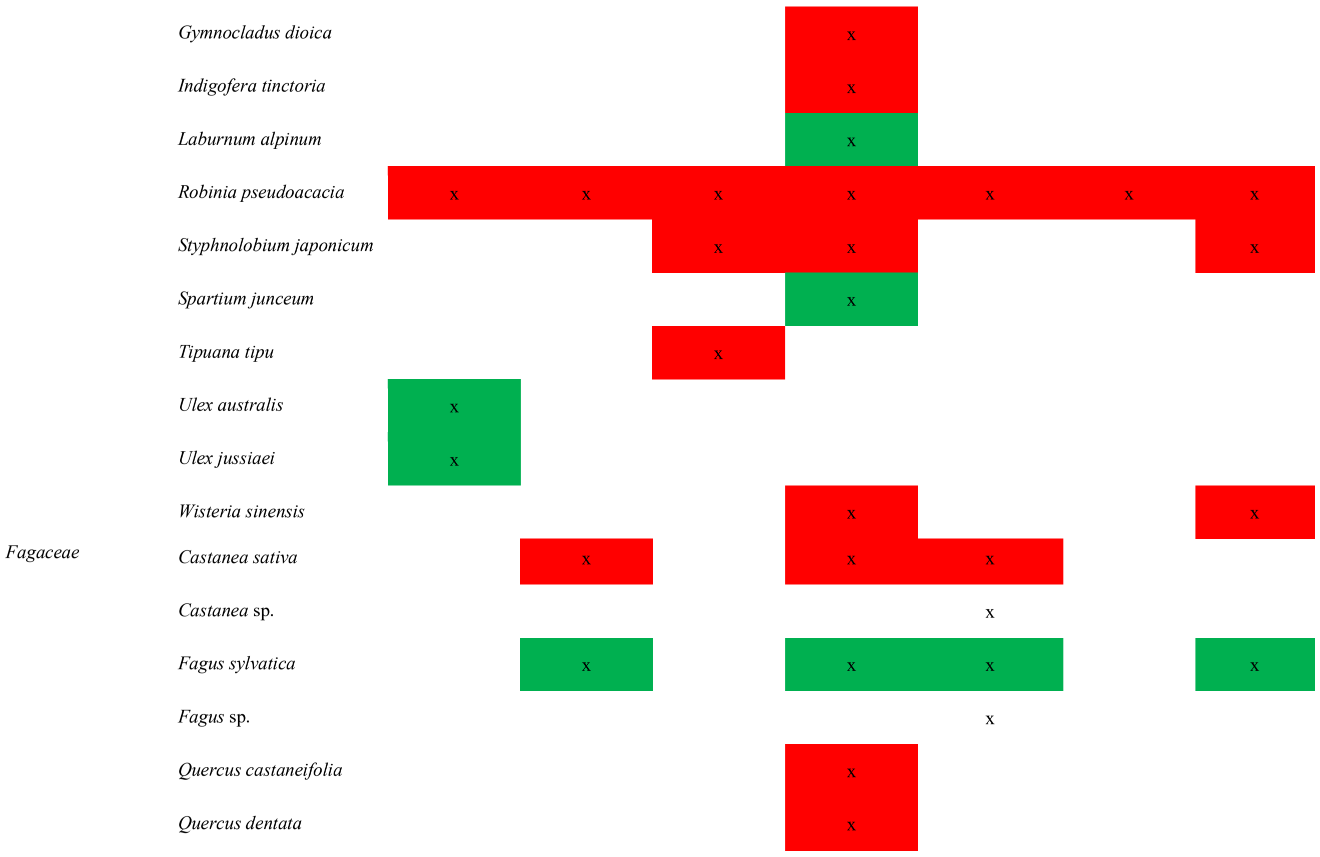
6

Cupressaceae	*Calocedrus decurrens*				🟥 x			
	Chamaecyparis lawsoniana		🟥 x					
	Chamaecyparis obtusa							🟥 x
	Chamaecyparis pisifera						🟥 x	
	Chamaecyparis sp.				🟥 x			x
	Cryptomeria japonica				🟥 x			
	Cunninghamia lanceolata							🟥 x
	Cupressus lusitanica			🟥 x				
	Cupressus macrocarpa			🟥 x				
	Cupressus nootkatensis							🟥 x
	Cupressus sempervirens	🟥 x		🟥 x	🟥 x			
	Cupressus sp.				x	x		
	Juniperus communis	🟩 x					🟩 x	
	Juniperus horizontalis			🟥 x				
	Juniperus sabina						🟥 x	🟩 x
	Juniperus sp.				x			x

7

	Metasequoia glyptostroboides		🟥 x		🟥 x			
	Microbiota decussata				🟥 x			
	Sequoia sempervirens				🟥 x			
	Sequoiadendron giganteum				🟥 x			
	Taxodium distichum				🟥 x			🟥 x
	Thuja occidentalis	🟥 x	🟥 x				🟥 x	🟥 x
	Thuja plicata							🟥 x
	Thuja sp.			x		x	x	x
Elaeagnaceae	*Elaeagnus angustifolia*	🟥 x		🟥 x	🟥 x			
	Elaeagnus commutata				🟥 x			
	Elaeagnus pungens				🟥 x			
	Elaeagnus sp.				x			
	Hippophae rhamnoides				🟩 x	🟩 x		
	Hippophae sp.					x		
Ericaceae	*Arbutus* sp.				x			

	Arbutus unedo	🟩 x		🟩 x	🟩 x			
	Calluna vulgaris		🟩 x					
	Rhododendron sp.		x	x	x			
Euphorbiaceae	*Euphorbia dendroides*							🟥 x
	Euphorbia sp.	x						
Fabaceae	*Acacia melanoxylon*			🟥 x				
	Acacia retinoides	🟥 x						
	Acacia saligna	🟥 x						
	Acacia sp.	x						
	Caragana arborescens				🟥 x		🟥 x	
	Caragana frutex						🟥 x	
	Ceratonia siliqua	🟥 x		🟥 x				
	Cercis siliquastrum	🟥 x		🟥 x	🟩 x			
	Coronilla glauca			🟩 x				
	Gleditsia triacanthos			🟥 x	🟥 x			



	Gymnocladus dioica				🟥 x			
	Indigofera tinctoria				🟥 x			
	Laburnum alpinum				🟩 x			
	Robinia pseudoacacia	🟥 x	🟥 x	🟥 x	🟥 x	🟥 x	🟥 x	🟥 x
	Styphnolobium japonicum			🟥 x	🟥 x			🟥 x
	Spartium junceum				🟩 x			
	Tipuana tipu			🟥 x				
	Ulex australis	🟩 x						
	Ulex jussiaei	🟩 x						
	Wisteria sinensis				🟥 x			🟥 x
Fagaceae	*Castanea sativa*		🟥 x		🟥 x	🟥 x		
	Castanea sp.					x		
	Fagus sylvatica		🟩 x		🟩 x	🟩 x		🟩 x
	Fagus sp.					x		
	Quercus castaneifolia				🟥 x			
	Quercus dentata				🟥 x			

10

	Quercus faginea			🟩 x				
	Quercus ilex				🟩 x			🟩 x
	Quercus palustris		🟥 x		🟥 x			
	Quercus petraea			🟥 x		🟩 x		
	Quercus phillyraeoides							🟥 x
	Quercus robur	🟩 x	🟩 x	🟩 x	🟩 x		🟩 x	🟩 x
	Quercus rotundifolia			🟩 x				
	Quercus rubra		🟥 x		🟥 x	🟥 x	🟥 x	🟥 x
	Quercus suber	🟩 x		🟩 x				
	Quercus sp.				x	x	x	x
Ficidae	*Ficus benjamina*			🟥 x				
	Ficus carica	🟩 x			🟥 x			
Garryaceae	*Aucuba japonica*				🟥 x			
Ginkgoaceae	*Ginkgo biloba*	🟥 x	🟥 x	🟥 x	🟥 x			🟥 x
Grossulariaceae	*Ribes alpinum*						🟩 x	
	Ribes nigrum				🟩 x		🟩 x	

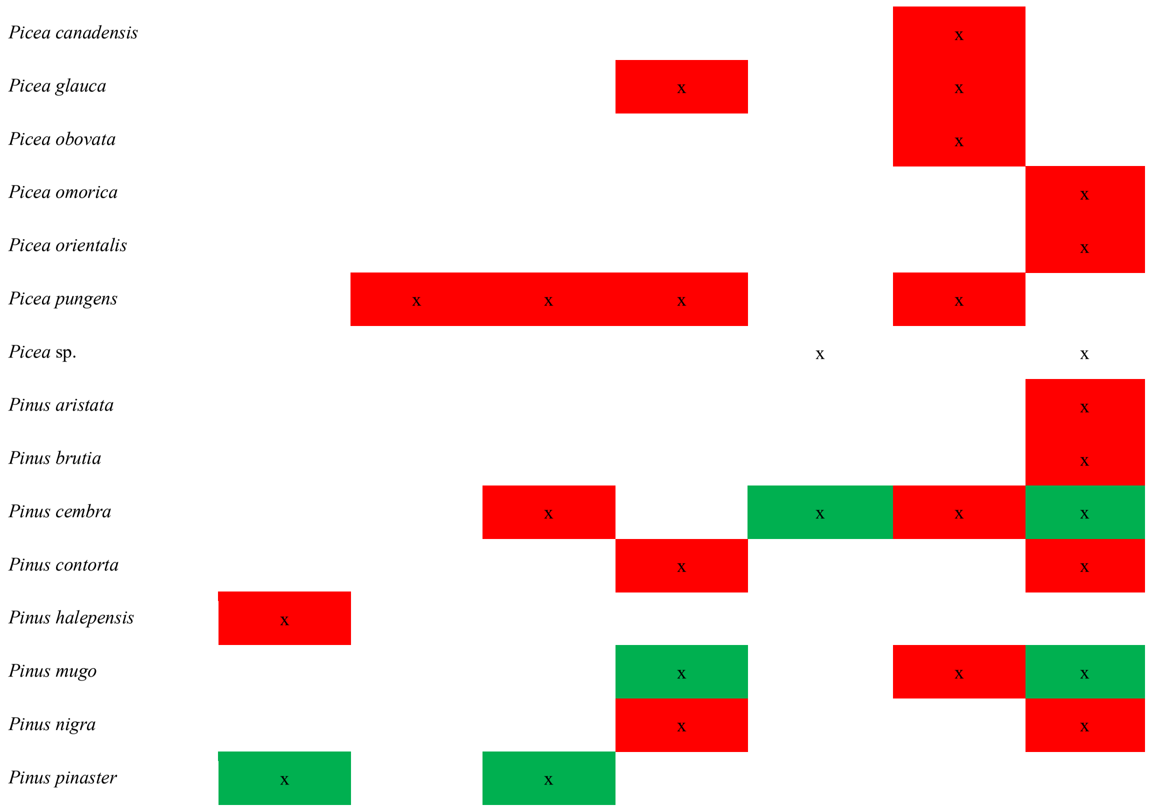
	Ribes rubrum					🟩 x	
	Ribes sp.						x
Hamamelidaceae	*Parrotia persica*			🟥 x			
Hydrangeaceae	*Deutzia* sp.			🟥 x			
	Forsythia sp.			x			
	Forsythia x intermedia	🟥 x					
	Philadelphus coronarius	🟥 x		🟥 x	🟥 x	🟥 x	🟥 x
	Philadelphus pubescens					🟥 x	
	Philadelphus sp.			x			
Hypericaceae	*Hypericum calycinum*			🟥 x			
	Hypericum sp.			x			
Juglandaceae	*Carya illinoinensis*			🟥 x			
	Juglans cinerea					🟥 x	
	Juglans mandshurica					🟥 x	🟥 x
	Juglans nigra			🟥 x			
	Juglans regia	🟥 x		🟥 x			

	Juglans sp.					x		x
	Pterocarya fraxinifolia				🟥 x			
Lamiaceae	*Lavandula stoechas*	🟩 x						
	Rosmarinus officinalis			🟩 x				
	Vitex agnus-castus				🟩 x			
Lauraceae	*Laurus nobilis*							🟥 x
Lythraceae	*Punica granatum*	🟥 x		🟥 x	🟥 x			
Magnoliaceae	*Liriodendron tulipifera*				🟥 x			
	Magnolia grandiflora			🟥 x	🟥 x			🟥 x
	Magnolia sp.			x	x			x
	Magnolia stellata							🟥 x
Malvaceae	*Brachychiton populneus*	🟥 x		🟥 x				
	Brachychiton sp.	🟥 x						
	Hibiscus syriacus	🟥 x						
	Tilia cordata		🟩 x		🟩 x		🟩 x	🟩 x
	Tilia platyphyllos		🟩 x		🟩 x		🟥 x	🟩 x

	Tilia tomentosa	🟥 x	🟥 x	🟥 x	🟥 x		🟥 x	🟥 x
	Tilia x europaea				🟩 x		🟥 x	
	Tilia sp.			x		x		x
Meliaceae	*Cedrus atlantica*		🟥 x		🟥 x			
	Cedrus deodara				🟥 x			
	Cedrus libani				🟥 x			
	Cedrus sp.				x			
	Melia azedarach				🟥 x			
Moraceae	*Broussonetia papyrifera*				🟥 x			
	Morus nigra			🟥 x	🟥 x			
Musaceae	*Musa balbisiana*			🟥 x				
Myrtaceae	*Eucalyptus* sp.	🟥 x		🟥 x				
	Myrtus communis	🟩 x						
Nyssaceae	*Nyssa sylvatica*				🟥 x			
Oleaceae	*Fraxinus angustifolia*	🟩 x		🟩 x	🟩 x			
	Fraxinus excelsior		🟩 x	🟥 x	🟩 x	🟩 x	🟩 x	🟩 x

	Fraxinus ornus				🟥 x			
	Fraxinus sp.			x		x		x
	Ligustrum japonicum	🟥 x						
	Ligustrum lucidum			🟥 x	🟥 x			
	Ligustrum obtusifolium							🟥 x
	Ligustrum vulgare	🟩 x	🟩 x		🟩 x			
	Ligustrum sp.	x		x		x		x
	Olea europaea	🟩 x		🟩 x	🟩 x			
	Olea maroccana			🟥 x				
	Phillyrea angustifolia	🟩 x		🟩 x				
	Phillyrea latifolia			🟩 x				🟥 x
	Syringa josikaea						🟥 x	
	Syringa reticulata						🟥 x	
	Syringa vulgaris				🟥 x	🟥 x	🟥 x	🟥 x
	Syringa sp.			x	x		x	
Paulowniaceae	*Paulownia tomentosa*				🟥 x			

Pentaphylacaceae	*Camellia japonica*		🟥 x			
	Camellia sp.		🟥 x			
Pinaceae	*Abies alba*				🟥 x	
	Abies balsamifera				🟥 x	
	Abies concolor				🟥 x	
	Abies pinsapo					🟥 x
	Abies sp.		x			x
	Larix decidua	🟥 x			🟥 x	🟩 x
	Larix gmelinii				🟥 x	
	Larix kaempferi					🟥 x
	Larix laricina					🟥 x
	Larix marschlinsii				🟥 x	
	Larix sibirica				🟥 x	
	Larix sp.	x		x	x	x
	Picea abies		🟩 x		🟩 x	🟩 x



Picea canadensis						🟥 x	
Picea glauca				🟥 x		🟥 x	
Picea obovata						🟥 x	
Picea omorica							🟥 x
Picea orientalis							🟥 x
Picea pungens		🟥 x	🟥 x	🟥 x		🟥 x	
Picea sp.					x		x
Pinus aristata							🟥 x
Pinus brutia							🟥 x
Pinus cembra			🟥 x		🟩 x	🟥 x	🟩 x
Pinus contorta				🟥 x			🟥 x
Pinus halepensis	🟥 x						
Pinus mugo				🟩 x		🟥 x	🟩 x
Pinus nigra				🟥 x			🟥 x
Pinus pinaster	🟩 x		🟩 x				

	Pinus pinea	🟩 x		🟩 x				
	Pinus sibirica						🟥 x	
	Pinus sylvestris		🟥 x		🟩 x		🟩 x	🟩 x
	Pinus wallichiana				🟥 x			
	Pinus sp.	x		x	x	x		x
	Pseudotsuga menziesii				🟥 x			
	Tsuga canadensis							🟥 x
Pittosporaceae	*Pittosporum tobira*	🟥 x		🟥 x	🟥 x			
	Pittosporum undulatum			🟥 x				
	Pittosporum sp.				x			
Plantaginaceae	*Veronica salicifolia*				🟥 x			
Platanaceae	*Platanus orientalis*				🟥 x			
	Platanus x hispanica	🟥 x	🟥 x	🟥 x	🟥 x			
	Platanus sp.					x		
Poaceae	*Bambusa* sp.			x				
Polyporaceae	*Davidia involucrata*							🟥 x

Proteaceae	*Grevillea robusta*	🟥 x		🟥 x				
Rhamnaceae	*Ceanothus* sp.				🟥 x			
	Ceanothus thyrsiflorus				🟥 x			
	Frangula alnus		🟩 x				🟩 x	
	Rhamnus alaternus			🟩 x				
	Rhamnus cathartica		🟩 x		🟩 x		🟩 x	
Rosaceae	*Amelanchier lamarckii*		🟥 x					
	Amelanchier sp.				x			x
	Amelanchier spicata						🟥 x	
	Aronia melanocarpa						🟥 x	🟥 x
	Chaenomeles japonica						🟥 x	
	Chaenomeles speciosa							🟥 x
	Cotoneaster horizontalis				🟥 x			
	Cotoneaster lacteus				🟥 x			
	Cotoneaster lucidus						🟥 x	🟥 x
	Cotoneaster sp.				x			

Crataegus laevigata		🟩 x					
Crataegus monogyna		🟩 x	🟩 x				
Crataegus pedicellata							🟥 x
Crataegus rhipidophylla						🟩 x	
Crataegus submollis						🟥 x	
Crataegus sp.			x	x	x	x	x
Eriobotrya japonica	🟥 x			🟥 x			
Eucalyptus camaldulensis	🟥 x						
Kerria japonica				🟥 x			
Malus domestica			🟥 x	🟥 x	🟥 x	🟥 x	🟥 x
Malus sylvestris		🟩 x				🟩 x	
Malus sp.				x			
Mespilus germanica				🟥 x			
Physocarpus opulifolius				🟥 x		🟥 x	🟥 x
Physocarpus sp.							x

20

Potentilla fruticosa				🟩 x		🟩 x	🟥 x
Prunus avium		🟩 x		🟩 x	🟩 x	🟥 x	
Prunus cerasifera	🟥 x			🟥 x	🟥 x		
Prunus cerasus	🟥 x			🟥 x	🟥 x		🟥 x
Prunus domestica					🟥 x	🟥 x	🟥 x
Prunus dulcis					🟥 x		
Prunus japonica				🟥 x			
Prunus laurocerasus		🟥 x		🟥 x			
Prunus lusitanica				🟩 x			
Prunus nipponica						🟥 x	
Prunus padus				🟩 x		🟩 x	🟩 x
Prunus persica			🟥 x				
Prunus serotina		🟥 x					
Prunus serrulata							🟥 x
Prunus spinosa					🟩 x	🟩 x	

Prunus sp.				x			
Pyracantha coccinea		🟥 x		🟩 x			
Pyrus communis	🟥 x		🟥 x		🟥 x	🟥 x	🟥 x
Pyrus pyraster							🟩 x
Pyrus salicifolia							🟥 x
Pyrus sp.				x			x
Rosa canina		🟩 x					🟩 x
Rosa maximowicziana							🟥 x
Rosa multiflora		🟥 x		🟥 x			
Rosa rugosa				🟥 x			
Rosa sp.			x	x	x	x	x
Rubus fruticosus		🟩 x					
Rubus ulmifolius	🟩 x						
Ruscus aculeatus				🟩 x			
Sorbaria sorbifolia				🟥 x			

	Sorbaria sp.		x					
	Sorbus aria		🟩 x					
	Sorbus aucuparia		🟩 x		🟩 x		🟩 x	🟩 x
	Sorbus intermedia				🟥 x		🟩 x	
	Sorbus torminalis			🟩 x				
	Sorbus sp.				x	x		
	Spiraea cantoniensis			🟥 x				
	Spiraea chamaedryfolia				🟥 x		🟥 x	
	Spiraea japonica				🟥 x	🟥 x		
	Spiraea sp.			x	x			
Rubiaceae	*Fuchsia* sp.				🟥 x			
Rutaceae	*Choisya ternata*				🟥 x			
	Citrus limon	🟥 x		🟥 x				
	Citrus trifoliata				🟥 x			
	Phellodendron amurense			🟥 x			🟥 x	
	Phellodendron						🟥 x	

	sachalinense						🟥	
	Phellodendron sp.				🟥 x			
Salicaceae	*Populus alba*	🟩 x	🟩 x	🟩 x	🟩 x		🟥 x	🟩 x
	Populus balsamifera				🟥 x			
	Populus canadensis		🟥 x					
	Populus nigra	x	x	x	x			
	Populus tremula		🟩 x	🟩 x	🟩 x	🟩 x	🟩 x	🟩 x
	Populus x canescens		🟩 x		🟩 x			
	Populus sp.			x		x	x	x
	Salix alba		🟩 x		🟩 x		🟥 x	🟩 x
	Salix babylonica		🟥 x	🟥 x	🟥 x			
	Salix caprea		🟩 x		🟩 x		🟩 x	🟩 x
	Salix cinerea				🟩 x		🟩 x	🟥 x
	Salix fragilis		🟩 x	🟩 x	🟩 x		🟩 x	
	Salix pentandra				🟩 x		🟩 x	
	Salix phylicifolia						🟩 x	

	Salix purpurea			🟩 x			
	Salix repens	🟩 x					
	Salix rosmarinifolia					🟩 x	
	Salix triandra					🟩 x	
	Salix viminalis			🟩 x		🟩 x	
	Salix x rubens			🟩 x			
	Salix sp.	x		x	x		x
Salticidae	*Cydonia oblonga*						🟥 x
	Erica sp.			x			
Sapindaceae	*Acer buergerianum*						x
	Acer campestre	🟩 x		🟩 x			🟩 x
	Acer cappadocium			🟥 x			
	Acer ginnala			🟥 x		🟥 x	
	Acer griseum			🟥 x			🟥 x
	Acer japonicum						🟥 x

Acer negundo	🟥 x		🟥 x	🟥 x	🟥 x	🟥 x	
Acer opulus				🟩 x			
Acer palmatum				🟥 x			
Acer platanoides		🟩 x		🟩 x	🟩 x	🟩 x	🟩 x
Acer pseudoplatanus	🟩 x	🟩 x		🟩 x	🟩 x	🟥 x	🟩 x
Acer saccharinum		🟥 x		🟥 x		🟥 x	🟥 x
Acer sempervirens				🟥 x			
Acer tataricum						🟥 x	
Acer sp.					x	x	x
Aesculus carnea			🟥 x	🟥 x			
Aesculus hippocastanum	🟥 x	🟥 x	🟥 x	🟥 x		🟥 x	🟥 x
Aesculus pavia				🟥 x			🟥 x
Aesculus sp.			🟥 x				🟥 x
Koelreuteria paniculata				🟥 x			

Scrophulariaceae	*Buddleja davidii*				🟥 x			
	Myoporum tenuifolium			🟥 x				
Simaroubaceae	*Ailanthus altissima*				🟥 x			
Sphingidae	*Amorpha fruticosa*				🟥 x			
Staphyleaceae	*Staphylea pinnata*				🟩 x			
Tamaricaceae	*Tamarix gallica*				🟩 x			
	Tamarix indica				🟥 x			
Taxaceae	*Taxus baccata*		🟩 x	🟩 x	🟩 x	🟩 x	🟩 x	🟩 x
Thymelaeaceae	*Daphne gnidium*	🟩 x						
Ulmaceae	*Ulmus glabra*		🟩 x		🟩 x		🟩 x	
	Ulmus laevis				🟩 x			
	Ulmus minor		🟩 x	🟩 x	🟩 x			
	Ulmus pumila				🟥 x			
	Ulmus sp.			x	x	x		x
	Zelkova serrata				🟥 x			
Verbenaceae	*Lantana camara*	🟥 x		🟥 x				
Vitaceae	*Parthenocissus quinquefolia*						🟥 x	🟥 x

27

Table S3. Regression coefficients and significances (*p<0.05; **p<0.01) of Figures 3, 4 and 5.

	Regressions coefficients of UGS size with			
	Woody species richness	Woody species density	Tree canopy cover	AGB
	R^2	R^2	R^2	R^2
Almada	0.11	0.90**	0.83**	0.66**
Lisbon	0.18*	0.89**	0.80**	0.43**
Antwerp	0.34*	0.80**	0.76**	0.59**
Paris	0.40*	0.87**	0.97**	0.76**
Tartu	0.17*	0.86**	0.92**	0.45*
Zurich	0.06	0.72**	0.89**	0.45*
Poznan	0.003	0.95**	0.85**	0.49**

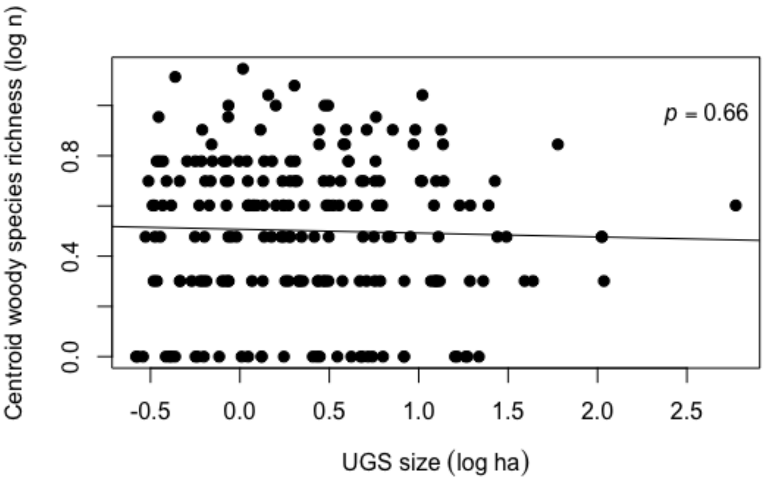


Figure S2. The relationship between the woody species richness in the centroid and UGS size, both on log-scale. Each dot is one UGS. The species richness data comprises all the woody species found in the five plots of each urban green space. The relationship is described by a linear regression line.

Linear regression model was carried out considering UGS size as independent variable and Woody species richness in the centroid of UGSs as a response variable for all the studied UGSs. Logarithmic transformations were applied to better fit linearity. Trend was represented in a scatter plot using ggplot2 package in R software. Woody taxonomic richness of the centroids did not show any significant relationship with UGS size ($p>0.05$).

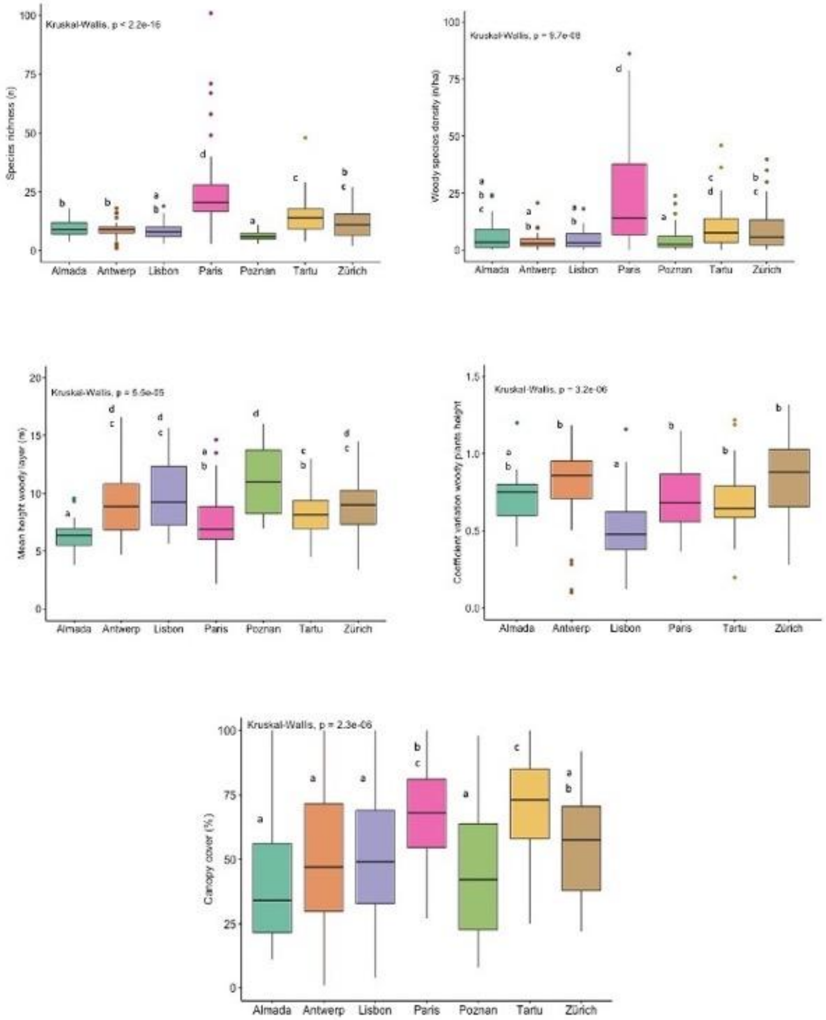


Figure S3. City-based comparison for five variables (i.e. woody species richness, woody species density, mean height of the woody layer, CV of woody plants height and percentage of canopy cover) displayed in boxplots. Box vertical size represents interquartile range (IQR). Transversal black line inside the box indicates the median value of the variable in each group. The box upper and lower limits are the 75th and 25th percentiles, respectively. Whiskers comprise both extremes of the data (1.5*IQR). The statistical differences were assessed using Kruskal-Wallis test for each variable. Different lowercase letters above the boxes indicate similarities in the variable between cities based on Dunn's multiple comparison tests.

Kruskal-Wallis rank sum test was used to test differences among groups for five of the variables. It is the non-parametric equivalent to ANOVA. Therefore, Kruskal-Wallis test assess for significant differences on a dependent variable (i.e. woody species richness, woody species density, mean height of the woody layer, CV of woody plants height and percentage of canopy cover) by a categorical independent variable or group (i.e. cities). Kruskall-Wallis test was performed in the R environment v. 3.6.1 (R Core Team, 2019) using the Kruskal.test function and the results evidenced significant differences among cities in the 5 variables. Following, post-hoc Dunn test for multiple comparisons of groups was performed using FSA v. 0.8.32 (Ogle et al., 2021) R-package. Output showed where these differences occurred, allowing to group cities according to their similarity for a given variable. Function cldList in rcompanion package in R was used to automatize the grouping.

Almada, Antwerp, Lisbon and Zurich were always grouped together when considering richness-based variables (i.e. total taxonomic richness and density) (Fig. S3). They displayed low values compared to other cities such as Tartu and Paris. No similarities were found between Paris and any other city in terms of woody taxonomic diversity. However, it was comparable to Tartu when the woody species density was considered. Poznan displayed the lowest values in both variables, being close to Lisbon in both cases and also to Almada and Antwerp for woody species density.

The distribution of woody layer height was quite heterogeneous among cities. Urban green spaces with lower height of their woody layer belonged to Almada and Paris, although Tartu and Zurich followed near. Cities with higher variation in woody layer height were Antwerp, Lisbon and Poznan.

CV did not display strong differences among cities, which were clustered in two groups. Biggest group contained all the cities except Lisbon, that was related to Almada in a smaller group. Therefore, canopy structure tends to be the same in urban green spaces independently of the city.

Every city had green areas fully covered by trees, although many of them (i.e. Almada, Antwerp, Lisbon and Poznan) had some UGSs with less than 25% of canopy cover. That seems to be the minimum threshold in UGSs from Paris, Tartu and Zurich, that showed some dissimilarities with the first group, with the exception of Zurich that also shared similar performances of canopy cover with the first group and with Paris separately.

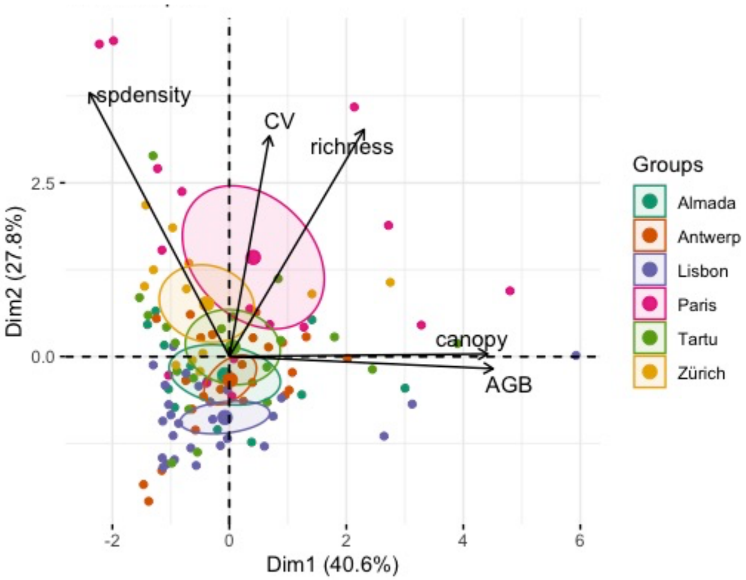


Figure S4. Principal component analysis (PCA) plot that characterizes the trends exhibited by the response variables (i.e. spdensity: species density; CV: coefficient of variation of woody plants height (i.e. standard deviation of the species-specific mean height at the site level and plant height measured in the plots divided by the heights average) used as a proxy of the vegetation structure of the UGSs; richness: woody species richness; canopy: absolute canopy cover; AGB: tree above-ground biomass) of our studied cities. Each dot represents an UGS and each color represents a city. NB: Poznan is not available.

Principal Component Analysis (PCA) was performed to analyze the direction and magnitude of our response variables (i.e. woody species richness, woody species density, mean height of the woody layer and percentage of canopy cover) in driving the variation of our dataset. PCA was performed in the R environment v. 3.6.1 (R Core Team, 2019) using factoextra package 1.0.7 (Kassambara and Mundt, 2020).

PCA explained almost 70% of the total variation of our dataset. PC1 explained around 41% of the total variation, that was mainly due to AGB and tree canopy cover, both variables closely correlated between them. PC2 explained almost 30% of the variation caused by CV, woody species richness and woody species density. Paris UGs were more characterized by their CV and woody species richness. UGSs in Zurich were better described by woody species density and CV.

III

Rocha, B., Matos, P., Giordani, P., Lõhmus, P., Branquinho, C.,
Casanelles-Abella, J., Aleixo, C., Deguines, N., Hallikma, T., Laanisto,
L., Moretti, M., **Alós Ortí, M.**, Samson, R., Tryjanowski, P., Pinho, P.
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Modelling the effects of broad scale air pollution and climate on urban ecosystem: through the lens of lichens

--Manuscript Draft--

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Corresponding Author:	Paula Matos PORTUGAL
First Author:	Bernardo Rocha
Order of Authors:	Bernardo Rocha
	Paula Matos
	Paolo Giordani
	Lõhmus Piret
	Cristina Branquinho
	Joan Casanelles-Abella
	Cristiana Aleixo
	Nicolas Deguines
	Tiit Hallikma
	Lauri Laanisto
	Marco Moretti
	Marta Alos Orti
	Roeland Samson
	Piotr Tryjanowski
	Pedro Pinho
Abstract:	To achieve more resilient cities, we need to understand the effects of global change drivers on urban ecosystems. Biodiversity-based ecological indicators (EI) can be used for that, as biodiversity is the basis of ecosystems structure, composition and functioning. Lichens have been used as EIs to monitor the effects of global change drivers on urban ecosystems, but on single city studies. Thus, we currently do not understand how lichens are affected by drivers working at the broad scale. Our aim was to quantify how much variance in lichen biodiversity-based metrics (taxonomic and trait-based) was explained by environmental drivers working at the broad spatial scale, in an urban context, where local drivers are superimposed. For that, we performed an unprecedented effort of sampling epiphytic lichens abundance in 219 green spaces, across a continental gradient from Portugal to Estonia. A total of 26 broad-scale drivers were retrieved, including air pollution and bioclimatic variables, and their dimensionality reduced by means of a principal component analysis. A total of 38 lichen metrics were then modelled against the first two axes scores of each PCA and its variance partitioned into pollution and climate components. For the first time, we determined that 15% of metrics variance was explained by broad scale drivers, with broad-scale air pollution showing to be more important than climate across majority of metrics. Taxonomic metrics were better explained by air pollution, as expected, while climate did not surpass air pollution in any of trait-based metrics groups. Consequently, 85% of metrics variance was shown to occur at the local scale. This suggests further work is necessary to unravel the effects of climate change, and that, although drivers working within cities are prevailing, both spatial scales must be considered

	simultaneously if we are to use lichens as EIs, in cities, at continental to global scales.
Suggested Reviewers:	Pilar Hurtado pilar.hurtado@urjc.es
	Christopher Ellis c.ellis@rbge.org.uk
	James Weldon james.weldon@slu.se
	Natalia Koch natalia.koch@ufms.br
	Maria João Pereira maria.pereira@ist.utl.pt
	Sarah Jovan sjovan@fs.fed.us
Response to Reviewers:	

Dear Editors,

Editors of Environmental Pollution Journal

First of all, and in behalf of all authors, I would like to apologise for the delay in the submission of our manuscript, now entitled “Modelling the effects of broad scale air pollution and climate on urban ecosystem: through the lens of lichens”. Unfortunately, due to the extent of reviews, necessary changes throughout the manuscript and the fact that we have to coordinate the revision of the manuscript with all the authors, particularly in the Easter time, proved to be very difficult and time consuming.

Nevertheless, we are optimistic that the time taken to fully and carefully address all comments and suggestions made by the most excellent editor and remaining reviewers have greatly improved our manuscript, thus placing it within the high-quality standards of Environmental pollution Journal.

Within the manuscript we have made profound changes, particularly in regard to the Abstract, Introduction and Discussion sections, taking in consideration all comments made by all reviewers. Figures 5 was also improved in terms of font size and relevant information was added to Supplementary Material. Furthermore, we have also changed the manuscript title, to better reflect the work comprised within it. Outside the manuscript file, you can also find a new graphical abstract, more aligned with the work and, in our opinion, much more explicit. Lastly, the highlights were also changed to better reflect the main findings of our work.

Within the response to reviewers file, we have fully addressed all comments and suggestions, giving quotations to the sentences which were changed in the manuscript in response to those comments, justifications to statistical approaches taken and references to justify some of our views, which are established in the manuscript itself.

We hope this renewed version of the manuscript pleases the editor and reviewers and we are open to answer any other questions that may arise in the future.

This manuscript and the work comprised within it has neither been published previously nor has it been submitted for publication elsewhere. We hope it fulfils the highest standards Environmental Pollution has accustomed its readers over the years and is consequently considered for revision. If any questions arise, please feel free to contact me at any time.

Respectfully,

Dra. Paula Matos

Modelling the effects of broad scale air pollution and climate on urban ecosystem: through the lens of lichens

Bernardo Rocha [1], Paula Matos [2*], Paolo Giordani [3], Lõhmus Piret [4], Cristina Branquinho [1], Joan Casanelles-Abella [5,6], Cristiana Aleixo [1], Nicolas Deguines [7], Tiit Hallikma [8], Lauri Laanisto [8], Marco Moretti [5], Marta Alos Orti [8], Roeland Samson [9], Piotr Tryjanowski [10] and Pedro Pinho [1]

[1] cE3c - Centre for Ecology, Evolution and Environmental Changes, FCUL, Campo Grande, 1749-016 Lisboa Portugal

[2] CEG - Centro de Estudos Geográficos do Instituto de Geografia e Ordenamento do Território da Universidade de Lisboa, 1600-276 Lisboa, Portugal

[3] DIFAR, University of Genova

[4] Institute of Ecology and Earth Science, University of Tartu, Lai st.40, Tartu, EE51005, Estonia

[5] Biodiversity and Conservation Biology, Swiss Federal Institute for Forest, Snow and Landscape Research WSL, 8903 Birmensdorf, Switzerland

[6] Department of Environmental Systems Science, Institute of Terrestrial Ecosystems, ETH Zürich, 8049 Zürich, Switzerland

[7] Université Paris-Saclay, CNRS, AgroParisTech, Ecologie Systématique Evolution, Orsay, France

[8] Chair of Biodiversity and Nature Tourism, Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, Kreutzwaldi 5, 51006 Tartu, Estonia

[9] Laboratory of Environmental and Urban Ecology, Departement of Bioscience Engineering, University of Antwerp, 2020 Antwerpen, Belgium

[10] Department of Zoology, Poznan University of Life Sciences, Woska Polskiego 71C, 60-625 Poznan

***** Correspondence: paula.matos@edu.ulisboa.pt; Phone: +351 21 044 30 00

Abstract: To achieve more resilient cities, we need to understand the effects of global change drivers on urban ecosystems. Biodiversity-based ecological indicators (EI) can be used for that, as biodiversity is the basis of ecosystems structure, composition and functioning. Lichens have been used as EIs to monitor the effects of global change drivers on urban ecosystems, but on single city studies. Thus, we currently do not understand how lichens are affected by drivers working at the broad scale. Our aim was to quantify how much variance in lichen biodiversity-based metrics (taxonomic and trait-based) was explained by environmental drivers working at the broad spatial scale, in an urban context, where local drivers are superimposed. For that, we performed an unprecedented effort of sampling epiphytic lichens abundance in 219 green spaces, across a continental gradient from Portugal to Estonia. A total of 26 broad-scale drivers were retrieved, including air pollution and bioclimatic variables, and their dimensionality reduced by means of a principal component analysis. A total of 38 lichen metrics were then modelled against the first two axes scores of each PCA and its variance partitioned into pollution and climate components. For the first time, we determined that 15% of metrics variance was explained by broad scale drivers, with broad-scale air pollution showing to be more important than climate across majority of metrics. Taxonomic metrics were better explained by air pollution, as expected, while climate did not surpass air pollution in any of trait-based metrics groups. Consequently, 85% of metrics variance was shown to occur at the local scale. This suggests further work is necessary to unravel the effects of climate change, and that, although drivers working within cities are prevailing, both spatial scales must be considered simultaneously if we are to use lichens as EIs, in cities, at continental to global scales.

Keywords: Urban macroecology; Spatial scales; Atmospheric pollution; Ecological indicator; Biodiversity-based metrics; Trait-based diversity.

1. Introduction

Humans are increasingly dwelling in cities, with projections estimating that 80% of the European population will be living in urban areas by 2050 (UN, 2019). This phenomenon has led to the fast expansion of cities, causing environmental degradation, pressuring populations and triggering human health and well-being problems (Singh et al., 2017). For that reason, governance must hence the transition to more sustainable and resilient cities (Cartalis, 2014), with several continental (e.g., European Union) to global (e.g., United Nations) actions already in place (Mori et al., 2019; WHO, 2016). Urban ecosystems play a crucial role in this transition, as they provide several ecosystem services that improve urban life quality (Tzoulas et al., 2007). Yet, like human populations, urban ecosystems are pressured by drivers working at the local scale (i.e., with a spatial scale of action at the city level), like the heat island effect (Tam et al., 2015) or land-use (Romero et al., 1999), and simultaneously by large scale drivers (e.g., climate change, which has a broad spatial range of action), (Dawson et al., 2017). Understanding how environmental pressures impact urban ecosystems, and monitoring the success of applied mitigation actions, requires being able to characterize the effects of global change drivers at both spatial scales. Nevertheless, we currently do not understand the effects of the drivers working at a broad spatial scale on urban ecosystems.

Standard physicochemical parameters (e.g., temperature, precipitation, pollutants concentration) are frequently used to measure environmental driver's change through time and space. However, these parameters are unable to quantify its effects in the ecosystems, i.e., on its biodiversity, structure or functioning. Ecological indicators are "measurable characteristics of the structure (e.g., genetic, population, habitat, and landscape pattern), composition (e.g., genes, species, populations, communities, and landscape types), or function (e.g., genetic, demographic/life history, ecosystem, and landscape disturbance processes) of ecological systems" (Niemi and Mcdonald, 2004). Within these, biodiversity-based ecological indicators relate to ecosystems' structure and functioning, being efficient tools to quantify the effects of environmental drivers at the ecosystems level, in a cost-efficient way.

Epiphytic lichens have long been used as ecological indicators, as they are known to respond to several global change drivers (Aptroot et al., 2021; Asta et al., 2002; Brunialti et al., 2012). Their extensive use has enabled the creation of a body of knowledge relating lichen biodiversity-based metrics (taxonomic and trait-based) to particular environmental drivers (Branquinho et al., 2015). Taxonomic-based diversity metrics (e.g., species richness or total species abundance) are particularly responsive to high-intensity drivers of change, like air pollution (Hauck et al., 2013; Lättman et al., 2014), due to a number of physiological characteristics (Nash and Gries, 1991). However, when drivers' intensity is lower, they primarily induce shifts in species composition rather than biodiversity loss per se (Ellis and Coppins, 2006). For that reason, taxonomic metrics have progressively been complemented by trait-based diversity metrics, as these are better to detect compositional shifts in the communities, potentially more universal, as they are not linked to species identity, and better indicators of ecosystem functioning quantification in response to global change drivers (Van Der Plas, 2019).

Understanding broad scale effects of environmental drivers on urban ecosystems imply the use of ecological indicators that can clearly signal the effects of broad scale drivers, despite the potential simultaneous local scale effects. However, this task may be particularly challenging. On one hand, local scale drivers' effects may be so intense that they can potentially overshadow broad scale drivers' effects, particularly if the last are drivers of lower intensity, like climate change (Branquinho et al., 2019). On the other hand, the same environmental driver, e.g., temperature, can act at both spatial scales, e.g., global increase in temperature due to climate change acting at the broad scale, and localized temperature increase inside cities due to the urban heat island effect (Jenerette et al., 2007). Thus, it could be potentially difficult to distinguish those drivers' broad scale action, from local scale ones. Lichens have been used as ecological indicators of drivers acting at the local scale on urban ecosystems, like urbanization (Lättman et al., 2014), air quality (McCarthy et al., 2009) and the urban heat island effect (Munzi et al., 2014). At the broad scale, they have also been used to track broad scale drivers like pollution (Mccune et al., 1997) and climate (Phinney et al., 2021). Nevertheless, this was done in natural and semi-natural ecosystems. Thus, we still do not know if these lichen biodiversity-based metrics will be able to signal the effects of broad scale drivers on urban ecosystems. This could potentially be tested by looking into epiphytic lichens' communities across multiple cities, where broad scale drivers (e.g., climate & large-scale air pollution) act superimposed. Nevertheless, such an endeavor has not yet been attempted.

The aim of this work was to quantify how much variance in lichen biodiversity-based metrics (taxonomic and trait-based) was explained by environmental drivers working at the broad spatial scale, in an urban context where local scale drivers are also present and can potentially overshadow their effects, if more intense. To address this, we sampled epiphytic lichens diversity, calculated several taxonomic and trait-based metrics, and applied them as ecological indicators of broad scale air pollution and climate. This was done across a large spatial gradient in Europe (seven cities in total from Lisbon to Tartu), representing a broad scale gradient of climate and pollution. Based on existing knowledge, we expect part of the metrics variance to be related to local scale drivers. Nevertheless, we believe that by exploring such a large spatial gradient, lichens metrics will also reflect the influence of urban broad scale drivers. Additionally, and within an urban context, broad scale air pollution intensity is expected to surpass that of climate, as pollutants, mainly emitted by industrial and traffic sources (Molina and Molina, 2004), as these pose a more harmful effect on lichens than climate (Evju and Bruteig, 2013). For that reason, we expect taxonomic metrics to better reflect the higher intensity drivers' effects, like broad scale air pollution, while trait-based to be more responsive to intermediate intensity drivers, like broad scale macroclimatic variations.

2. Materials and Methods

2.1. Study areas. Lichen communities were sampled across seven European cities, in 2018, under the BIOVEINS project (BiodivERsA32015014). Almada and Lisbon (Portugal), Paris (France), Zurich

(Switzerland), Antwerp (Belgium), Poznan (Poland), and Tartu (Estonia) were chosen to represent a large spatial gradient of climate, air pollution and local city characteristics (Fig. 1).

The selected cities present very distinct spatial extensions, namely at the Local Administrative Unit Level 2 (LAU-2 Level) (http://ec.europa.eu/eurostat/web/nuts/local-administrative-units). Therefore, to ensure spatial extent consistency, some cities were used to their full extent (e.g., Tartu) while in others (e.g., Paris), only a section was used. In all cases though, it was ensured that the sampling sites represented a gradient of urban density.

2.2. Sampling site selection. Sampling sites were selected within the "Green Urban Areas" class of the pan-European land-cover classification, the European Urban Atlas (EEA, 2018). This ensured land-use typology and intensity were consistent across Europe. For each patch of "Green Urban Areas", patch size and the connectivity index (Gustafson and Parker, 1992) were calculated (see below). Sites were classified into six size classes ([0 - 0.6[, [0.6 – 1.2[, [1.2 – 2.4[, [2.4 – 4.8[, [4.8 – 9.6[and >9.6 ha) and six classes of connectivity ([0 – 18000[, [18000 – 36000[, [36000 – 72000[, [72000 – 144000[, [144000 – 288000[and >288000 – no units). From the initially available 1582 patches (across all cities), up to 36 were selected for each city, stratified by size and by the proximity index. Selection within each combination of classes (maximum of 36 combinations) was done randomly. This resulted in a total of 219 sampling sites across all cities. For some cities (Figure 1) less than 36 patches were selected as some combinations were not available.

The proximity index (Gustafson and Parker, 1992) is a measure of fragmentation/isolation of each focal patch. Briefly, it quantifies the amount of available habitat in neighboring patches, each neighbor patch area being weighted by the square of the distance to the focal patch. The neighborhood of each focal patch is defined by user-specified radius. In this case, we selected a 5000 m area to include the maximum distance for which Urban Atlas was available. Note that because the distance to each patch is squared, nearby patches have a much higher weight on the index than those further away from the focal patch, thus, looking at longer distances would cause insignificant changes in this metric. Based on previous knowledge, we expected all neighboring patches with trees to influence lichens in the focal patches, e.g., due to its mitigation of the urban heat-island (Munzi et al., 2014) or air pollution (Matos et al., 2019). To account for this, all land-cover types that could host a significant number of trees were included as potential habitat in the calculation of the proximity index, namely "Discontinuous Low-Density Urban Fabric" and "Discontinuous very-low-density urban fabric" (mainly small houses with gardens), "Permanent Crops" (orchards), and "Forests". The Proximity Index takes the highest values when the focal patch is surrounded by nearby large similar habitats and takes the value of zero when the focal patch has no neighbors of the same habitat.

2.3. Data collection

2.3.1. Field Sampling. Epiphytic lichens diversity was sampled following the European Standard Method, developed to assess lichen diversity response to overall environmental change (Asta et al., 2002; Cristofolini et al., 2014b) (Figure 2). The use of a standard method for lichen sampling is unprecedented in urban areas, at this scale, and greatly contributed to reducing variability due to disparate sampling protocols. Within each patch, the point furthest from the margin was taken as the patch centroid. The nearest area with at least 30% cover by trees and grass, within a 50 m radius buffer, was then selected as the sampling site. On each sampling site, the four trees closest to the centroid were selected, ensuring they were within the range of conditions required by the sampling protocol: healthy trees with an upright main trunk (< 20º deviation from vertical), without branches or injuries up to two meters, with circumference at the sampling height (one to two meters from the ground) between 50 and 250 cm. A maximum distance of 50 m between trees was established.

It is important to highlight that to reduce the sampling variability to the feasible minimum, tree bark and tree size were homogenized as much as possible: as it is not possible to select a single phorophyte species across all cities, sampling was narrowed to phorophytes sharing the same bark roughness (intermediate roughness was chosen as it could be found in all cities). Additionally, tree size was limited to medium size trees (50 to 250 cm perimeter at sampling height). On each tree, a sampling grid (50 x 10 cm, divided into 5 squares) was placed on the four main aspects (N, S, E, W, total 2000 cm^2 sampling area per tree). All lichens within the grid were either identified on location or collected for later laboratory identification. Species abundance was determined based on the number of squares on which they occur (max. 20), and then averaged by site. Nomenclature followed (Nimis and Martellos, 2021). Species nomenclature follows (Mayrhofer and Moberg, 2002; Randlane and Saag, 2004; Smith et al., 2009). A total of 140 species were identified, nine of which to the genus level only.

2.3.2. Biodiversity-based metrics. Taxonomic and trait-based metrics were computed**.** Regarding the taxonomic metrics, eight metrics were calculated. Species richness corresponds to the total number of species per site. The number of rare species corresponds to the number of rare species per site, i.e., if present in less than 5% of the total sampling sites. The Shannon diversity Index is a measure of species diversity in a community, as is the Inverse-Simpson Index. In both diversity indices, higher values correspond to higher species diversity. Total species abundance corresponds to the sum of all lichen species abundance per site (same as the Lichen Diversity Value in the lichen European Standard Method). To analyze the communities' dissimilarity, Bray-Curtis, Jaccard and Morisita-Horn dissimilarity indices were calculated. These indices were chosen to reflect changes in community composition giving both relevance to rare (Bray-Curtis and Jaccard) or dominant species (Morisita-Horn), (Barwell et al., 2015). In these three metrics, values vary from 0 to 1, with values of 1 indicating complete dissimilarity between sites, I.e., no shared species. R software (Team, 2020) was used to calculate taxonomic diversity metrics, using functions *diversity* and *vegdist* from the Vegan package (Oksanen et al., 2011). Given the similar patterns of variation between species richness and number of rare species, between Shannon and Inverse-Simpson, between and Jaccard and Bray-Curtis and Morisita-Horn, we present only results for species richness, Shannon, total abundance and Jaccard. Results of the remaining metrics are shown in supplementary material (Figure S1).

Regarding the trait-based metrics, indices representing both functional diversity and functional structure were computed taken only into consideration species identified to the species level. This was done based on seven categorical traits known to respond to climate and/or air pollution (Table 1). Growth form, main photobiont type (green algae other than *Trentepohlia*, *Trentepohlia* and cyanobacteria), species substrate pH tolerance, tolerance to solar irradiation, tolerance to aridity, tolerance to eutrophication and poleotolerance. Trait information was retrieved from the ITALIC database (Nimis and Martellos, 2021), and the maximum value for each species was used (trait classification are ordinal in the database – Table 1). These traits were selected as they respond to environmental change influencing lichen growth, survival and, ultimately, fitness. Growth form and the main photobiont type traits are known to respond to both air pollution and climate (Aptroot and Van Herk, 2007; Koch et al., 2019; Matos et al., 2015). Substrate pH was used as a proxy for air pollution, as deposition of particles and gases affect natural trees' bark pH, a key factor influencing lichen communities (Larsen et al., 2007). Note that substrate pH does not reflect raw bark pH values, as these were not measured, but rather lichens species tolerance to substrate pH. Eutrophication tolerance shows species' tolerance to nitrogen in the environment and has also been used to track air pollution (Giordani and Malaspina, 2017; Pinho et al., 2011) while the poleotolerance trait groups species based on its tolerance to different degrees of human disturbance, being used successfully in the past as an ecological indicator of the integrated effects of environmental disturbances (Rocha et al., 2019). Lastly, solar irradiation and aridity traits are known to respond to climatic conditions (Munzi et al., 2014). Species that could not be identified to the species level and for which we could not retrieve specific trait classification were excluded from trait-based metrics calculation (Table S1). In terms of functional diversity metrics, we calculated functional richness and Rao's quadratic entropy (RaoQ), both as multi-trait indices, computed only with the traits and corresponding functional groups (the different categories of each categorical trait) included in the results section. Functional richness represents the amount of functional space occupied by the different functional groups (per sampling site), the trait diversity tally of species richness. RaoQ corresponds to the functional dispersion, reflecting the variety of functional strategies, weighted by abundance. The community weighted mean (CWM) was included to represent the communities' functional structure and represents the mean trait value in the community weighted by the abundance, i.e., the proportion of summed species abundances belonging to the same functional group of each trait. The two lower classes of the irradiation, eutrophication and poleotolerance traits were merged prior to calculations as they presented similar correlation trends with both climate and air pollution PCA axes (Figure S2). Like for some taxonomic metrics, main photobiont type, pH of the substrate and the poleotolerance traits were excluded from the main results and are only presented in the supplementary material. The main photobiont showed no variation, as green algae were dominant across all cities (they represent on average 97.43% of all photobiont types). The poleotolerance and species substrate pH requirement were excluded as they showed the same patterns as the eutrophication trait (Figure S1 and S2). Results for squamulose, leprose and cyanobacteria functional groups are also only presented in the supplementary material, as they showed very low overall abundance (less than 5 %). Trait-based indices were calculated with R software (Team, 2020), function *dbFD* from the FD package (Laliberté et al., 2014).

2.3.3. Environmental variables. To quantify the overall importance of broad scale drivers on each biodiversity-based metric, a set of 26 environmental variables were gathered. These are intended to depict two main broad scale drivers in urban environments, air pollution and climate (Harlan and Ruddell, 2011). Note that both pollution and climate were derived from models working at continental scale, thus climate and air pollution values show little variance within each city sites, i.e., they represent environmental gradients working at the broad spatial scale. Climate and air pollution values were extracted for each of the 219 sampling sites (the average values, per city, can be seen in Table S3).

To characterize broad scale climatic conditions, 19 bioclimatic variables representing air temperature and precipitation annual and seasonal values, were retrieved from the CHELSA database (Karger D.N. et al., 2018; Karger et al., 2017), at the maximum available spatial resolution of 1 km, and corresponding to modelled average values for the 1979-2013 time period (Table S2). These were preferred over raw maximum, mean and minimum temperature and precipitation variables as the former are potentially biologically more meaningful (Title and Bemmels, 2018). More detailed information on each climatic variable can be seen in (O'Donnell and Ignizio, 2012). For broad scale air pollution, redN and OxN deposition (mg.m^{-2}) and NH_3, SO_2, NO_x, PM2.5 and PM10 air concentration (µg.m^{-3}), for the year 2018, were retrieved from the EMEP (Fagerli et al., 2019) at the maximum available spatial resolution (11 km). These pollutants were selected as they have been seen to impact the diversity of epiphytic lichen vegetation across Europe (Loppi and Pirintsos, 2000; Van Herk et al., 2003). Long-term averages of climate, contrasting with short-term (annual) air pollution values, were used as we expect lichens to respond rapidly to changes in air quality, because it is a high intensity environmental driver, capable of causing species loss (Lättman et al., 2014); while for climate the response of lichen is expected to be slower than for pollution (van Herk et al., 2002). Still, because we are dealing with macro scale gradients, we do not expect that the relative position of cities along the continental spatial gradient regarding climate would change if we used climate annual data. A common European model was used for pollution and climate to avoid the pitfalls of using national or city specific models, that would use different modelling approaches. Thus, this ensured that all values are of the same quality and can be used to compare sites and cities.

To account for the remaining broad scale variability, not represented by climate and air pollution, an additional factor ("other", corresponding to city identity and meant to represent all other potential drivers working at the broad scale, aside from air pollution and climate) was added to the analysis. This factor is expected to represent the remaining city characteristics varying at the broad scale (i.e., differentiating cities), such as city size, air pollution legacy, or management policies.

2.4. Data analysis. All analyses were performed in R software v. 4.0.3 (Team, 2020) using RStudio v. 1.4.1103 (Team, 2021). Two Principal Components Analysis (PCA) were performed, one on the set of 19 climate variables and another on the set of 7 air pollution variables, to reduce the large number of variables in each set. For each main driver, climate and air pollution, the sets of variables were reduced to two dimensions (two axes), representing most of the information of the original dataset. The site scores of these first two PCA axes were henceforth used as climate and air pollution variables in the subsequent analyses. The second axis of the climate PCA isolated Zurich sampling sites in the precipitation gradient, suggesting that a log-transformation of the precipitation climate variables (supplementary Table S2) prior to the PCA process should be tested. The resulting PCA was similar to the non-log-transformed climate PCA (data not shown), thus results report to a PCA without these variables log-transformation. PCAs were computed using the *prcomp* function from the stats package.

Spearman correlations were used to make a preliminary exploration of the relationships between air pollution and macroclimate PCA axes and biodiversity metrics (Figure S2). As detailed in 2.3.2, this procedure was used to shorten the number of biodiversity metrics shown to prevent overcrowding.

Interquartile range (25-75), minimum, maximum, average and median of each taxonomic, functional diversity and functional structure metric was calculated by city and represented as boxplots.

Linear regressions were used to model the response of each biodiversity metrics to the four climate and air pollution variables (sites scores of the first two axes of each driver' PCA). To ensure that the linear model approach was adequate we checked the residuals distribution (normality) and homogeneity of distribution (Quantile-quantile and density plots) of the linear models (Figures S3 to S7). The residuals showed a good distribution in terms of normality and homogeneity, thus attesting to the adequacy of the use of linear models.

The potential interactions between the four broad scale pollution and climate variables (by means of multiplicative linear models) were not tested here as our focus was on the individual effect of each broad scale driver on each lichen biodiversity-based metric.

A variable named "Other", coded as the city name, was also tested both as a fixed and a random factor in the linear models. Firstly, it was tested as a fixed factor with the four climate and air pollution variables, as an attempt to represent the remaining drivers other than pollution and climate, acting at the broad scale (Biodiversity metric ~ Climate PCA1 + Climate PCA2 + Pollution PCA1 + Pollution PCA2 + Other). The variable "Other" was highly collinear with the remaining four variables (VIF > 150000), and the resulting model wasn't better in terms of fit, thus this variable was excluded as fixed predictor. This result suggested that all broad scale variance could be accounted for by looking only to climate and pollution, and the city did not apport any extra information. The remaining four variables (climate and pollution) presented low collinearity (VIF < 1.5) (Zuur et al., 2010), and were kept in the model. Secondly, "Other" was also fitted as a random term in a linear model [(Biodiversity metric ~ Climate PCA1 + Climate PCA2 + Pollution PCA1 + Pollution PCA2 + (1|Other)]. Across all modelled metrics, the variable "Other" explained the majority of the variance that was previously explained by air pollution and climate, thus effectively cancelling their effect, without adding new information. Thus, the linear models used to quantify the biodiversity metrics response to the broad scale drivers did not include "Other" [(Biodiversity-based metric ~ Climate PCA1 + Climate PCA2 + Pollution PCA1 + Pollution PCA2]. For each model, the total R^2 variance was partitioned to assess the proportion of variance explained by each of the predictors working at the broad scale. The remaining variance ($1- R^2$) was interpreted as unaccounted variance associated to drivers working at a local scale, without further detail (i.e., local scale drivers were not investigated as this was not the objective of this work). Variance partitioning is presented for each biodiversity metrics and averaged by group (taxonomic, functional diversity and functional structure for each trait) and main broad scale driver to summarize the variance explained by each, to facilitate the clarification of the work expectations. This was done assuming that all metrics value the same. To prevent overcrowding, metrics that had very similar responses are omitted from Figure 4 and 5. Results of the remaining metrics are presented in supplementary material (Figure S8). Models were considered significant for $p < 0.05$. Models were performed with the *lm* function from the stats package and the variance partitioning corresponds to the sum of squares of each predictor divided by the total (i.e., sum of squares of all predictors). As previously stated, the remaining unexplained variance in the model, i.e., not explained by any of the variables working at a broad scale, was interpreted as most likely being driven by variables working at the local scale (acting at the city spatial scale). We are confident of this interpretation of variance partitioning between broad and local scale. The results (see above) of using "other" as a fixed term in the model allowed us to assume that city identity represents all possible sources of variance at the broad scale (e.g., climate and pollution but also geology, other climate variables, daylength, city age or city environmental policies). Thus, though we did not include other broad scale drivers, the fact that city identity accounted for the same amount of variance in lichen biodiversity metrics as pollution and climate (data not shown), gives us confidence that the four broad scale variables used are in fact the most important ones acting at the broad scale. In addition, these results allow us also to assume that this way we were able to extract most of the variance that could be accounted for at a broad scale and, that, the remaining unexplained variance in lichen metrics can be attributed to the local scale (e.g., caused by local air pollution, surrounding land-use, park or tree characteristics).

3. Results

3.1 Summarizing the climate and air pollution continental scale gradients

The PCA of climate variables (Figure 3a) showed a main gradient of temperature on the first axis (58.8%), and a gradient of precipitation in the second axis (21.6%). Together, they represented most of the variance in climate (80.4%), with sampling sites clustering in cities along the temperature axis. Almada and Lisbon overlap over the warmest temperature side of the continental scale climate gradient, as expected given their close geographical proximity. Paris and Antwerp follow in the middle part of the temperature gradient, with Zurich and Poznan right next to them. Tartu stands on the opposite side of the temperature gradient as the coldest city in our dataset. In relation to the precipitation gradient (second axis), Zurich is the wettest city in our dataset, while the remaining cities present similar precipitation levels on the driest part of the gradient.

The PCA of air pollution variables (Figure 3b) showed a clear main gradient of overall increasing air pollution loads on the positive side of the first axis (57.6%), and a second one (20.8%) representing a gradient of type of pollutants. The second axis can be generally interpreted as representing a gradient of sites dominated by N-based compounds (corresponding to eutrophication) and sites dominated by sulfur dioxide and particulate matter (corresponding to acidification). Together the axes represented most of the variance in air pollution (78.4%). Cities do not appear clustered so clearly by pollution as they did with climate. In terms of overall broad scale air pollution load, Paris, Antwerp and Zurich are the most polluted cities, followed by Poznan, Lisbon and Almada, with Tartu represented in the less polluted part of the gradient. In terms of type of pollutants, Paris, Antwerp and Zurich appear more dominated by N compounds, while Almada, Lisbon and Poznan seem to be more related to sulfur dioxide and particulate matter.

3.2 Characterization of lichen taxonomic and trait-based metrics

A total of 140 species were identified across all cities. We found Lisbon, Tartu and Zurich to harbor the more species-rich lichen communities, while Poznan the poorest (Figure 4). Shannon diversity was also highest (i.e., more diverse) in Lisbon, Tartu and Zurich. The total abundance of lichens was also the highest in these three cities, and the lowest in Almada and Poznan (Figure 4). All cities show high spatial dissimilarity values. Almada was on average the most dissimilar, while Lisbon, Paris and Zurich showed the lowest spatial dissimilarity (Figure 4).

In terms of functional-structure, foliose narrow lobed lichens were the dominant growth form in all cities, while crustose and foliose broad lobed lichens were present in lower and similar proportion (Figure 4). The exception was Almada, where crustose lichens co-dominate with foliose narrow lobed lichens, followed by foliose broad lobed. Fruticose lichens represent a small proportion across all cities (< 5% abundance). Communities were also dominated by lichens tolerant to high solar radiation in all cities, with the highest tolerance level accounting for more than 75% of the total lichen abundance (Figure 4). The exception was, again, Almada, where medium-tolerant species accounted also for 25% of the abundance. Regarding aridity, the pattern was different (Figure 4). Species less tolerant to arid conditions (i.e., more hygrophytic) were nearly absent from all cities except Almada (13%). Poznan was totally dominated by species with medium-high tolerance to aridity, with Antwerp, Lisbon, Paris and Zurich also presenting high values (> 60 %). In Almada, Tartu and medium tolerant species dominated. Lichens more tolerant to eutrophication were clearly dominant (representing usually more than 50% of the total) in Paris, Zurich, Poznan and Lisbon (Figure 4). These were also the cities where species with lower eutrophication tolerance were scarcer. In Antwerp high, but especially, medium-high eutrophication tolerant lichens dominated. Tartu and Almada showed a more evenly distribution of species abundance between the different levels of eutrophication tolerance (Figure 4). Similar to species richness, functional richness values were also highest in Tartu, and lowest in Poznan, while the remaining cities rank in the middle with similar values (Figure 4). Regarding the functional dispersion, Almada showed the highest values and Poznan the lowest (Figure 4).

3.3 Partitioning the proportion of biodiversity metrics variance explained by the broad and local scale

The vast majority of the models (Figure 5 and S4) were found to be highly significant, showing a p-value lower than 0.001, strongly supporting their use to interpret the data. Across all biodiversity metrics (Figure 5), the four considered broad scale drivers explained an average of 15%. The remaining unexplained variance was on average 85% and assumed to represent all drivers that are not working at the broad scale, and that can thus be interpreted as local scale variation (i.e., acting at the city scale). For six biodiversity metrics, broad scale drivers explained more than 20% of the variance. Only the Jaccard, low tolerance to irradiation and high tolerance to aridity models were not significant.

Considering the main the broad scale drivers (pollution and climate), and all biodiversity metrics together, air pollution accounted for most of the variance found at the broad scale, explaining on average 11.3% of the variance, while climate explained 6.7% (Figure 5b). When metrics were grouped into taxonomical, functional structure or functional diversity (i.e., by type of metric, Figure 5b), broad scale pollution surpassed climate across the three metrics groups. When considering each metric individually, air pollution also surpassed climate across 14 of the total 22 biodiversity-based metrics.

Within the taxonomic metrics group, composed of species richness, Shannon index, total abundance and Jaccard dissimilarity index, air pollution explained more variance (7.8%) in comparison to climate (6.3%). Nevertheless, not all taxonomic metrics responded equally (Figure 5a). Within the significant models, species richness responded almost exclusively to the air pollution broad scale gradient (17.5%), the Shannon-index similarly to both pollution and climate (7.6% and 7.5%, respectively) and the total abundance mainly to climate (16.3% out of 19.9%).

Air pollution also explained the majority of the functional diversity metrics variance (21.3% on average, Figure 5b). Nevertheless, like taxonomic diversity, each functional diversity metrics responded differently. While functional richness variance was almost exclusively explained by broad scale air pollution (24.3%), for the RaoQ metric both pollution and climate were equally relevant (18.4% and 14.2% respective, forming a total of 32.6%).

Regarding the functional structure, the relevance of each broad scale driver was also different depending on the trait considered and even among functional groups within the same trait (Figure 5b). Growth form explained variance was mostly attributed to the air pollution gradient (7.2%, versus 4.3% of climate). Considering each growth form (Figure 5a), air pollution was more important than climate for crustose, foliose narrow lobed lichens (9.7% in 13.4% and 12.8% in 19%, respectively), and the only explaining fruticose (5.4%). For foliose broad lobed lichens, climate was the most important driver (7.1%, out of 8.1). For the irradiance trait (Figure 5a), when the average of all functional groups of the trait are considered, the variance explained was almost equally divided between the two broad scale drivers. Within the significant models, the medium irradiance tolerance metric was mainly explained by air pollution (19.9% in 24.3%) and was one of the six models where broad scale drivers jointly explained more than 20% of the variance. Contrarily, in both the medium-high and high metrics variance was better explained by climate (19.9% in 24.3% and 6.4% in 10.2%, respectively). For the aridity trait, air pollution explained, on average, twice as much as climate (12.6% versus 5.5%, Figure 5b). In the medium-low, medium and medium-high metrics variance, air pollution surpassed climate (14.4% in 22.2%, 17.9% in 25.1% and 17% in 20.4%, respectively). Finally, for the eutrophication trait, most variance was also explained by broad scale pollution (10.3%, versus 3.8% of climate, Figure 5b). Within the medium-low and medium metrics, air pollution was in fact the main broad scale driver (13.2% in 19% and 8.7% in 11.8%, respectively), while in the medium-high the importance was similarly shared with climate (5.6% and 6.1%, respectively).

5. Discussion

Cities adaptation and compliance with the United Nations Sustainable Development Goals (SDGs) (UN, 2015) must necessarily focus on a key aspect of urban areas, the urban ecosystems (Maes et al., 2019). For that, it is fundamental to evaluate global change drivers' effects at the ecosystem level, and this can only be fulfilled by comparing cities across large areas (i.e., continental to global) and looking at drivers working at the broad scale using ecological indicators (Hák et al., 2016). To the best of our knowledge, this is the first time that lichens biodiversity-based metrics are used as an ecological indicator to quantify the importance of broad scale drivers in an urban context. Our work found that broad scale drivers accounted for an average of 15% across all lichen metrics variance. Furthermore, within the broad scale drivers included, air pollution (10%) was more important than climate (5%) across all metrics groups. Consequently, and as expected, taxonomic metrics were better explained by the broad scale air pollution driver. However, and contrary to our expectation, broad scale climate was less important than broad scale air pollution for trait-based metrics.

Broad scale drivers (nearly homogeneous within the city and thus with little variance between sampling sites), accounted for an average of 15% in lichen metrics variance, reaching a maximum of 33% in the RaoQ metric. The effects of broad scale drivers on lichen communities are well documented (Geiser et al., 2021; Phinney et al., 2021), although these studies were conducted on natural or semi-natural environments only. For that reason, we expected urban lichens metrics variance partitioning to reflect, to some extent, the influence of these broad scale drivers. Despite broad scale drivers playing a role in shaping urban lichen diversity, the unexplained variance suggests that this effect may be overshadowed by drivers acting at the local scale. These local scale drivers are known to act as high intensity drivers and are well documented in cities, although only for single cities studies (Davies et al., 2007; Koch et al., 2019; Munzi et al., 2007). Along the urbanization process, lichen communities are driven towards species more tolerant to high intensity local drivers' effects (Hawksworth, 1990; LiŠKa and Herben, 2008), to a point where the effects of other, less intense drivers (i.e., broad scale climate), are overshadowed. Thus, one potential solution to better isolate broad scale drivers effects on lichens communities is by standardizing for such local scale effects. This could be done for example by homogenizing the characteristics of sampling sites (e.g. green areas with the same size). Another possibility is to include more cities with a broader gradient of broad scale pollution and climate. Still, and because the effects of broad scale drivers are statistically significant across majority of metrics, both spatial scales must be considered simultaneously to interpret lichen data derived from multi-city studies.

Within the broad scale, and as expected, the air pollution gradient was overall more significant (10% out of 15% of the total broad scale variance) to lichen metrics than climate. Air pollution has long been a high intensity driver in urban areas, due to the presence of local industrial and traffic pollutants sources within our nearby cities (Babiy et al., 2003; Fenger, 1999), which translates to increased pollutants concentration/deposition (Krzyzanowski et al., 2014; Riga-Karandinos and Saitanis, 2005). Despite the role of specific pollutants has been observed in several local scale studies (Llop et al., 2017; Varela et al., 2018), our results suggest that at the broad scale, when multiple pollutants are superimposed, lichens respond to pollution overall rather than to specific pollutants. As lichens absorb pollutants from wet and dry atmospheric deposition (Van Der Wat and Forbes, 2015), increased air pollution levels translate to overall harmful effect on most lichen species and consequent species loss, as reported by several authors in single-city studies (Gary, 2010; Koch et al., 2016; Munzi et al., 2007). Here we confirm that this pattern is also visible at the broad scale, as the influence of broad scale air pollution largely surpassed that of climate on species richness, one of the largest across all metrics, while for both the Shannon index and total abundance metrics, pollution importance in relation to climate decreased. Furthermore, and contrarily to our initial expectations, air pollution was also the main broad scale driver across both functional structure and functional diversity metrics groups, reaching a maximum of 24% with the functional richness metric. These results reinforce the idea that, high intensity drivers, like pollution, act as a filter for lichen, promoting species loss and the overall narrowing of functional groups. Thus, metrics based on presence (i.e., species richness or functional richness) are more suitable to track the effects of high intensity drivers, regardless of being taxonomic or trait-based in nature. Based on our results we can also suggest that air pollution, in Europe, is still above critical levels and loads for lichens (Cape et al., 2009), i.e., pollution is above the threshold for causing significant changes in lichen biodiversity, which is reflected in communities composed of mostly pollution or disturbance tolerant species. This goes in accordance with other works (Llop et al., 2012; Llop et al., 2017), but was seen for the first time for multiple cities and broad scale air pollution. We highlight that the air pollution model used (EMEP MSC-W) includes not only pollution sources and concentration, but also climatic information. Thus, the broad scale air pollution data is expected to be richer than the climate one, which could help explain why it surpassed climate across all metric groups. This cannot be avoided, as it represents, as accurately as possible, both broad scale pollution and climate. However, if climate alone had no effect on lichens, we would not retrieve models based mostly on pollution. Thus, this reinforces the interpretation that air pollution is the main driver of lichens at the broad scale, although climate is very likely to have an indirect effect, by affecting pollutants dispersion and deposition (Fiore et al., 2015; Kinney, 2008). Although not tested here, future works should aim at assessing the effects of the interactions between both broad scale drivers on urban ecosystems. Still, to do that, sampling must be extended to a larger number of cities, which may be unfeasible. The effects of the broad scale climate were, as expected, lower than pollution across all metrics and metrics groups (average of 5% out of 15%). Despite the large continental gradient representing a broad range of climatic conditions (mean annual temperature and annual precipitation ranging from, respectively, a maximum of 17 ºC and 1071 mm, to a minimum of 5 ºC and 517 mm), its importance on all lichen metrics was still low. Lichens response to broad scale climate change is well documented (Concostrina-Zubiri et al., 2014; Di Nuzzo et al., 2021; Hurtado et al., 2020; Matos et al., 2015), although studies were done mostly in natural and semi-natural environments. However, our work suggests that, in urban contexts, air pollution is probably still the most limiting factor to lichens, overshadowing climate's effect. In fact, the two less polluted cities, Almada and Tartu, showed high abundance of lichens more sensitive to aridity, suggesting that climate can become an important driver of lichen diversity when air pollution is not prevalent. Such phenomenon has already been detected in a previous work in Almada (Munzi et al., 2014), where the effects of the urban heat island were only detected when air pollution was low. The effects of climate on lichens are expected to be of lower intensity, in comparison to air pollution, thus primarily inducing compositional shifts in lichens communities, which should be reflected more on the trait-based metrics rather than on taxonomic ones (Ellis and Coppins, 2006). For that reason, we expected a higher contribution of broad scale climate across the trait-based metrics, particularly in climate related traits (e.g., irradiance, aridity). Broad scale air pollution nevertheless surpassed the contribution of climate also in these metrics' groups, emphasizing the still prevalent role of other high intensity drivers, like air pollution, in cities. Furthermore, low to intermediate intensity drivers, like climate, are expected to lead to changes in the abundance of lichen species (Branquinho et al., 2019), rather than species loss. Here, we confirm that view, as metrics based on abundance (i.e., total abundance, RaoQ) reflected a high contribution from broad scale climate. However, we reinforce that to develop ecological indicators for the effects of climate in cities, future research must also focus on either proposing alternative metrics, or to develop statistical methodologies to disentangle the effects of the prevailing environmental driver (e.g., air pollution) before looking at the effects of climate. Such need has already been raised (Branquinho et al., 2015), but remains unanswered. Although this problem is foreseen to decrease in the future – with the increasing importance of climate change together with a decrease in air pollution loads across Europe (Ortiz et al., 2020), disentangling climate from the remaining urban global change drivers is fundamental to establish a baseline of effects at the broad scale (Ellis and Coppins, 2010; Nascimbene et al., 2012).

Whitin the explored urban areas, the importance of local scale drivers across all tested metrics, assumed here to represent the proportion of variance not explained by the broad-scale drivers, averaged at 85%. These could comprehend local pollution sources (e.g., industry facility or traffic), green urban area management and history (e.g., parks created from existing woodland) and phorophyte species and age (although this last was partially controlled trough the field sampling phorophyte restrictions), all which have been seen to impact urban lichen communities (Matos et al., 2019; McDonald et al., 2017; Munzi et al., 2014). These results show the need to further detail the local drivers, and their sources. To do so, one requires the use of local environmental data, which should be derived from common methods, rather than local-based information sources, such as city-specific cartography or single city studies. Furthermore, other methods, such as lichens elemental analysis, can complement the application of lichens as ecological indicators, as these possess the capacity to detail local pollution sources and origins (Jeran et al., 2002; Van Der Wat and Forbes, 2015). However, this is a more costly approach and contrary to ecological indicators, uncappable to reflect environmental drivers' effects at the ecosystem level. These findings thus stress that, for future European (EU) and global (UN- 11th SDG) efforts towards more sustainable and resilient cities, development of indicators to monitor global change drivers' effects on urban ecosystems must be able to detect the effects of drivers working at both scales and to be applied over wide continental to global gradients (Hák et al., 2016; Klopp and Petretta, 2017). Despite all limitations and future challenges, biodiversity-based ecological indicators are a valuable tool to quantify the effects of broad scale drivers on urban ecosystems structure and properties. As they are based on biodiversity, the backbone of ecosystem functioning, they can reflect these global change drivers' effects on urban ecosystem services and functioning, which analytical methods (i.e., pollutants concentration, air temperature, precipitation and humidity levels monitoring) alone are not capable to translate. Furthermore, their cost-effectiveness allows to extensively monitor these effects over multiple cities.

6. Conclusions

For the first time, we were able to quantify the amount of variance of lichen biodiversity metrics explained by broad scale drivers associated with pollution and climate in urban areas. Overall, broad scale drivers explained 15% of variance of lichen metrics, suggesting these were overshadowed by the effects of local drivers. Thus, our work supports the need to quantify the effects of drivers working at the local scale even in multi cities studies. At the broad scale, air pollution was more important than climate, suggesting that urban lichen communities are primarily driven by pollution. This had only been shown before for single cities studies and was shown here also, in a multi city design. Results also suggest that only when pollution decreases, the effects of climate can be detected. In our study, the effects of broad scale drivers had a statistical significance effect on lichen metrics variances, and thus broad scale drivers must be considered alongside local drivers. From an ecological indicator perspective, the overall low contribution of broad scale drivers across most metrics suggests that the tested lichens biodiversity-based metrics and statistical approach are hard to apply directly, i.e., independently of local context, to characterize the effects of broad scale drivers. Still, ecological indicators capacity to reflect the effects at the ecosystem level makes them valuable tools toward achieving UN conventions goals on urban areas, e.g., those related to air pollution (CLRTAP) or climate change (UNFCCC). Their application can help overcome the lack of baseline characterization of pollution and climate effects, especially in southern European cities (Reckien et al., 2015), and thus, help create more resilient cities to face future climate change effects as well as strategies to measure the efficacy of adopted measures. But first, metrics must be compared across cities, and for that, broad- and local-scale drivers' effects must be simultaneously considered. Thus, if we are to use them to evaluate the effects of broad scale drivers in urban ecosystems, alternative sampling designs or statistical approaches must be considered first.

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References:

Aptroot, A., Stapper, N.J., Košuthová, A., van Herk, K., 2021. Chapter 23 - Lichens as an indicator of climate and global change, in: Letcher, T.M. (Ed.), Climate Change (Third Edition). Elsevier, pp. 483-497.

Aptroot, A., Van Herk, C.M., 2007. Further evidence of the effects of global warming on lichens, particularly those with Trentepohlia phycobionts. Environmental Pollution 146, 293-298.

Asta, J., Erhardt, W., Ferretti, M., Fornasier, F., Kirschbaum, U., Nimis, P.L., Purvis, O.W., Pirintsos, S., Scheidegger, C., van Haluwyn, C., Wirth, V., 2002. Mapping lichen diversity as an indicator of environmental quality, in: Nimis, P., Scheidegger, C., Wolseley, P. (Eds.), Monitoring with Lichens-Monitoring Lichens. Kluwer Academic Publisher, The Netherlands, pp. 273-279.

Babiy, A.P., Kharytonov, M.M., Gritsan, N.P., 2003. Connection Between Emissions and Concentrations of Atmospheric Pollutants, in: Melas, D., Syrakov, D. (Eds.), Air Pollution Processes in Regional Scale. Springer Netherlands, Dordrecht, pp. 11-19.

Barwell, L.J., Isaac, N.J.B., Kunin, W.E., 2015. Measuring β-diversity with species abundance data. Journal of Animal Ecology 84, 1112-1122.

Branquinho, C., Matos, P., Pinho, P., 2015. Lichens as ecological indicators to track atmospheric changes: future challenges. Indicators and surrogates of biodiversity and environmental change. CSIRO Publishing, Melbourne, CRC Press, London, 77-87.

Branquinho, C., Serrano, H.C., Nunes, A., Pinho, P., Matos, P., 2019. Essential Biodiversity Change Indicators for Evaluating the Effects of Anthropocene in Ecosystems at a Global Scale, History, Philosophy and Theory of the Life Sciences. Springer International Publishing, pp. 137-163.

Brunialti, G., Frati, L., Loppi, S., 2012. Fragmentation of Mediterranean oak forests affects the diversity of epiphytic lichens. Nova Hedwigia 96, 265-278.

Cartalis, C., 2014. Toward resilient cities – a review of definitions, challenges and prospects. Advances in Building Energy Research 8, 259-266.

Concostrina-Zubiri, L., Pescador, D.S., Martínez, I., Escudero, A., 2014. Climate and small scale factors determine functional diversity shifts of biological soil crusts in Iberian drylands. Biodiversity and Conservation 23, 1757-1770.

Cristofolini, F., Brunialti, G., Giordani, P., Nascimbene, J., Cristofori, A., Gottardini, E., Frati, L., Matos, P., Batic, F., Caporale, S., Fornasier, M.F., Marmor, L., Merinero, S., Zapata, J.N., Torra, T., Wolseley, P., Ferretti, M., 2014a. Towards the adoption of an international standard for biomonitoring with lichens-Consistency of assessment performed by experts from six European countries. Ecological Indicators 45, 63-67.

Cristofolini, F., Brunialti, G., Giordani, P., Nascimbene, J., Cristofori, A., Gottardini, E., Frati, L., Matos, P., Batič, F., Caporale, S., Fornasier, M.F., Marmor, L., Merinero, S., Nuñez Zapata, J., Tõrra, T., Wolseley, P., Ferretti, M., 2014b. Towards the adoption of an international standard for biomonitoring with lichens—Consistency of assessment performed by experts from six European countries. Ecological Indicators 45, 63-67.

Davies, L., Bates, J.W., Bell, J.N.B., James, P.W., Purvis, O.W., 2007. Diversity and sensitivity of epiphytes to oxides of nitrogen in London. Environmental Pollution 146, 299-310.

Dawson, R., Hall, J., Barr, S., Batty, M., Bristow, A., Carney, S., Dagoumas, A., Evans, S., Ford, A., Harwatt, H., Köhler, J., Tight, M., Walsh, C., Zanni, A., 2017. A blueprint for the integrated assessment of climate change in cities: The Urban War against Climate Change, pp. 32-51.

Di Nuzzo, L., Vallese, C., Benesperi, R., Giordani, P., Chiarucci, A., Di Cecco, V., Di Martino, L., Di Musciano, M., Gheza, G., Lelli, C., Spitale, D., Nascimbene, J., 2021. Contrasting multitaxon responses to climate change in Mediterranean mountains. Scientific Reports 11.

EEA, 2018. Copernicus Land Monitoring Service - Urban Atlas, in: Agency, E.E. (Ed.), www.eea.europa.eu/data-and-maps/data/copernicus-land-monitoring-service-urban-atlas.

Ellis, C.J., Coppins, B.J., 2006. Contrasting functional traits maintain lichen epiphyte diversity in response to climate and autogenic succession. Journal of Biogeography 33, 1643-1656.

Evju, M., Bruteig, I.E., 2013. Lichen community change over a 15-year time period: effects of climate and pollution. The Lichenologist 45, 35-50.

Fagerli, H., Tsyro, S., Jonson, J.E., Nyíri, Á., Gauss, M., Simpson, D., Wind, P., Benetictow, A., Klein, H., Mortier, A., Aas, W., Hjellbrekke, A.-G., Solberg, S., Platt, S.M., Yttri, K.E., Tørseth, K., Gaisbauer, S., Mareckova, K., Matthews, B., Schindlbacher, S., Sosa, C., Tista, M., Ullrich, B., Wankmüller, R., Scheuschner, T., Bergström, R., Johanson, L., Jalkanen, J.-P., Metzger, S., van der Gon, H.A.C.D., Kuenen, J.J.P., Visschedijk, A.J.H., Barregård, L., Molnár, P., Stockfelt, L., 2019. Transboundary particulate matter, photo-oxidants, acidifying and eutrophying components, EMEP Report 1/2019. METEOROLOGISK iNSTITUTT Norwegian Meteorological Institute, p. 44.

Fenger, J., 1999. Urban air quality. Atmospheric Environment 33, 4877-4900.

Fiore, A.M., Naik, V., Leibensperger, E.M., 2015. Air Quality and Climate Connections. Journal of the Air & Waste Management Association 65, 645-685.

Gary, B.P., 2010. Bioassessing air pollution effects with epiphytic lichens in Raleigh, North Carolina, U.S.A. The Bryologist 113, 39-50.

Geiser, L.H., Root, H., Smith, R.J., Jovan, S.E., St Clair, L., Dillman, K.L., 2021. Lichen-based critical loads for deposition of nitrogen and sulfur in US forests. Environmental Pollution 291, 118187.

Giordani, P., Malaspina, P., 2017. Do tree-related factors mediate the response of lichen functional groups to eutrophication? Plant Biosystems-An International Journal Dealing with all Aspects of Plant Biology 151, 1062-1072.

Gustafson, E.J., Parker, G.R., 1992. Relationships between landcover proportion and indices of landscape spatial pattern. Landscape Ecology 7, 101-110.

Harlan, S.L., Ruddell, D.M., 2011. Climate change and health in cities: impacts of heat and air pollution and potential co-benefits from mitigation and adaptation. Current Opinion in Environmental Sustainability 3, 126-134.

Hauck, M., Bruyn, U.d., Leuschner, C., 2013. Dramatic diversity losses in epiphytic lichens in temperate broad-leaved forests during the last 150years. Biological Conservation 157, 136-145.

Hawksworth, D., 1990. The long-term effects of air pollutants on lichen communities in Europe and North America. The Earth in transition: patterns and processes of biotic impoverishment. Cambridge University Press, Cambridge, 45-64.

Hurtado, P., Matos, P., Aragón, G., Branquinho, C., Prieto, M., Martínez, I., 2020. How much matching there is in functional, phylogenetic and taxonomic optima of epiphytic macrolichen communities along a European climatic gradient? Science of The Total Environment 712, 136533.

Hák, T., Janoušková, S., Moldan, B., 2016. Sustainable Development Goals: A need for relevant indicators. Ecological Indicators 60, 565-573.

Jenerette, G.D., Harlan, S.L., Brazel, A., Jones, N., Larsen, L., Stefanov, W.L., 2007. Regional relationships between surface temperature, vegetation, and human settlement in a rapidly urbanizing ecosystem. Landscape Ecology 22, 353-365.

Jeran, Z., Jaćimović, R., Batič, F., Mavsar, R., 2002. Lichens as integrating air pollution monitors. Environmental Pollution 120, 107-113.

Karger D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Zimmermann, N.E., Linder, H.P., Kessler, M., 2018. Data from: Climatologies at high resolution for the earth's land surface areas. Dryad Digital Repository.

Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Zimmermann, N.E., Linder, H.P., Kessler, M., 2017. Climatologies at high resolution for the earth's land surface areas. Scientific Data 4, 170122.

Kinney, P.L., 2008. Climate Change, Air Quality, and Human Health. American Journal of Preventive Medicine 35, 459-467.

Klopp, J.M., Petretta, D.L., 2017. The urban sustainable development goal: Indicators, complexity and the politics of measuring cities. Cities 63, 92-97.

Koch, N.M., Branquinho, C., Matos, P., Pinho, P., Lucheta, F., Martins, S.M., Vargas, V.M., 2016. The application of lichens as ecological surrogates of air pollution in the subtropics: a case study in South Brazil. Environmental Science and Pollution Research 23, 20819-20834.

Koch, N.M., Matos, P., Branquinho, C., Pinho, P., Lucheta, F., Martins, S.M.d.A., Vargas, V.M.F., 2019. Selecting lichen functional traits as ecological indicators of the effects of urban environment. Science of The Total Environment 654, 705-713.

Krzyzanowski, M., Apte, J.S., Bonjour, S.P., Brauer, M., Cohen, A.J., Prüss-Ustun, A.M., 2014. Air Pollution in the Mega-cities. Current Environmental Health Reports 1, 185-191.

Laliberté, E., Legendre, P., Shipley, B., 2014. FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-12. Vienna, Austria: R Foundation for Statistical Computing.

Larsen, R.S., Bell, J.N.B., James, P.W., Chimonides, P.J., Rumsey, F.J., Tremper, A., Purvis, O.W., 2007. Lichen and bryophyte distribution on oak in London in relation to air pollution and bark acidity. Environmental Pollution 146, 332-340.

LiŠKa, J., Herben, T., 2008. Long-term changes of epiphytic lichen species composition over landscape gradients: an 18 year time series. The Lichenologist 40, 437-448.

Llop, E., Pinho, P., Matos, P., Pereira, M.J., Branquinho, C., 2012. The use of lichen functional groups as indicators of air quality in a Mediterranean urban environment. Ecological indicators 13, 215-221.

Llop, E., Pinho, P., Ribeiro, M.C., Pereira, M.J., Branquinho, C., 2017. Traffic represents the main source of pollution in small Mediterranean urban areas as seen by lichen functional groups. Environmental Science and Pollution Research 24, 12016-12025.

Loppi, S., Pirintsos, S., 2000. Effect of dust on epiphytic lichen vegetation in the Mediterranean area (Italy and Greece). Israel Journal of Plant Sciences 48, 91-95.

Lättman, H., Bergman, K.-O., Rapp, M., Tälle, M., Westerberg, L., Milberg, P., 2014. Decline in lichen biodiversity on oak trunks due to urbanization. Nordic Journal of Botany 32, 518-528.

Maes, M.J.A., Jones, K.E., Toledano, M.B., Milligan, B., 2019. Mapping synergies and trade-offs between urban ecosystems and the sustainable development goals. Environmental Science & Policy 93, 181-188.

Matos, P., Pinho, P., Aragon, G., Martínez, I., Nunes, A., Soares, A.M., Branquinho, C., 2015. Lichen traits responding to aridity. Journal of Ecology 103, 451-458.

Matos, P., Vieira, J., Rocha, B., Branquinho, C., Pinho, P., 2019. Modeling the provision of air-quality regulation ecosystem service provided by urban green spaces using lichens as ecological indicators. Science of the Total Environment, 705-713.

Mayrhofer, H., Moberg, R., 2002. Nordic Lichen Flora Volume 2. Physciaceae.

McCarthy, D.P., Craig, B., Brand, U., 2009. Chapter 10 Lichen Monitoring of Urban Air Quality, Hamilton, Ontario, in: Legge, A.H. (Ed.), Developments in Environmental Science. Elsevier, pp. 247-267.

Mccune, B., Dey, J., Peck, J., Heiman, K., Will-Wolf, S., 1997. Regional Gradients in Lichen Communities of the Southeast United States. The Bryologist 100, 145.

McDonald, L., Van Woudenberg, M., Dorin, B., Adcock, A.M., McMullin, R.T., Cottenie, K., 2017. The effects of bark quality on corticolous lichen community composition in urban parks of southern Ontario. Botany 95, 1141-1149.

Molina, M.J., Molina, L.T., 2004. Megacities and Atmospheric Pollution. Journal of the Air & Waste Management Association 54, 644-680.

Mori, I., Group, T., Associati, E., 2019. Assessment Study of the Urban Agenda for the European Union (UAEU). European Commission, https://ec.europa.eu/regional_policy/en/information/publications/studies/2019/assessment-study-of-the-urban-agenda-for-the-european-union-uaeu, p. 195.

Munzi, S., Correia, O., Silva, P., Lopes, N., Freitas, C., Branquinho, C., Pinho, P., 2014. Lichens as ecological indicators in urban areas: beyond the effects of pollutants. Journal of Applied Ecology 51, 1750-1757.

Munzi, S., Ravera, S., Caneva, G., 2007. Epiphytic lichens as indicators of environmental quality in Rome. Environmental Pollution 146, 350-358.

Nash, T.H., Gries, C., 1991. Lichens as Indicators of Air Pollution, in: Gries, C., Lipfert, F.W., Lippmann, M., Nash, T.H. (Eds.), Air Pollution. Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 1-29.

Niemi, G.J., Mcdonald, M.E., 2004. Application of Ecological Indicators. Annual Review of Ecology, Evolution, and Systematics 35, 89-111.

Nimis, P.L., Martellos, S., 2021. ITALIC - The Information System on Italian Lichens. Version 5.0. University of Trieste, Dept. of Biology, (http://dryades.units.it/italic).

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'hara, R., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2011. vegan: Community ecology package. R package version, 117-118.

O'Donnell, M.S., Ignizio, D.A., 2012. Bioclimatic predictors for supporting ecological applications in the conterminous United States. US Geological Survey Data Series 691, 4-9.

Phinney, N.H., Gauslaa, Y., Palmqvist, K., Esseen, P.-A., 2021. Macroclimate drives growth of hair lichens in boreal forest canopies. Journal of Ecology 109, 478-490.

Pinho, P., Dias, T., Cruz, C., Sim Tang, Y., Sutton, M.A., Martins-Loução, M.A., Máguas, C., Branquinho, C., 2011. Using lichen functional diversity to assess the effects of atmospheric ammonia in Mediterranean woodlands. Journal of Applied Ecology 48, 1107-1116.

Randlane, T., Saag, A., 2004. Eesti pisisamblikud (Estonian Microlichens). Tartu Ülikooli Kirjastus, Tartu.

Reckien, D., Flacke, J., Olazabal, M., Heidrich, O., 2015. The Influence of Drivers and Barriers on Urban Adaptation and Mitigation Plans—An Empirical Analysis of European Cities. PLOS ONE 10, e0135597.

Riga-Karandinos, A.-N., Saitanis, C., 2005. Comparative assessment of ambient air quality in two typical Mediterranean coastal cities in Greece. Chemosphere 59, 1125-1136.

Rocha, B., Pinho, P., Vieira, J., Branquinho, C., Matos, P., 2019. Testing the Poleotolerance Lichen Response Trait as an Indicator of Anthropic Disturbance in an Urban Environment. Diversity 11, 55.

Romero, H., Ihl, M., Rivera, A., Zalazar, P., Azocar, P., 1999. Rapid urban growth, land-use changes and air pollution in Santiago, Chile. Atmospheric Environment 33, 4039-4047.

Singh, R., Srivastava, V., Singh, A., 2017. Environmental Issues Surrounding Human Overpopulation.

Smith, C.W., Aptroot, A., Coppins, B.J., Fletcher, A., Gilbert, O.L., James, P.W., Wolseley, P.A., 2009. The Lichens of Great Britain and Ireland. British Lichen Society.

Tam, B.Y., Gough, W.A., Mohsin, T., 2015. The impact of urbanization and the urban heat island effect on day to day temperature variation. Urban Climate 12, 1-10.

Team, R., 2021. RStudio: Integrated Development Environment for R. RStudio, 1.4.1103 ed, PBC, Boston.

Team, R.C., 2020. R: A language and environment for statistical computing, Vienna, Austria: R Foundation for Statistical Computing.

Title, P.O., Bemmels, J.B., 2018. ENVIREM: an expanded set of bioclimatic and topographic variables increases flexibility and improves performance of ecological niche modeling. Ecography 41, 291-307.

Tzoulas, K., Korpela, K., Venn, S., Yli-Pelkonen, V., Kaźmierczak, A., Niemela, J., James, P., 2007. Promoting ecosystem and human health in urban areas using Green Infrastructure: A literature review. Landscape and Urban Planning 81, 167-178.

UN, 2015. United Nations: Sustainable development knowledge platform. United Nations: Department of Economic and Social Affairs, https://sdgs.un.org/goals.

UN, 2019. World Urbanization Prospects: The 2018 Revision. United Nations, New York.

Van Der Plas, F., 2019. Biodiversity and ecosystem functioning in naturally assembled communities. Biological Reviews.

Van Der Wat, L., Forbes, P.B.C., 2015. Lichens as biomonitors for organic air pollutants. TrAC Trends in Analytical Chemistry 64, 165-172.

Van Herk, C., Mathijssen-Spiekman, E., De Zwart, D., 2003. Long distance nitrogen air pollution effects on lichens in Europe. The Lichenologist 35, 347-359.

van Herk, C.M., Aptroot, A., van Dobben, H.F., 2002. Long-Term Monitoring in the Netherlands Suggests that Lichens Respond to Global Warming. The Lichenologist 34, 141-154.

Varela, Z., López-Sánchez, G., Yáñez, M., Pérez, C., Fernández, J.A., Matos, P., Branquinho, C., Aboal, J.R., 2018. Changes in epiphytic lichen diversity are associated with air particulate matter levels: The case study of urban areas in Chile. Ecological Indicators 91, 307-314.

WHO, 2016. Health as the pulse of the new urban agenda: United Nations conference on housing and sustainable urban development, Quito, October 2016. World Health Organization, Geneva.

Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1, 3-14.

Figures and Tables:

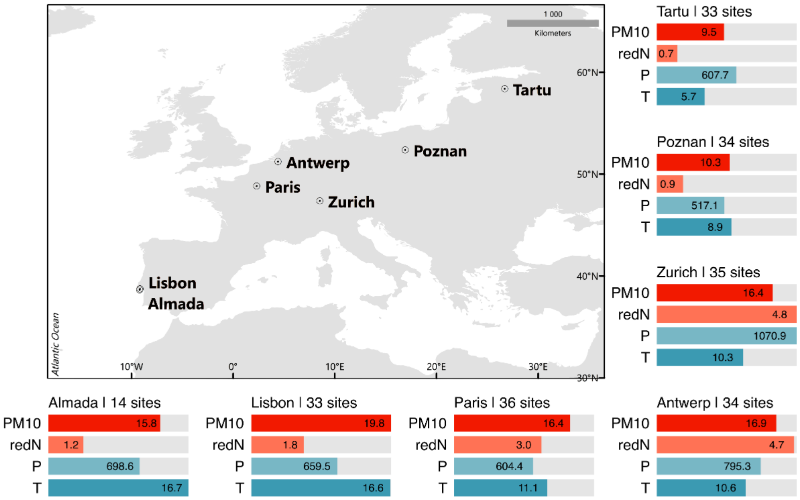
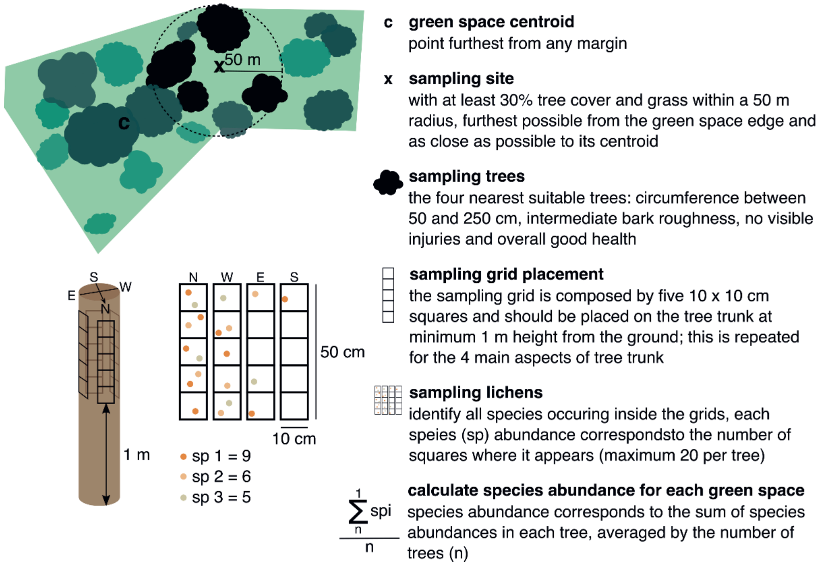


Figure 1: Map of the seven sampled European cities along a continental gradient of pollution and climate, characterized by average annual particulate matter concentration (PM10, inµg.m^{-3}), reduced nitrogen deposition (redN, in mg.m^{-2}), mean annual precipitation (P, in mm) and annual mean temperature (T, in °C). The number of green spaces sampled in each city was derived from the random sampling selection of parks, stratified by size and fragmentation (N=219).



c green space centroid
point furthest from any margin

x sampling site
with at least 30% tree cover and grass within a 50 m radius, furthest possible from the green space edge and as close as possible to its centroid

sampling trees
the four nearest suitable trees: circumference between 50 and 250 cm, intermediate bark roughness, no visible injuries and overall good health

sampling grid placement
the sampling grid is composed by five 10 x 10 cm squares and should be placed on the tree trunk at minimum 1 m height from the ground; this is repeated for the 4 main aspects of tree trunk

sampling lichens
identify all species occuring inside the grids, each speies (sp) abundance correspondsto the number of squares where it appears (maximum 20 per tree)

$$\frac{\sum_{n}^{1} spi}{n}$$

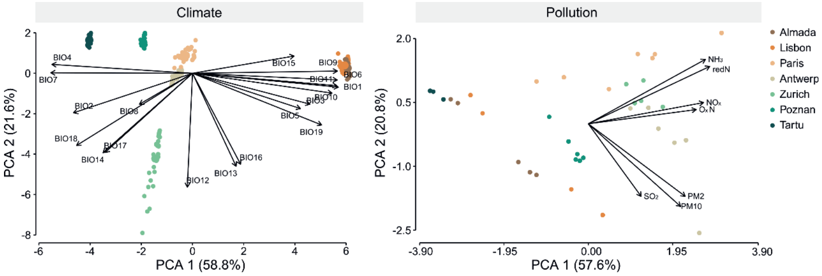
calculate species abundance for each green space
species abundance corresponds to the sum of species abundances in each tree, averaged by the number of trees (n)

Figure 2. Selection of sampling site inside a green space patch and sampling scheme for epiphytic lichens, according to the European Standard Method (Asta et al., 2002; Cristofolini et al., 2014a).

Table 1: Lichen species traits and related functional groups (with categorical and correspondent ordinal classification) used in the study, described following *(Nimis and Martellos, 2021)*. For species trait classification see Table S1.

Trait	Functional group	Description
growth form	crustose	thallus firmly and entirely attached to the substrate by the lower surface
	foliose broad-lobed	thallus partly attached to the substrate, with distinct upper and lower surfaces and broad lobes
	foliose narrow-lobed	thallus partly attached to the substrate, with distinct upper and lower surfaces and narrow lobes
	fruticose	thallus attached to the substrate by one single point and with rounded or flattened branches
	leprose	thallus like crustose but surface thallus with a granular mass appearance and always decorticated
	squamulose	thallus composed of small scales
main photobiont	cyanobacteria	lichens with cyanobacteria

type	green algae	lichens with green algae other than *Trentepohlia*
	trentepohlia	lichens with *Trentepohlia* (green algae)
species substrate pH tolerance	low (1)	occurs in very acid substrata
	medium-low (2)	occurs in acid substrata
	medium (3)	occurs in subacid to sub neutral substrata
	medium-high (4)	occurs in slightly basic substrata
	high (5)	occurs in basic substrata
solar irradiation tolerance	low (1)	occurs in very shaded situations
	medium-low (2)	occurs in shaded situations
	medium (3)	occurs in sites with plenty of diffuse light but scarce direct solar irradiation
	medium-high (4)	occurs in sun-exposed sites
	high (5)	occurs in very high direct solar irradiation
aridity tolerance	low (1)	Hygrophytic
	medium-low (2)	rather hygrophytic
	medium (3)	mesophytic
	medium-high (4)	xerophytic
	high (5)	very xerophytic
eutrophication tolerance	low (1)	occurs in sites with no eutrophication
	medium-low (2)	occurs in sites with very weak eutrophication
	medium (3)	occurs in sites with weak eutrophication
	medium-high (4)	occurs in sites with rather high eutrophication
	high (5)	occurs in sites with very high eutrophication
poleotolerance	low (0)	occurs in undisturbed forests
	medium-low (1)	occurs in natural or semi-natural habitats
	medium (2)	occurs in moderately disturbed areas
	high (3)	occurs in heavily disturbed areas



(a) (b)

Figure 3: Principal Components Analysis showing the ordination of sampling sites (N=219) along climate (a) and air pollution (b) gradients. In the climate PCA (a), the first axis (PCA 1) represents a temperature gradient while the second one (PCA 2) represents a precipitation gradient. Decoding of bioclimatic variables can be seen in Table S2. In the air pollution PCA (b), the first axis (PCA 1) represents a gradient of increasing air pollution while the second one (PCA 2) distinguishes between sites polluted by N-based compounds on one side and sulfur dioxide and particulate matter on the other. Pollutant's deposition: redN - reduced nitrogen and OxN - oxidized nitrogen. Pollutant's air concentration: NH3 – ammonia, SO2 - sulfur dioxide, NOx - nitrogen oxide. PM2.5 and PM10 are atmospheric particulate matter of less than, respectively, 2.5 and 10 micrometres in diameter. Sites overlap in PCA (b) due to the lower spatial resolution of air pollution variables.

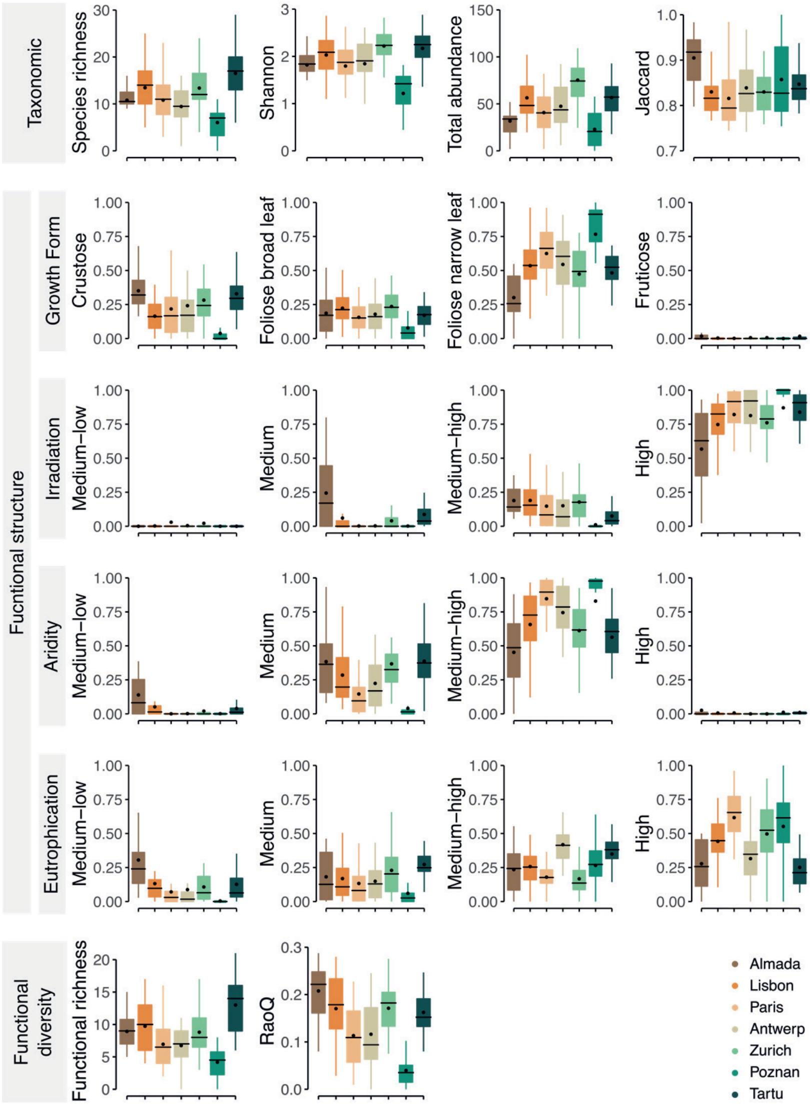


Figure 4: Boxplots representing the distribution of taxonomic, functional structure and functional diversity metrics in the seven European cities, ordered here from the warmest (Almada to the coldest (Tartu), as indicated in the first axis of the PCA. Shannon, Jaccard and Rao's Q indices values range from 0 to 1. The functional structure, represented here by the CWM of each functional group (Table 1) belonging to the same trait (growth form, tolerance to irradiation, tolerance to aridity, tolerance to eutrophication) ranges also from 0 to 1 (the sum of all functional groups from the same trait is 1 at site

level). Boxes display first to third interquartile ranges, the black lines the median, the dots the average, and the whiskers the maximum and minimum (N=219).

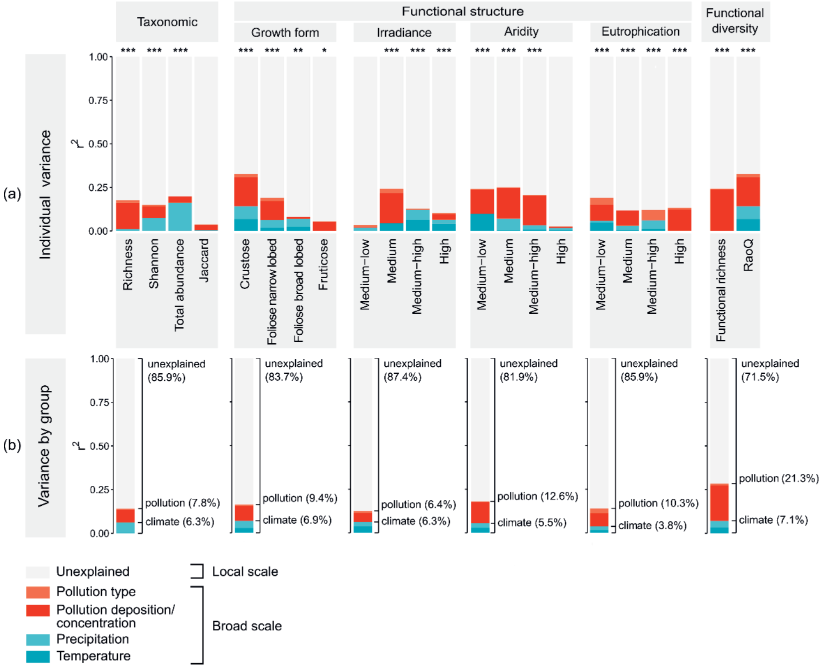


Figure 5: Variance partitioning of broad scale drivers for each (a) lichen biodiversity metrics and (b) the average variance partitioning for each group of metrics. Metrics are grouped into taxonomic and trait-based, the latter sub-divided into functional diversity and functional structure by trait (growth form and tolerance to irradiance, aridity and eutrophication). Temperature reflects the first climate PCA axis, related to a broad scale temperature gradient. Precipitation reflects the second climate PCA axis, related to a broad scale precipitation gradient. Air pollution deposition/concentration reflects the first air pollution PCA axis, related to a broad scale gradient of air pollution. Air pollution type reflects the second air pollution PCA axis, related to a broad scale gradient of air pollution ranging from N-based pollutants on one side, to sulfur dioxide and particulate matter compounds on the other. Significance of the model is indicated in superscript: * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$. Averaged variance (%), per spatial scale and metric group, was calculated assuming all metrics to value the same when evaluating changes in lichens community structure.

Supplement of

Testing lichens as ecological indicators of the effects of multiple global change drivers in European cities at the broad spatial scale

Bernardo Rocha [1], Paula Matos [2*], Paolo Giordani [3], Lõhmus Piret [4], Cristina Branquinho [1], Joan Casanelles-Abella [5,6], Cristiana Aleixo [1], Nicolas Deguines [7], Tiit Hallikma [8], Lauri Laanisto [8], Marco Moretti [5], Marta Maria Alos Orti [8,] Roeland Samson [9], Piotr Tryjanowski [10], and Pedro Pinho [1]

[1] cE3c - Centre for Ecology, Evolution and Environmental Changes, FCUL, Campo Grande, 1749-016 Lisboa Portugal; brerocha@fc.ul.pt

[2] CEG - Centro de Estudos Geográficos do Instituto de Geografia e Ordenamento do Território da Universidade de Lisboa, 1600-276 Lisboa, Portugal; psmatos@fc.ul.pt

[3] DIFAR, University of Genova; giordani@difar.unige.it

[4] Institute of Ecology and Earth Science, University of Tartu, Lai st.40, Tartu, EE51005, Estonia; piret.lohmus@ut.ee

[5] Biodiversity and Conservation Biology, Swiss Federal Institute for Forest, Snow and Landscape Research WSL, 8903 Birmensdorf, Switzerland; joan.casanelles@wsl.ch

[6]Department of Environmental Systems Science, Institute of Terrestrial Ecosystems, ETH Zürich, 8049 Zürich, Switzerland

[7] Université Paris-Saclay, CNRS, AgroParisTech, Ecologie Systématique Evolution, Orsay, France.; nicolas.deguines@univ-poitiers.fr

[8] Chair of Biodiversity and Nature Tourism, Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, Kreutzwaldi 5, 51006 Tartu, Estonia; martaalosorti@gmail.com

[9] Laboratory of Environmental and Urban Ecology, Departement of Bioscience Engineering, University of Antwerp, 2020 Antwerpen, Belgium; roeland.samson@uantwerpen.be

[10] Department of Zoology, Poznan University of Life Sciences, Woska Polskiego 71C, 60-625 Poznan; piotr.tryjanowski@gmail.com

***** Correspondence: psmatos@fc.ul.pt. Phone: +351 21 044 30 00

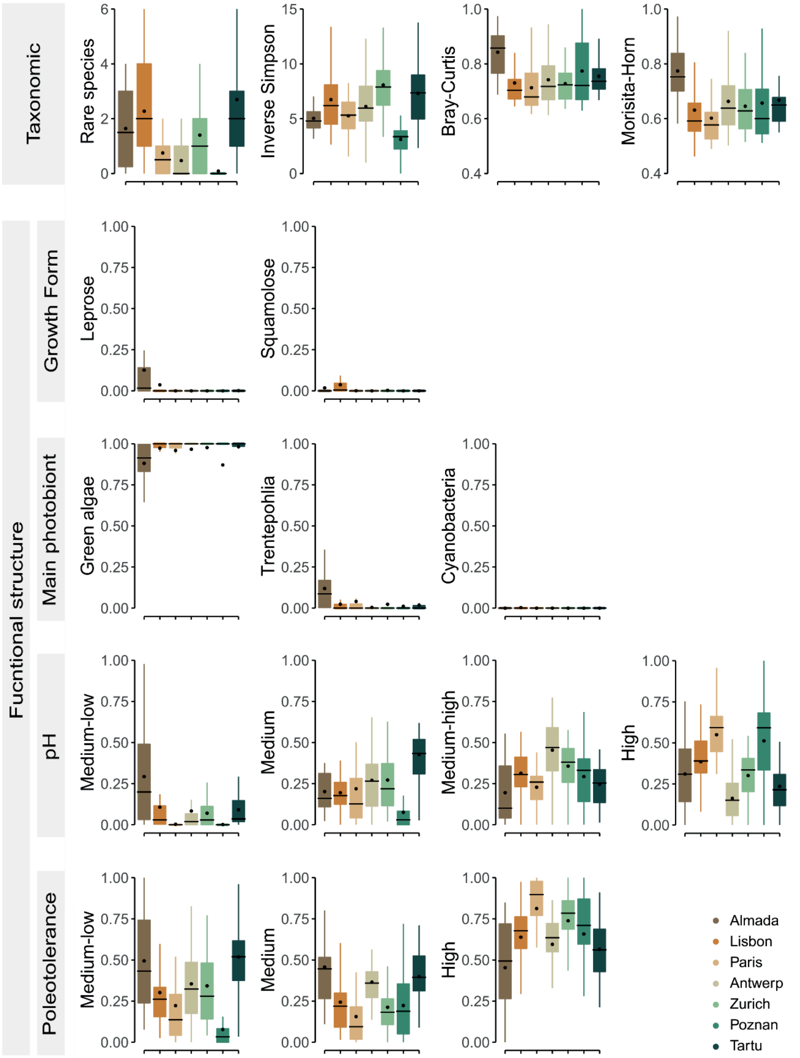


Figure S1: Boxplots representing the distribution of remaining taxonomic (rare species, inverse Simpson, Bray-Curtis and Morisita-Horn) and functional structure (Growth form, main photobiont type, species substrate pH tolerance and poleotolerance) metrics in the seven European cities, ordered here from the warmest (Almada to the coldest (Tartu), as indicated in the first axis of the PCA. Bray-Curtis and Morisita-Horn indices values range from 0 to 1. The functional structure (Table 1), represented here by the CMW of each functional group belonging to the same trait (growth form, species substrate pH tolerance and poleotolerance) ranges also from 0 to 1 (the sum of all functional groups from the same trait is 1 at site level). Boxes display first to third interquartile ranges, the black lines the median, the dots the average, and the whiskers the maximum and minimum (N=219). Only metrics not represent on the main text (Figure 4) are shown here.

Table S1: List of total species identified (N=140) and respective functional characterization based on the growth form, type of algae, main reproduction type, and tolerance to different levels of substrate pH requirement, solar irradiation, aridity, eutrophication and poleotolerance. Nomenclature followed [1].

Scientific name	**Growth form**[1]	**Photobiont**[2]	**Reproduction**[3]	**pH**[4]	**Irradiation**[5]	**Aridity**[6]	**Eutrophication**[7]	**Poleotolerance**[8]
Acrocordia cavata	c	t	se	3	3	2	1	0
Alyxoria varia	c	t	se	3	3	3	2	2
Amandinea punctata	c	g	se	3	5	4	4	3
Arthonia sp. *	-	-	-	-	-	-	-	-
Arthonia mediella	c	t	se	2	3	3	1	1
Arthonia radiata	c	t	se	3	4	3	3	3
Athallia cerinelloides	c	g	se	4	5	4	4	2
Athallia pyracea	c	g	se	4	5	4	4	2
Arthopyrenia sp. *	-	-	-	-	-	-	-	-
Bacidia arceutina	c	g	se	3	4	3	2	1
Bacidia rubella	c	g	se	3	4	3	3	2
Bacidia subincompta	c	g	se	3	3	2	2	1
Bacidina arnoldiana	c	g	se	3	3	2	3	2
Biatoridium monasteriense	c	g	se	3	3	2	3	2
Buellia griseovirens	c	g	se	2	4	3	1	2

Scientific name	Growth form[1]	Photobiont[2]	Reproduction[3]	pH[4]	Irradiation[5]	Aridity[6]	Eutrophication[7]	Poleotolerance[8]
Caloplaca cerina	c	g	se	4	4	4	4	3
Candelaria concolor	fn	g	so	4	5	4	5	3
Candelariella reflexa	c	g	so	4	5	3	5	3
Candelariella vitellina	c	g	se	3	5	4	5	3
Candelariella xanthostigma	c	g	se	3	5	3	3	3
Catapyrenium psoromoides	sq	g	se	3	4	3	2	1
Catillaria nigroclavata	c	g	se	3	4	3	3	2
Chaenotheca chrysocephala	c	g	se	2	4	3	1	1
Chaenotheca furfuracea	c	g	se	2	3	2	1	2
Chaenotheca phaeocephala	c	g	se	2	3	2	1	1
Chaenotheca stemonea	c	g	se	2	3	1	1	1
Chaenotheca trichialis	c	g	se	2	3	2	1	1
Chaenotheca xyloxena	c	g	se	2	3	2	1	1
Chrysothrix candelaris	l	g	so	2	3	3	1	2
Cladonia sp. *	-	-	-	-	-	-	-	-

Scientific name	Growth form[1]	Photobiont[2]	Reproduction[3]	pH[4]	Irradiation[5]	Aridity[6]	Eutrophication[7]	Poleotolerance[8]
Cladonia fimbriata	f	g	so	3	4	3	3	2
Coenogonium pineti	c	t	se	3	3	3	2	2
Coenogonium tavaresianum	c	t	se	2	3	1	1	0
Collema furfuraceum	fb	c	is	3	4	2	3	1
*Cyphelium sp. **	-	-	-	-	-	-	-	-
Dendrographa decolorans	c	t	so	2	3	2	3	2
Diploicia canescens	c	g	so	5	5	3	4	2
Evernia prunastri	f	g	so	3	5	3	3	2
Flavoparmelia caperata	fb	g	so	3	4	3	3	2
Flavoparmelia soredians	fb	g	so	3	5	3	3	2
Flavoplaca citrina	c	g	so	5	5	4	5	3
Gyalecta fagicola	c	t	se	3	3	2	1	0
Hyperphyscia adglutinata	fn	g	so	5	5	4	5	3
Hypogymnia physodes	fn	g	so	3	4	3	2	3
Hypogymnia tubulosa	fn	g	so	2	3	3	2	2
Hypogymnia tubulosa f. farinosa	fn	g	so	2	3	3	2	2

Scientific name	Growth form[1]	Photobiont[2]	Reproduction[3]	pH[4]	Irradiation[5]	Aridity[6]	Eutrophication[7]	Poleotolerance[8]
Hypotrachyna revoluta	fb	g	so	2	3	3	3	2
Lecania cyrtella	c	g	se	3	5	4	3	3
Lecania naegelii	c	g	se	3	4	3	3	2
Lecanographa amylacea	c	t	se	2	4	2	1	0
Lecanographa lyncea	c	t	se	2	4	2	1	0
*Lecanora sp. **	-	-	-	-	-	-	-	-
Lecanora albella	c	g	se	2	3	2	1	1
Lecanora allophana	c	g	se	3	5	4	3	2
Lecanora argentata	c	g	se	3	4	3	2	2
Lecanora carpinea	c	g	se	3	5	4	3	3
Lecanora chlarotera	c	g	se	3	5	4	5	3
Lecanora conizaeoides	c	g	se	2	5	3	3	3
Lecanora expallens	c	g	so	2	4	3	2	2
Lecanora populicola	c	g	se	3	4	3	4	1
Lecanora pulicaris	c	g	se	2	5	4	2	2
Lecanora strobilina	c	g	se	2	3	3	1	1
Lecanora symmicta	c	g	se	2	4	3	2	2

Scientific name	Growth form[1]	Photobiont[2]	Reproduction[3]	pH[4]	Irradiation[5]	Aridity[6]	Eutrophication[7]	Poleotolerance[8]
Lecidella elaeochroma	c	g	se	4	5	5	4	3
Lecidella euphorea	c	g	se	3	4	4	3	2
Lepra albescens	c	g	so	3	4	3	3	2
Lepra amara	c	g	so	3	3	3	3	3
*Lepraria sp. **	-	-	-	-	-	-	-	-
Lepraria lobificans	l	g	so	3	4	4	1	1
Leprocaulon quisquiliare	fn	g	is	3	5	3	3	2
Leptogium brebissonii	fb	c	is	3	3	2	2	1
*Melanelixia sp. **	-	-	-	-	-	-	-	-
Melanelixia glabratula	fb	g	is	3	4	3	3	3
Melanelixia subaurifera	fb	g	so	3	4	3	3	2
Melanohalea exasperatula	fb	g	is	3	5	3	3	3
Melanohalea laciniatula	fb	g	is	2	3	2	3	1
Micarea prasina	c	g	se	2	3	2	1	1
Myriolecis dispersa	c	t	se	5	5	5	4	3
Myriolecis hagenii	c	g	se	5	5	5	4	3
Myriolecis sambuci	c	g	se	4	5	3	3	2

Scientific name	Growth form[1]	Photobiont[2]	Reproduction[3]	pH[4]	Irradiation[5]	Aridity[6]	Eutrophication[7]	Poleotolerance[8]
Normandina pulchella	sq	g	so	3	4	3	3	2
Ochrolechia szatalaensis	c	g	se	2	3	3	1	1
Opegrapha vulgata	c	t	se	3	3	2	1	2
Parmelia saxatilis	fb	g	is	2	4	3	3	2
Parmelia sulcata	fb	g	so	3	5	3	3	3
Parmelina tiliacea	fb	g	is	2	4	3	3	3
Parmeliopsis ambigua	fn	g	so	2	5	4	1	2
Parmotrema hypoleucinum	fb	g	so	3	5	2	2	1
Parmotrema perlatum	fb	g	so	2	4	3	2	2
Parmotrema robustum	fb	g	so	2	4	2	1	0
Pertusaria sp. *	-	-	-	-	-	-	-	-
Pertusaria heterochroa	fn	g	so	5	5	4	5	2
Pertusaria hymenea	c	g	se	3	5	3	2	2
Phaeophyscia cernohorskyi	fn	g	so	3	5	4	4	1
Phaeophyscia endophoenicea	fn	g	se	3	3	3	3	1

Scientific name	Growth form[1]	Photobiont[2]	Reproduction[3]	pH[4]	Irradiation[5]	Aridity[6]	Eutrophication[7]	Poleotolerance[8]
Phaeophyscia hirsuta	fn	g	so	4	5	4	4	2
Phaeophyscia nigricans	fn	g	is	4	5	4	4	2
Phaeophyscia orbicularis	fn	g	so	5	5	4	5	3
Phlyctis argena	c	g	so	2	3	3	2	2
Physcia adscendens	fn	g	so	5	5	4	5	3
Physcia aipolia	fn	g	se	3	5	3	4	3
Physcia caesia	fb	g	so	5	5	4	5	2
Physcia clementei	fn	g	is	3	5	3	3	2
Physcia dubia	fn	g	so	4	5	4	5	3
Physcia stellaris	fn	g	se	3	5	3	4	2
Physcia tenella	fn	g	so	4	5	4	4	2
Physcia tribacioides	fn	g	so	3	5	2	3	1
*Physciaceae sp. **	-	-	-	-	-	-	-	-
Physciella chloantha	fn	g	so	5	4	3	4	2
Physconia distorta	fn	g	se	4	5	4	4	3
Physconia enteroxantha	fn	g	so	3	5	3	4	2
Physconia grisea	fn	g	so	4	5	3	5	3

Scientific name	Growth form[1]	Photobiont[2]	Reproduction[3]	pH[4]	Irradiation[5]	Aridity[6]	Eutrophication[7]	Poleotolerance[8]
Physconia perisidiosa	fn	g	so	3	4	3	3	2
Platismatia glauca	fb	g	is	2	5	3	2	2
Pleurosticta acetabulum	fb	g	se	3	5	4	3	3
Polycauliona polycarpa	fn	g	se	3	5	4	3	2
Porina aenea	c	t	se	3	2	3	1	1
Pseudoschismatomma rufescens	c	t	se	3	3	2	1	1
Punctelia jeckeri	fb	g	so	4	4	3	3	3
Punctelia subrudecta	fb	g	so	4	4	3	3	3
Pyrenula macrospora	c	t	se	3	3	2	1	1
Ramalina calicaris	f	g	se	2	4	2	2	1
Ramalina farinacea	f	g	so	3	5	2	2	2
Ramalina fastigiata	f	g	se	3	5	3	3	2
Ramalina fraxinea	f	g	se	3	5	3	3	1
Ramalina lacera	f	g	so	3	5	2	3	1
Rinodina capensis	c	g	se	3	4	3	2	1
Rinodina ficta	c	g	se	3	5	4	4	2
Rinodina oleae	c	g	se	3	5	4	3	1

Scientific name	Growth form[1]	Photobiont[2]	Reproduction[3]	pH[4]	Irradiation[5]	Aridity[6]	Eutrophication[7]	Poleotolerance[8]
Rinodina pyrina	c	g	se	3	5	3	3	2
Ropalospora viridis	c	g	so	2	4	2	1	1
Sclerophora pallida	c	t	se	3	3	2	1	0
Scoliciosporum chorococcum	c	g	se	3	3	3	3	2
Teloschistes chrysophthalmos	f	g	se	3	5	4	3	1
Trapeliopsis flexuosa	c	g	se	2	5	4	2	2
Usnea rubicunda	f	g	so	2	4	2	2	0
Waynea stoechadiana	sq	g	se	2	4	3	3	1
Xanthomendoza fulva	fn	g	so	3	5	4	4	1
Xanthoparmelia conspersa	fb	g	is	3	5	4	3	2
Xanthoria parietina	fb	g	se	4	5	4	4	3

[*] Species only identified to the genus level

[1] c – crustose; fn - foliose narrow lobe; fb - foliose broad lobe; sq – squamulose; l – leprose; f – fruticulose.

[2] g – green; c – cyano; t – trentepohlia.

[3] se – sexual; so – soredia; is - isidia

[4] 2 - on acid substrata, such on non-eutrophicated bark of Quercus; 3 - on subacid to sub neutral substrata (e.g. on bark of Sambucus); 4 - on slightly basic substrata, such as dust-covered bark; 5 - on basic substrata, e.g. pure limestone.

[5] 2 - in shaded situations, such as on the northern side of boles in close-canopied deciduous forests; 3 - in sites with plenty of diffuse light but scarce direct solar irradiation, such as in rather open-canopied deciduous woodlands; 4 - in sun-exposed sites, but avoiding extreme solar irradiation; 5 - in sites with very high direct solar irradiation, e.g. on the southern side of isolated boles.

[6] 1 - hygrophytic, in sites with a very high frequency of fog; 2 - rather hygrophytic, intermediate between 1 and 2; 3 – mesophytic; 4 - xerophytic but absent from extremely arid stands; 5 - very xerophytic.

[7] 1 - no eutrophication; 2 - very weak eutrophication; 3 - weak eutrophication; 4 - rather high eutrophication; 5 - very high eutrophication.

[8] 0 - species which exclusively occur on old trees in ancient, undisturbed forests; 1 - species occurring in natural or semi-natural habitats; 2 - species occurring in moderately disturbed areas (agricultural areas, small settlements etc.); 3 - species occurring in heavily disturbed areas, incl. large towns.

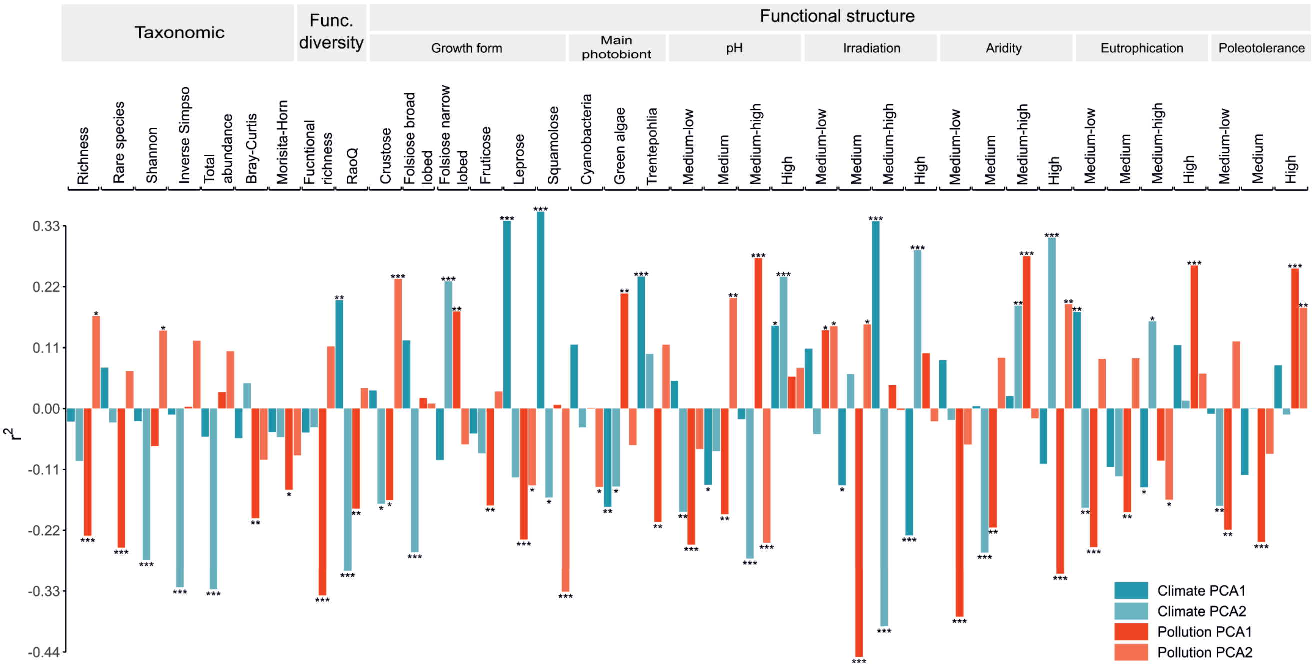


Figure S2: Spearman correlation coefficients between air pollution and macroclimate PCA axes (Climate A1, Climate A2, Pollution A1 and Pollution A2) and epiphytic lichens biodiversity metrics. N=219

Table S2: Climate variables used, divided by group (temperature; precipitation), type (annual range; seasonal) and described based on [2,3].

Variable group	Type	Variable	Description
Air temperature	annual	Bio 1	annual mean temperature
		Bio 2	mean diurnal range
		Bio 3	isothermality
		Bio 7	temperature annual range
	seasonal	Bio 4	temperature seasonality
		Bio 5	maximum mean temperature of warmest month
		Bio 6	minimum temperature of coldest month
		Bio 8	mean temperature of wettest quarter
		Bio 9	mean temperature of driest quarter
		Bio 10	mean temperature of warmest quarter
		Bio 11	mean temperature of coldest quarter
Precipitation	annual	Bio 12	annual precipitation
	seasonal	Bio 13	precipitation of wettest month
		Bio 14	precipitation of driest month
		Bio 15	precipitation seasonality
		Bio 16	precipitation of wettest quarter
		Bio 17	precipitation of driest quarter
		Bio 18	precipitation of warmest quarter
		Bio 19	precipitation of coldest quarter

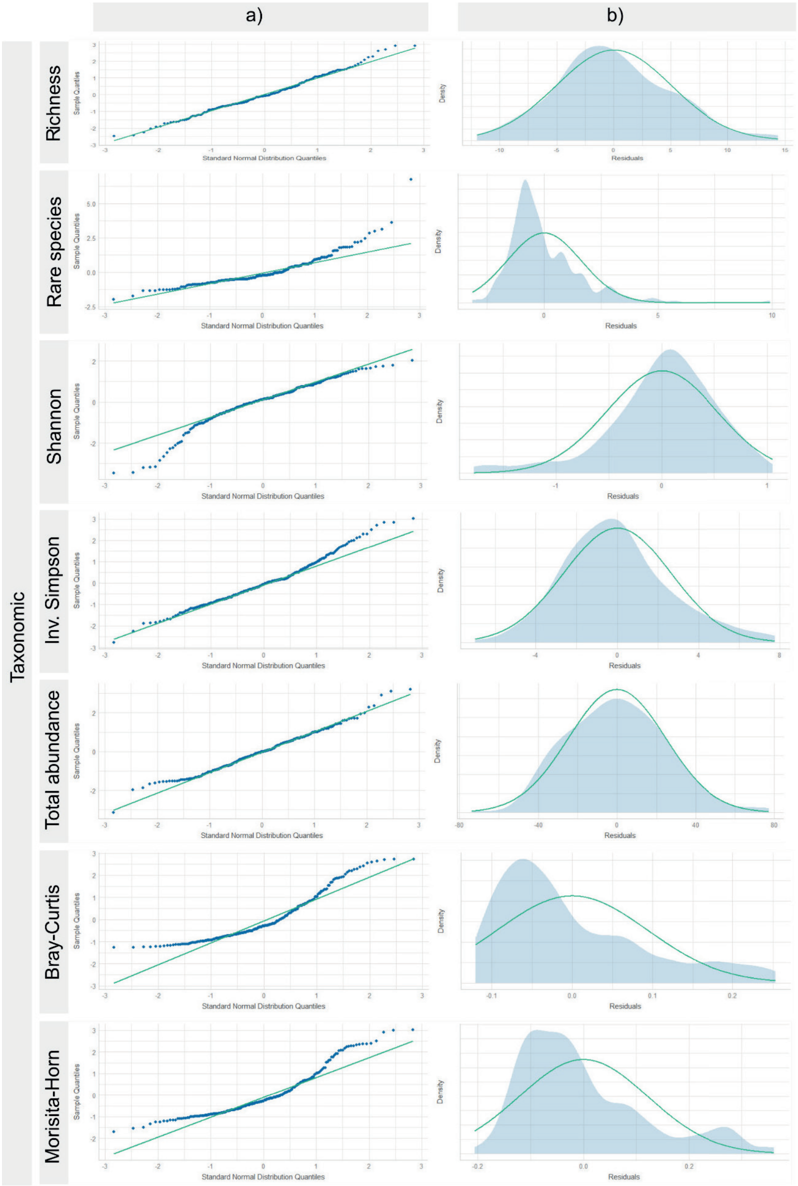


Figure S3: Linear regression model (Figure 5) residuals normality plots for each lichen taxonomic-based metric, useful for determining if the residuals follow a normal distribution. a) Quantile-quantile plot, representing the probability of the linear regression models residuals to follow a normal distribution. The more the dots (blue) fall along the straight line (green), the highest the likelihood of the residuals to follow a normal distribution. b) Density plots, representing the distribution of the linear regression models residuals. The closest the resemble between the residuals distribution (blue) to the normal curve (green), the highest the likelihood of the residuals to follow a normal distribution.

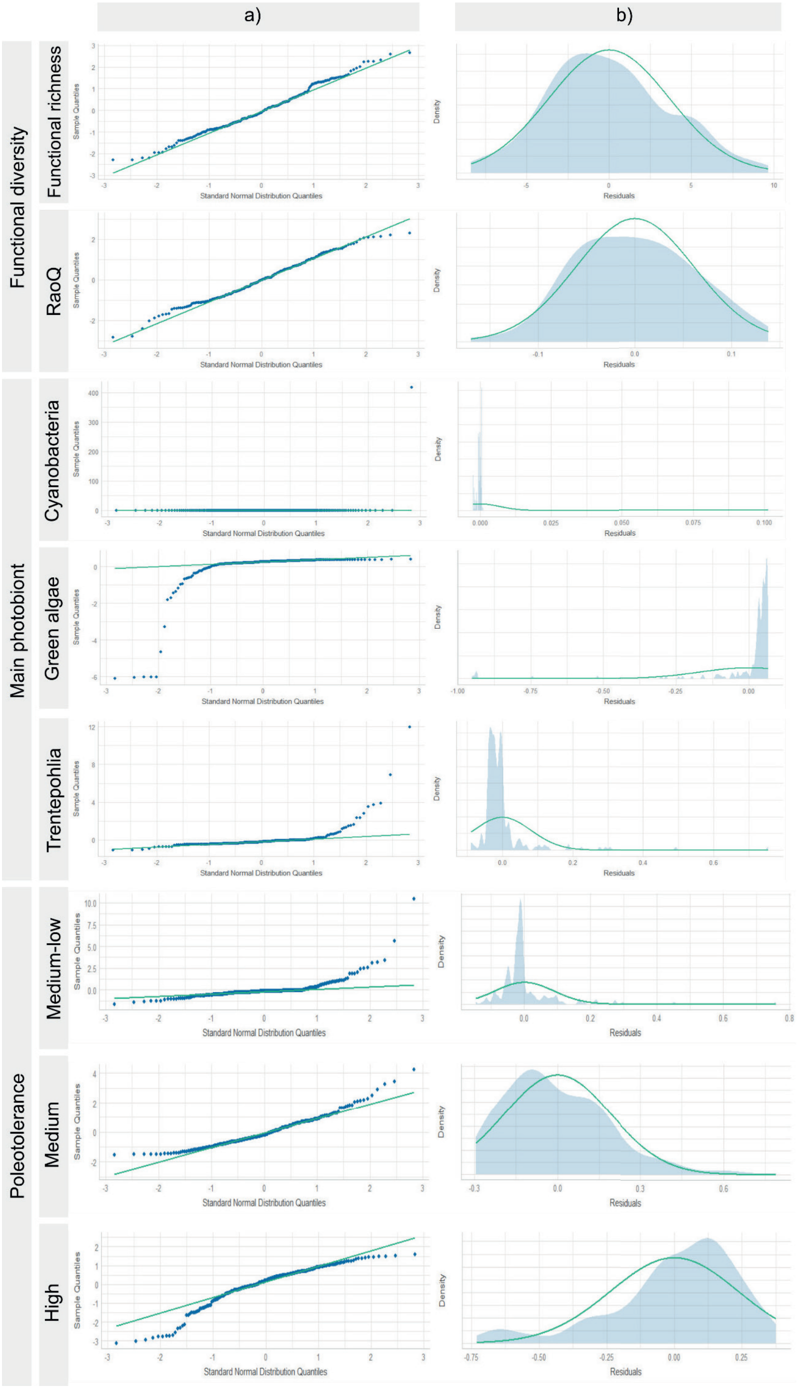

a)
b)
Functional diversity
Functional richness
RaoQ
Main photobiont
Cyanobacteria
Green algae
Trentepohlia
Poleotolerance
Medium-low
Medium
High
Sample Quantiles
Standard Normal Distribution Quantiles
Density
Residuals

Figure S4: Linear regression model (Figure 5) residuals normality plots for each lichen functional diversity and functional structure (main photobiont and poleotolerance traits) -based metric, useful for determining if the residuals follow a normal distribution. a) Quantile-quantile plot, representing the probability of the linear regression models residuals to follow a normal distribution. The more the dots (blue) fall along the straight line (green), the highest the likelihood of the residuals to follow a normal distribution. b) Density plots, representing the distribution of the linear regression models residuals. The closest the resemble between the residuals distribution (blue) to the normal curve (green), the highest the likelihood of the residuals to follow a normal distribution.

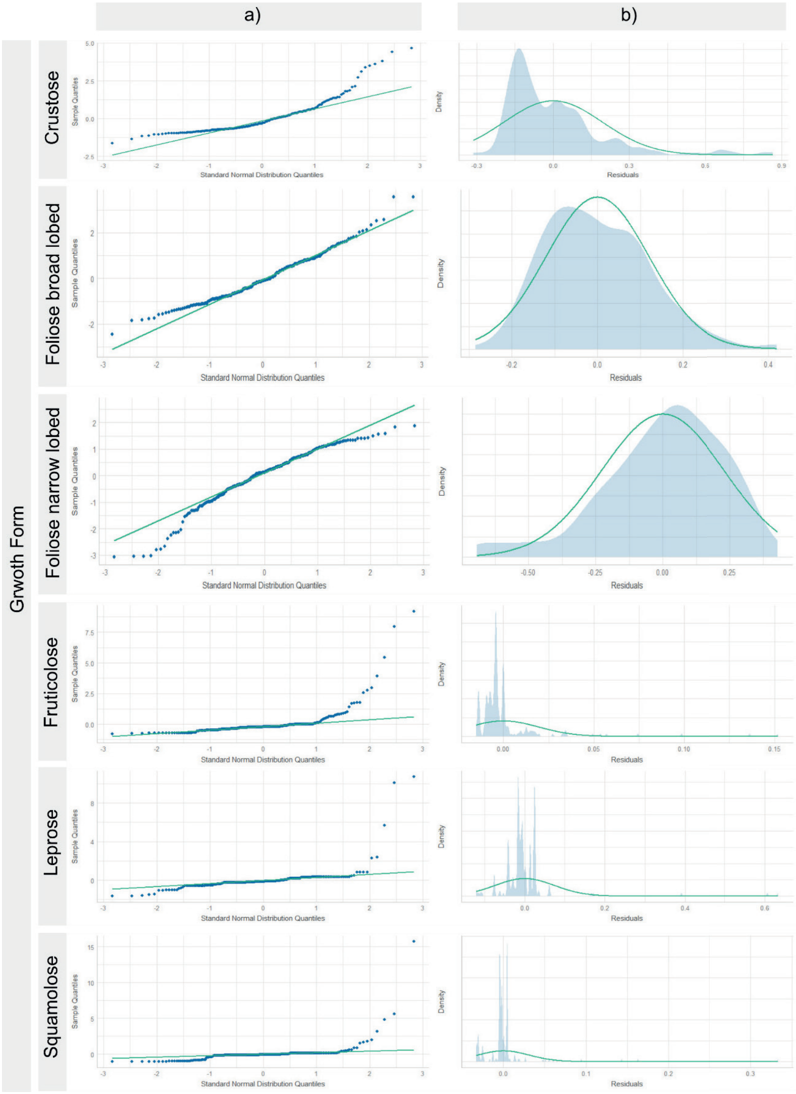


Figure S5: Linear regression model (Figure 5) residuals normality plots for each lichen functional diversity and functional structure (growth form) -based metric, useful for determining if the residuals follow a normal distribution. a) Quantile-quantile plot, representing the probability of the linear regression models residuals to follow a normal distribution. The more the dots (blue) fall along the straight line (green), the highest the likelihood of the residuals to follow a normal distribution. b) Density plots, representing the distribution of the linear regression models residuals. The closest the resemble between the residuals distribution (blue) to the normal curve (green), the highest the likelihood of the residuals to follow a normal distribution.

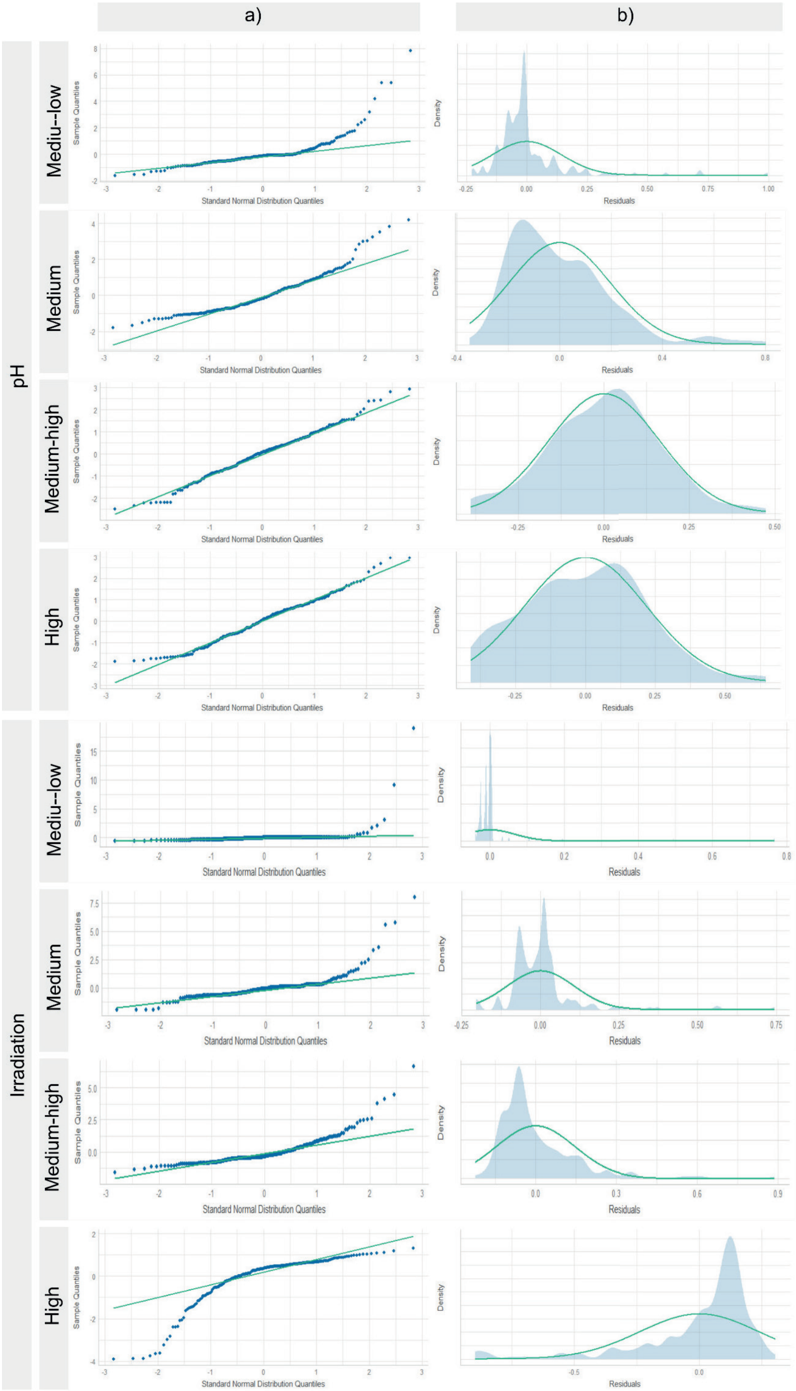

a)
b)
pH
Irradiation
Mediu--low
Medium
Medium-high
High
Mediu--low
Medium
Medium-high
High
Sample Quantiles
Standard Normal Distribution Quantiles
Density
Residuals

Figure S6: Linear regression model (Figure 5) residuals normality plots for each functional structure (species substrate pH tolerance (pH) and irradiation traits) -based metric, useful for determining if the residuals follow a normal distribution. a) Quantile-quantile plot, representing the probability of the linear regression models residuals to follow a normal distribution. The more the dots (blue) fall along the straight line (green), the highest the likelihood of the residuals to follow a normal distribution. b) Density plots, representing the distribution of the linear regression models residuals. The closest the resemble between the residuals distribution (blue) to the normal curve (green), the highest the likelihood of the residuals to follow a normal distribution.

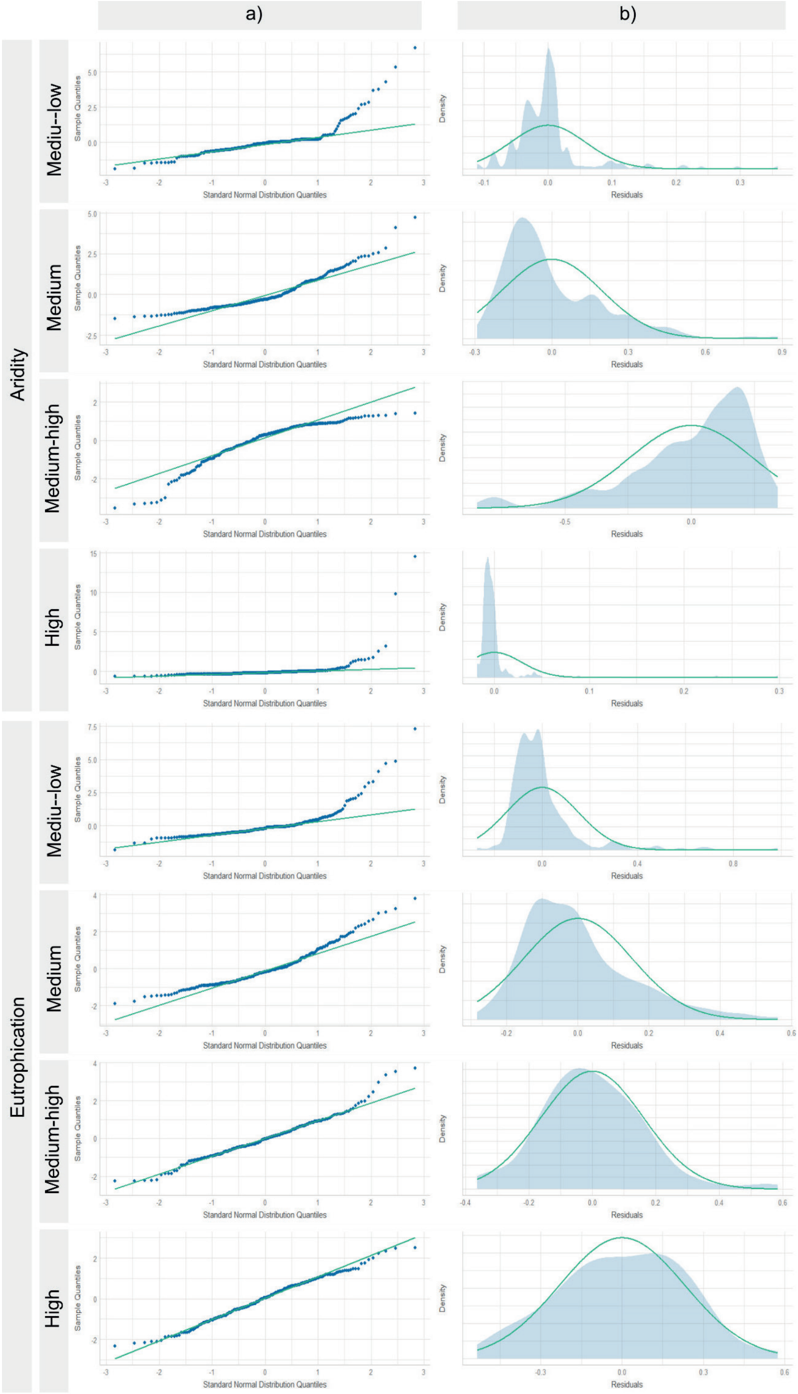

a)
b)
Aridity
Eutrophication
Mediu--low
Medium
Medium-high
High
Sample Quantiles
Standard Normal Distribution Quantiles
Density
Residuals

Figure S7: Linear regression model (Figure 5) residuals normality plots for each functional structure (aridity and eutrophication traits) -based metric, useful for determining if the residuals follow a normal distribution. a) Quantile-quantile plot, representing the probability of the linear regression models residuals to follow a normal distribution. The more the dots (blue) fall along the straight line (green), the highest the likelihood of the residuals to follow a normal distribution. b) Density plots, representing the distribution of the linear regression models residuals. The closest the resemble between the residuals distribution (blue) to the normal curve (green), the highest the likelihood of the residuals to follow a normal distribution.

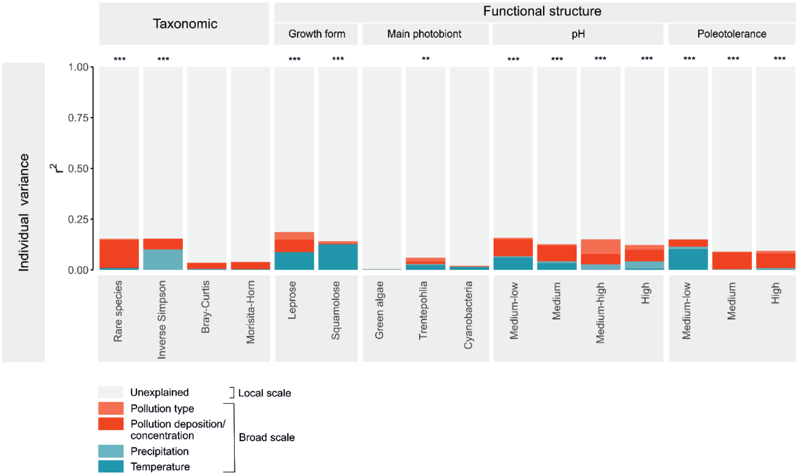


Figure S8: Variance partitioning of broad scale drivers for each lichen biodiversity metrics. Metrics are grouped into taxonomic (Rare species, Inverse Simpson, Bray-Curtis and Morisita-Horn) and functional structure (Growth form, Main photobiont type, Species substrate pH tolerance and Poleotolerance). Only metrics not represent on the main text (Figure 5) are shown here. Temperature reflects the first climate PCA axis, related to a broad scale temperature gradient. Precipitation reflects the second climate PCA axis, related to a broad scale precipitation gradient. Air pollution deposition/concentration reflects the first air pollution PCA axis, related to a broad scale gradient of air pollution. Air pollution type reflects the second air pollution PCA axis, related to a broad scale gradient of air pollution ranging from N-based pollutants on one side, to sulfur dioxide and particulate matter compounds on the other. Significance of the model is indicated in superscript: * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

References:

1. Nimis, P.L.; Martellos, S. ITALIC - The Information System on Italian Lichens. Version 5.0. University of Trieste, Dept. of Biology, (http://dryades.units.it/italic). **2021**.
2. Karger D.N.; Conrad, O.; Böhner, J.; Kawohl, T.; Kreft, H.; Soria-Auza, R.W.; Zimmermann, N.E.; Linder, H.P.; Kessler, M. Data from: Climatologies at high resolution for the earth's land surface areas. Dryad Digital Repository. **2018**, doi:http://dx.doi.org/doi:10.5061/dryad.kd1d4.
3. Karger, D.N.; Conrad, O.; Böhner, J.; Kawohl, T.; Kreft, H.; Soria-Auza, R.W.; Zimmermann, N.E.; Linder, H.P.; Kessler, M. Climatologies at high resolution for the earth's land surface areas. *Scientific Data* **2017**, *4*, 170122, doi:10.1038/sdata.2017.122.

IV

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RESEARCH ARTICLE

How wild bees find a way in European cities: Pollen metabarcoding unravels multiple feeding strategies and their effects on distribution patterns in four wild bee species

Joan Casanelles-Abella[1,2] | Stefanie Müller[1,3] | Alexander Keller[4] | Cristiana Aleixo[5] | Marta Alós Orti[6] | François Chiron[7] | Nicolas Deguines[7,8] | Tiit Hallikma[6] | Lauri Laanisto[6] | Pedro Pinho[5] | Roeland Samson[9] | Piotr Tryjanowski[10] | Anskje Van Mensel[9] | Loïc Pellissier[2,11] | Marco Moretti[1]

[1]Biodiversity and Conservation Biology, Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland

[2]Institute of Terrestrial Ecosystems, ETH Zurich, Zurich, Switzerland

[3]Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, Switzerland

[4]Organismic and Cellular Interactions, Biocenter, Faculty of Biology, Ludwig-Maximilians-Universität München, Martinsried, Germany

[5]Centre for Ecology, Evolution and Environmental Changes (cE3c), Faculdade de Ciências, Universidade de Lisboa, Lisboa, Portugal

[6]Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, Tartu, Estonia

[7]Université Paris-Saclay, CNRS, AgroParisTech, Ecologie Systématique Evolution, Orsay, France

[8]Laboratoire Ecologie et Biologie des Interactions, Equipe Ecologie Evolution Symbiose, Université de Poitiers, UMR CNRS, Nouvelle-Aquitaine, France

[9]Laboratory of Environmental and Urban Ecology, Department of Bioscience Engineering, University of Antwerp, Antwerp, Belgium

[10]Department of Zoology, Poznan University of Life Sciences, Poznań, Poland

Abstract

1. Urban ecosystems can sustain populations of wild bees, partly because of their rich native and exotic floral resources. A better understanding of the urban bee diet, particularly at the larval stage, is necessary to understand biotic interactions and feeding behaviour in urban ecosystems, and to promote bees by improving the management of urban floral resources.
2. We investigated the larval diet and distribution patterns of four solitary wild bee species with different diet specialization (i.e. *Chelostoma florisomne*, *Osmia bicornis*, *Osmia cornuta* and *Hylaeus communis*) along urban intensity gradients in five European cities (Antwerp, Paris, Poznan, Tartu and Zurich) using two complementary analyses. Specifically, using trap-nests and pollen metabarcoding techniques, we characterized the species' larval diet, assessed diet consistency across cities and modelled the distribution of wild bees using species distribution models (SDMs).
3. Our results demonstrate that urban wild bees display different successful strategies to exploit existing urban floral resources: not only broad generalism (i.e. *H. communis*) but also intermediate generalism, with some degree of diet conservatism at the plant family or genus level (i.e. *O. cornuta* and *O. bicornis*), or even strict specialization on widely available urban pollen hosts (i.e. *C. florisomne*). Furthermore, we detected important diet variation in *H. communis*, with a switch from an herbaceous pollen diet to a tree pollen diet with increasing urban intensity.
4. Species distribution modelling indicated that wild bee distribution ranges inside urban ecosystems ultimately depend on their degree of specialization, and that broader diets result in less sensitivity to urban intensity.

Loïc Pellissier and Marco Moretti—Joint senior position.

[11]Land Change Science, Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland

Correspondence
Joan Casanelles-Abella
Email: joan.casanelles@wsl.ch

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5. *Policy implications*. Satisfying larval dietary requirements is critical to preserving and enhancing wild bee distributions within urban gradients. For high to intermediate levels of feeding specialization, we found considerable consistency in the preferred plant families or genera across the studied cities, which could be generalized to other cities where these bees occur. Identifying larval floral preferences (e.g. using pollen metabarcoding) could be helpful for identifying key plant taxa and traits for bee survival and for improving strategies to develop bee-friendly cities.

KEYWORDS
cavity-nesting bees, feeding behaviour, remote sensing, species distribution models, trap-nests, urban biodiversity, urbanization

1 | INTRODUCTION

Wild bees are responsible for major ecosystem functions and make many contributions relevant to people, including pollination and maintenance of ecosystem stability, and they represent social and cultural values (e.g. Potts et al., 2016). Over the last decades, bee populations have dramatically decreased (Zattara & Aizen, 2021). Multiple causes have been identified (Goulson et al., 2015), and the loss of floral resources is among the most important (Goulson et al., 2015). Wild bees critically depend on large amounts of nectar and pollen to survive and reproduce during their life cycle, and most species display some degree of fidelity to specific plant taxa (Goulson, 1999; Vanderplanck et al., 2014). Consequently, diet specialization and diet preference are two key traits determining the sensitivity to land-use changes (e.g. urbanization; Dharmarajan et al., 2021) and the distribution patterns of wild bees (e.g. Fournier et al., 2020).

Urban ecosystems can harbour large and diverse bee communities, helping to preserve and promote wild bee diversity. Although urbanization has major negative impacts on biodiversity (Theodorou et al., 2020), a significant number of wild bee species can thrive in cities. Documentation of wild bees in urban ecosystems has frequently indicated diverse wild bee communities (Baldock et al., 2015; Casanelles-Abella, Chauvier, et al., 2021), although this ultimately depends on each species' traits and its response to urbanization. Urban ecosystems are warmer (Roth et al., 1989), have higher landscape heterogeneity (Turrini & Knop, 2015) and are generally less polluted by pesticides (Scheyer et al., 2007) than intensive agricultural areas. Moreover, while intensified agricultural systems have impoverished floral resources, in cities these resources might be maintained, thanks to social investment, high availability of woody species (e.g. street trees) in highly urbanized areas, and the presence of flower-rich habitats (Somme et al., 2016; Tew et al., 2021). In both public and private urban greenspaces, there are important efforts to establish and maintain flowering plant assemblages, with each phase reflecting the preferences and needs of the specific owners and managers (Harrison & Winfree, 2015). Therefore, there is a major opportunity to promote wild bee fitness and reproduction by increasing and improving wild bee habitats.

Urban ecosystems can induce dietary changes in species, due to their distinct availability of various food resources. In urban ecosystems, natural food resources are complemented with anthropogenic food resources (Faeth et al., 2005), whose accessibility is modulated by each species' diet specialization. Urban floral resources are especially diverse in cities, due to gardening and horticultural activities, with many native and exotic species planted for different purposes. Some of these species provide additional sources of food for pollinators within their range of foraging preference, phenology and trait matching (Garbuzov & Ratnieks, 2014; Harrison & Winfree, 2015). Therefore, generalist wild bee species with a broad dietary range might be better able to exploit the existing urban resources, access and forage on a greater variety of patches, and consequently be more widely distributed.

Knowledge on bee diet preferences could reveal which plant species are important for their survival and reproduction and could be translated into important decisions concerning the planning and management of floral resources, for example, what species to plant. Plant identification with DNA metabarcoding techniques has increased in diet studies and provides new knowledge about the feeding preferences of animals, which can help us to understand their distribution along environmental gradients (Pitteloud et al., 2021). So far, diet preferences have mostly been assessed indirectly through observations of adult bee plant visitation (e.g. Marquardt et al., 2021) or through the morphological identification of pollen grains (Haider et al., 2013; Sedivy et al., 2011). Nonetheless, specific sampling methodologies, such as trap-nests that allow standardized sampling (Staab et al., 2018), combined with metabarcoding techniques promise to be a powerful tool to characterize and study larval bee diets (Bell et al., 2016; Keller et al., 2015). Trap-nests target larval pollen and thus can better describe bee diet preferences than measurements of adult visitation, while pollen metabarcoding techniques can identify a larger number of taxa with a higher taxonomic resolution than pollen morphological identification; this is particularly useful in urban ecosystems with unique and rich plant pools. Metabarcoding techniques reduce the need for taxonomic expertise associated with pollen morphological identification, thus broadening its application across multiple sites.

Here, we investigated the larval diet and distribution of four widespread wild bee species of urban ecosystems, representing a gradient of decreasing diet specialization (*Chelostoma florisomne*, *Osmia bicornis*, *Osmia cornuta* and *Hylaeus communis*), along urban intensity gradients in five European cities (Antwerp, Paris, Poznan, Tartu and Zurich). In particular, we asked the following questions: (a) What is the taxonomic and trait-based composition of the bee diets in different urban areas? (b) How consistent are the bee diets across urban areas? (c) How does diet specialization influence the bee distribution in urban ecosystems? We expected that specialized bee species (i.e. *C. florisomne*) would have strong preferences for specific plant taxa and thus a highly consistent diet across urban areas and within urban gradients. Conversely, we predicted that more generalist bees (i.e. *O. cornuta*, *O. bicornis* and *H. communis*) would have a more flexible diet and be capable of switching to alternative floral resources, including exotic taxa, and thus have a higher turnover in the diet composition (at the plant family, genus and species levels) and a less consistent diet. Finally, we hypothesized that bee species with greater diet specialization would have low flexibility in terms of switching their diet to other plant taxa and thus would be more sensitive to urban intensity.

2 | MATERIALS AND METHODS

2.1 | Cities and study sites

We investigated wild bee diets in five cities in Europe: Antwerp (Belgium), Greater Paris (France, hereinafter referred as Paris), Poznan (Poland), Tartu (Estonia) and Zurich (Switzerland), covering a large part of the climatic variability in mainland Europe. Site selection followed Casanelles-Abella, Frey, et al. (2021). Overall, we selected sites from the urban green areas mapped and defined in the pan-European Urban Atlas (EEA, 2012). We used an orthogonal gradient of patch area and connectivity. In particular, we calculated connectivity using the proximity index (PI), which considers the area and the distance to all nearby patches with a favourable habitat, within a given search radius. We considered as favourable habitat the land cover classes urban green areas, forest and low urban density with <30% impervious surface. We set the search radius to 5 km from each focal patch, the maximum value possible with the available cartography. This resulted in the final selection of 80 sites: 32 in Zurich and 12 in each of the remaining four cities (Figure S1; Table S1). We maintained a minimum distance of 500 m between selected sites (except for two sites in Zurich selected based on their position in the patch and connectivity gradient, which were separated by 260 m).

2.2 | Bee sampling

At each site, we installed trap-nests in trees, and in three cases (one in Paris, one in Tartu and one in Zurich) in other vertical structures (e.g. lamp post). We constructed trap-nests with reeds and cardboard tubes (Figure S1). Our sampling trap-nests consisted of a standardized wood box with three plastic pipes 15 cm in diameter and 20 cm long. We assembled the first two pipes using 200–300 reeds from *Phragmites australis* (Cav.) Trin. and 5–10 bamboo reeds with diameters of 1–10 mm and a length of 20 cm to cover all requirements of the cavity-nesting bee community. We assembled the third pipe only using cardboard tubes of 7.5 mm diameter specific for *Osmia* spp. (WAB Mauerbienenzucht; Konstanz, Germany). We installed trap-nests at 2.5–3.5 m height with direct sunlight and SE or SW exposition, and kept them in the field from January until October 2018. In October, we collected the trap-nests and stored them at *c.* 5°C until February 2019, and then transferred them to a new room at ambient temperature to recreate spring-like conditions. Bees hatched and were identified to the species level from February to June 2019.

2.3 | Study organisms

We collected pollen from the nests of four solitary bee species, *Chelostoma florisomne* (Linnaeus, 1758), *Hylaeus communis* (Nylander, 1852), *Osmia bicornis* (Linnaeus, 1758) and *Osmia cornuta* (Latreille, 1805). These species encompass a gradient of diet specialization (i.e. the number of different plant families exploited as resources, from the oligolectic *C. florisomne* to the highly polylectic *H. communis*), differ in phenology, and are common species in urban areas in Europe. In our study, each species was present in at least three of the studied cities. For more details about the ecology of these four wild bee species, see Text S1.

2.4 | Pollen identification

We extracted a total of 464 pollen samples (Table S1) from undeveloped cells (i.e. where the larva had died) in nests where at least one adult had emerged and thus taxonomic identification of the bees was possible. Specifically, for *C. florisomne* we used 121 samples distributed in 3 cities and 18 sites (2 in Antwerp, 1 in Tartu and 15 in Zurich), for *O. cornuta* we used 66 samples distributed in 3 cities and 20 sites (6 in Antwerp, 5 in Paris and 9 in Zurich), for *O. bicornis* we used 176 samples distributed in 5 cities and 37 sites (3 in Antwerp, 10 in Paris, 8 in Poznan, 1 in Tartu and 15 in Zurich), and for *H. communis* we used 101 samples distributed in 5 cities and 33 sites (4 in Antwerp, 6 in Paris, 6 in Poznan, 9 in Tartu and 8 in Zurich). DNA metabarcoding (isolation, amplification and sequencing) was performed by AllGenetics laboratories (AllGenetics & Biology SL; A Coruña, Spain). We followed the method described by Sickel et al. (2015) and Vierna et al. (2017) to produce a pooled amplicon library on the ITS2 genomic region for the Illumina platform (Illumina). See Text S3 for details on the laboratory procedure of pollen metabarcoding. Bioinformatics followed mainly the procedure described in Campos et al. (2021) with minor modifications: We used VSEARCH v2.14.2 (Rognes et al., 2016) to join paired ends of forward and reverse reads. We also used VSEARCH to remove reads shorter than 200 bp, complete quality filtering (EE < 1; Edgar & Flyvbjerg, 2015) and de-novo chimera filtering, and define amplicon sequence variants (ASVs), as previously done successfully for pollens (e.g. Wilson et al., 2021). The ITS2 rDNA reads were first directly mapped with VSEARCH global alignments and an identity cut-off threshold of 97% against a floral ITS2 reference database generated with the BCdatabaser (Keller et al., 2020), which consisted of plants recorded within the study regions. For the remaining unclassified reads, we first used global alignments against a global reference database (Ankenbrand et al., 2015; Keller et al., 2015). For reads that were still unclassified, we used SINTAX (Edgar, 2016a, 2016b) to assign taxonomic levels as deep as possible but a maximum of genus level with the same global reference database. In total, 82% of species recorded at the sites were present in the local database and 83% of species in the global database (direct classification). Furthermore, 92% of genera were covered by the global database for hierarchical classification. Please note that the global database contains 112,115 unique species, 11,321 genera and 710 families in total, with a very high likelihood of coverage for species and genera of any interest for anthropogenic use, including exotic garden species.

2.5 | Environmental variables

We assembled variables that were potential drivers of bee diets and distributions and that represented different aspects of the urban environmental gradients. Specifically, we focused on proxies of stress (particularly thermal stress), amount of habitat and resource availability at different spatial scales. We inferred resource availability at the local scale by performing floristic inventories on standardized plots, as explained in Casanelles-Abella, Frey, et al. (2021) and in Supplementary Text S4. Furthermore, we collected information on two functional plant traits sensitive to bee–plant interactions, that is, growth form (Tables S2 and S3) and blossom type (Tables S2 and S3) using information available in Casanelles-Abella, Frey, et al. (2021). See Text S4 and Tables S2 and S3 for additional information on the definition of the traits.

We used local and landscape connectivity metrics, local land cover metrics and landscape remote-sensing-based indices to infer thermal stress and the amount of available habitat, particularly regarding resource availability. As connectivity metrics, we used patch size and the proximity index. We obtained the local land cover metrics by mapping grasslands, artificial surfaces, bare land, coniferous trees and deciduous broad-leaved trees and then calculating their proportions at different spatial scales (i.e. 8, 16 and 32 m) from the focal trap-nest (see Text S5 for additional details). Finally, we used remote-sensing-based indices on land surface temperature, impervious surfaces, soil, water and vegetation at different spatial scales (50, 100, 200, 400, 800, 1,600 m). Specifically, we used land surface temperature (LST), the urban index (UI), the colour index (CI), the normalized difference water index (NDWI) and the normalized difference vegetation index (NDVI), which can be used to characterize existing vegetation and urban infrastructure. In addition, we performed a principal component analysis (PCA) on the explanatory variables to define new meaningful underlying variables while reducing the dimensionality of the data set (see Section 2.6). See Text S6 for details on the calculation of the remote-sensing-based indices and Figure S2 for the distribution of values of each predictor in each city.

2.6 | Statistical analysis

We conducted all analyses in R version 4.0.2 (R Core Team, 2021) with RStudio version 1.4.1106 (RStudio Team, 2020).

2.6.1 | Species diet analysis

We performed taxonomic and trait-based metrics on the bee diets at the city and site levels. Specifically, we computed the proportion of different plant taxa at the family, genus and species levels (Table S4). Furthermore, we calculated the species, genus and family richness and the Shannon diversity index. Concerning trait-based responses, we calculated the proportion of the different categories of the three studied traits (Table S5). For each of the four studied bees, we performed Pearson correlations to investigate the relationships between the taxonomic and the trait-based diet metrics with the proxies of urban intensity, habitat amount and resource availability. We assessed these relationships (a) for each single city and (b) for all the cities combined.

We calculated the pairwise correlations between cities for each bee species to study diet consistency. Specifically, we first assembled binary trophic interaction matrices between the four bee species and the plant taxa at the family, genus and species levels and then calculated the Pearson correlations of the binary trophic interaction matrices between pairs of cities for each bee and plant level. However, the trophic interaction matrix for a given city, and thus the pairwise correlations between cities, is influenced by the available plant pool. To avoid effects of plant composition, we first created a list with the plant pool occurring in each city at the family, genus and species levels. We used the plant species sampled within a 100-m buffer by Casanelles-Abella, Frey, et al. (2021) and complemented with the plant species recorded in GBIF (2021) at each city for the period 2000–2018 (Figure S3). If a plant family, genus or species was missing in one of the plant pools of a pair of cities, we removed the interaction when performing the correlations. Moreover, we computed a Chi-squared (χ^2) test on the family and trait composition between cities' plant species pools (Text S7, Table S6).

2.6.2 | Species distribution of urban gradients

We studied bee distribution patterns with species distribution models (SDMs). We assembled occurrence matrices indicating the occurrence of each bee species in the different sites. From the candidate environmental predictors, we evaluated the statistical relevance of each predictor using the predictive power (D^2; Table S7) and then manually picked three predictors that had correlations <0.7 to avoid collinearity (Figure S4) for each bee separately. We used an ensemble of two common modelling techniques to account for model uncertainty and specificity (Buisson et al., 2010). Specifically, we used two regression-based models, that is, generalized linear models (GLMs) and generalized additive models (GAMs), and two tree-based models, that is, gradient boosting machines (GBMs) and random forests (RFs), that show a higher complexity in their fitting procedures than GLMs and GAMs. We used city as a fixed factor to account for the nested structure of the data with a binomial probability distribution. We parameterized each modelling technique in the following way: we calibrated GLMs with first-order polynomials, GAMs with a spline smoothing term of intermediate complexity ($k = 4$), RFs with a node size of 5 (nodesize = 5) and 1,000 trees, and GBMs with an interaction depth of 1, a shrinkage of 0.001 and 1,000 trees. We ran the models using the R packages MGCV version 1.8-30, RANDOMFOREST version 4.6-14 and GBM version 2.1.5. We randomly split the species records of the four bees into two sets containing 80% of the data for model calibration and 20% of the data for model evaluation. We repeated the procedure five times. We assessed model performance with the True Skill Statistic (TSS; Allouche et al., 2006). TSS evaluates model skill in distinguishing absences from presences. The predictive performance of the different models was deemed acceptable when TSS > 0.4, following a commonly used minimum threshold (Thuiller et al., 2019). Thus, we discarded models with TSS values lower than 0.4. We used the selected models of each studied bee species to predict the probability of occurrence over the environmental space of the studied cities.

3 | RESULTS

3.1 | Species diet analysis

A total of 41 plant families, 93 genera and 135 species were identified from the nests of the four bee species (Figure 1; Tables S8 and S9). Over half of the species were native (55%), there were more herbs (42%) than trees (34%), and dish-bowl blossoms were more common (56%) (Figures S6–S8; Table S9). The number of plant species per bee nest was similar among bee species (Table S9). The total number of collected plant taxa varied greatly among bee species, reflecting their differences in diet specialization: 1 family and 4 species in *C. florisomne*, 12 families and 33 species in *O. cornuta*, 18 families and 51 species in *O. bicornis*, and 32 families and 81 species in *H. communis* (Figure 1; Table S9). At the city level, we found dominance patterns in pollen abundance for some bees (Figure 1). In *O. bicornis*, the most abundant species in pollen were *Quercus robur* (Antwerp, 70%) and *Acer pseudoplatanus* (Paris, 64%; Poznan, 44%; and Zurich, 33%). In *H. communis*, *Styphnolobium japonicum* was the most abundant species in pollen but only in Paris (52%) and Poznan (32%), with the vast majority of species representing 1%–14% of the pollen abundance. Interestingly, in *C. florisomne*, the most abundant *Ranunculus* spp. in pollen changed between cities (*R. acris* in Antwerp, *R. repens* in Tartu and *R. bulbosus* in Zurich). Finally, in *O. cornuta*, no species made up more than 37%, being the most abundant ones *A. pseudoplatanus* (Antwerp, 37%; Paris, 21%; and Zurich, 24%) and *Prunus lusitanica* (Paris, 33%). In addition, very few nests were dominated by a single plant species and mostly in *C. florisomne* (Figure S6).

We found different levels of diet conservatism across cities at the plant family and plant genus levels, according to the bee specialization degree and taxonomic resolution of the plant taxa (Figure 2). At the family and genus levels, diet consistency was high for *C. florisomne* and declined with broader feeding niches, particularly at the genus level (Figure 2a; Table S10). Conversely, we found major variation at the plant species level, which was particularly prominent for the broad generalist *H. communis*, which switched from herbaceous pollen to tree pollen with increasing urbanization (Figure 3b).

The extent to which bee diet taxonomic and trait-based composition were conserved also varies according to the degree of specialization. *Chelostoma florisomne* had the most conserved diet, composed exclusively of native *Ranunculus* spp. (Figures 1 and 2a; Tables S8 and S9). *Osmia cornuta* primarily collected the pollen of native tree and shrub species, mainly with dish-bowl or brush type blossoms, from the families Sapindaceae, Salicaceae and Rosaceae (Figure 1; Figures S7–S10; Tables S4, S5, S8–S11). Nevertheless, in Paris and Zurich, we also found a considerable proportion of Ranunculaceae (Figure 1b). Both *C. florisomne* and *O. cornuta* taxonomic and trait-based metrics showed no or little variation along urban intensity gradients (Figure S11; Table S12). In *O. bicornis*, native tree species with dish-bowl or brush blossoms from the families Sapindaceae and Fagaceae represented a large part of the diet (Figure 1; Figures S7–S10; Tables S4, S5, S8–S11), but we found some variation across cities concerning the remaining species in the diet (Figure 1b; Figure S10).

Hylaeus communis had the most diverse and variable diet. The Fabaceae family represented 34% in Paris and 42% in Poznan of the species found in the larval diet (Figure 1b) and a minor part in the remaining cities (Figure 1b). Furthermore, exotic species were more frequent for *H. communis* than for the other three bee species (Figure 3a; Figure S7; Tables S5 and S9). In addition, we found family richness, species richness and pollen diversity to be positively correlated with NDVI for *H. communis* for all cities except Poznan (Figure S11; Table S12). Finally, in Paris, an important part of the diet was trees with flag type blossoms (Figure 3b), in part due to the contribution of *Styphnolobium japonicum* (Figure 1a; Table S8), which became more dominant in the diet with increasing urban intensity (e.g. decreasing NDVI and increasing UI and CI at different scales; Figure 3; Table S12).

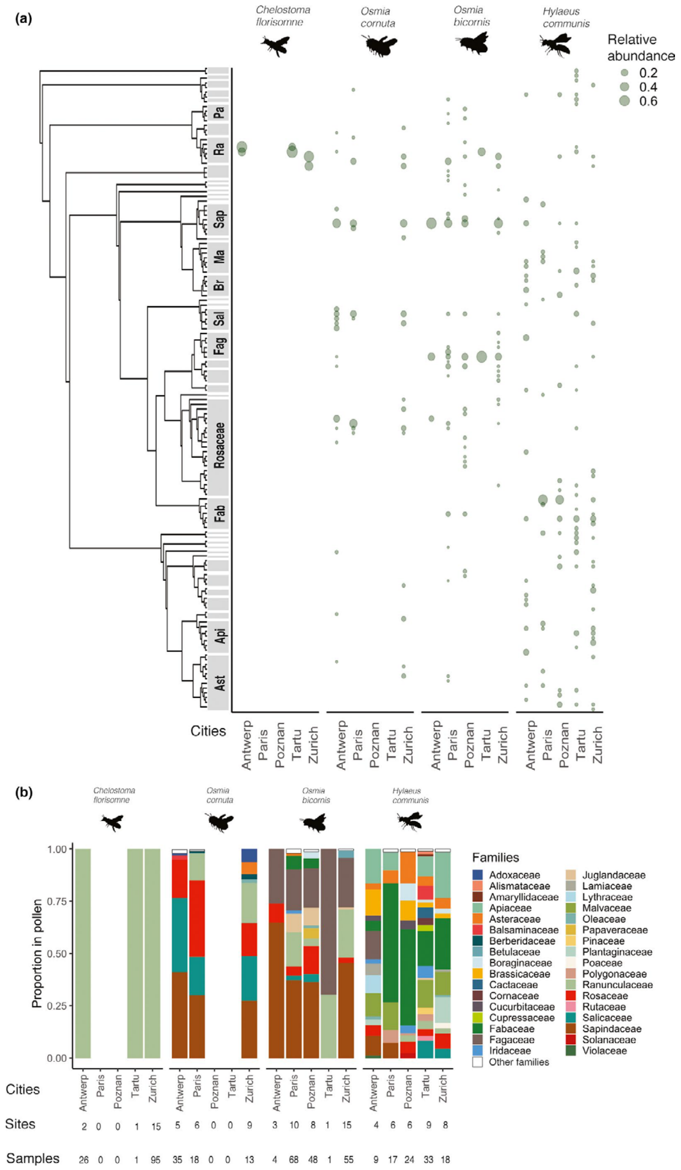
(a)
Chelostoma florisomne
Osmia cornuta
Osmia bicornis
Hylaeus communis
Relative abundance
0.2
0.4
0.6
Pa
Ra
Sap
Ma
Br
Sal
Fag
Rosaceae
Fab
Api
Ast
Cities
Antwerp
Paris
Poznan
Tartu
Zurich
(b)
Chelostoma florisomne
Osmia cornuta
Osmia bicornis
Hylaeus communis
Proportion in pollen
1.00
0.75
0.50
0.25
0.00
Families
Adoxaceae
Alismataceae
Amaryllidaceae
Apiaceae
Asteraceae
Balsaminaceae
Berberidaceae
Betulaceae
Boraginaceae
Brassicaceae
Cactaceae
Cornaceae
Cucurbitaceae
Cupressaceae
Fabaceae
Fagaceae
Iridaceae
Other families
Juglandaceae
Lamiaceae
Lythraceae
Malvaceae
Oleaceae
Papaveraceae
Pinaceae
Plantaginaceae
Poaceae
Polygonaceae
Ranunculaceae
Rosaceae
Rutaceae
Salicaceae
Sapindaceae
Solanaceae
Violaceae
Cities
Antwerp Paris Poznan Tartu Zurich
Sites
2 0 0 1 15
5 6 0 0 9
3 10 8 1 15
4 6 6 9 8
Samples
26 0 0 1 95
35 18 0 0 13
4 68 48 1 55
9 17 24 33 18

FIGURE 1 Bee larval diet composition in the studied cities. (a) For each bee species, the collected plant species in each city where the bee species was recorded (three cities for *Chelostoma florisomne* and *Osmia cornuta*, five cities for *Osmia bicornis* and *Hylaeus communis*) are shown. The size of the circle represents the mean relative abundance of plant species contributing to pollen samples per city and bee species. (b) For each bee species, the proportion in the pollen of the different collected plant families in the studied cities is shown (mean relative abundance of plant species contributing to pollen samples per city and bee species). Only families with a proportion in pollen ≥ 0.01 are plotted, whereas the remaining ones are represented in the category 'Other families'. Note that the proportion in pollen for *O. bicornis* in Antwerp and Tartu was obtained using only four and one samples, respectively. For each bee and city, we provide the number of sites where pollen samples were taken, and the total number of samples. Information on the computation of the phylogenetic tree can be found in Text S2 and Figure S5. Data supporting (a) can be found in Table S8. Ast, Asteraceae; Api, Apiaceae; Fab, Fabaceae; Fag, Fagaceae; Sal, Salicaceae; Br, Brassicaceae; Ma, Malvaceae; Sap, Sapindaceae; Ra, Ranunculaceae; Pa, Papaveraceae

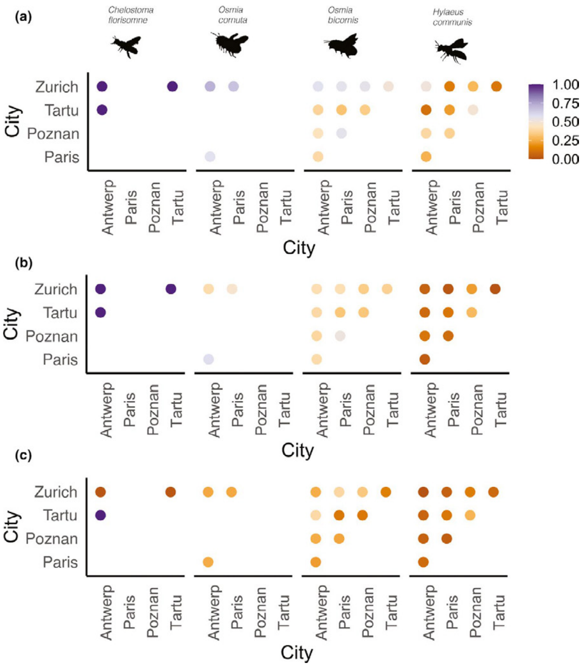

FIGURE 2 Pairwise correlations of the larval diet composition among cities. For each of the four studied bee species, the city pairwise correlations of the collected plant taxa are shown at the family (a), genus (b) and species (c) levels. The colour of the dots indicates the value of the correlation, with lower and higher values in orange and blue, respectively. Note that the correlation values are expressed as absolute values. Note also that the pollen for *Osmia bicornis* in Antwerp and Tartu was obtained using only four and one samples, respectively. Data supporting Figure 2 can be found in Table S10

3.2 | Species distributions along urban gradients

The PCA conducted on the explanatory variables returned two main axes that explained 38% and 12% of the variation, respectively. The first axis was composed of remotely sensed variables, with larger values of the PC axis indicating less vegetation (i.e. higher UI, CI and LST, and lower NDVI; Figure S12) independently of the landscape scale considered. The second axis was mostly composed of local land cover variables and metrics representing the available floral resources. Specifically, larger values on the PC axis indicated larger proportions of grasslands and lower proportions of deciduous trees and artificial surfaces, independently of the local scale considered (Figure S12).

We found two distinct distribution patterns of the four bee species along urban intensity gradients. The first type of response was composed of *C. florisomne*, *O. cornuta* and *O. bicornis*. The probability of occurrence of these three bee species decreased rapidly with increasing urban intensity at the landscape scale (Figure 4a,b; Figure S13) and increased with higher proportions of grasslands at the local scale (Figure 4c,d). Strikingly, the probability

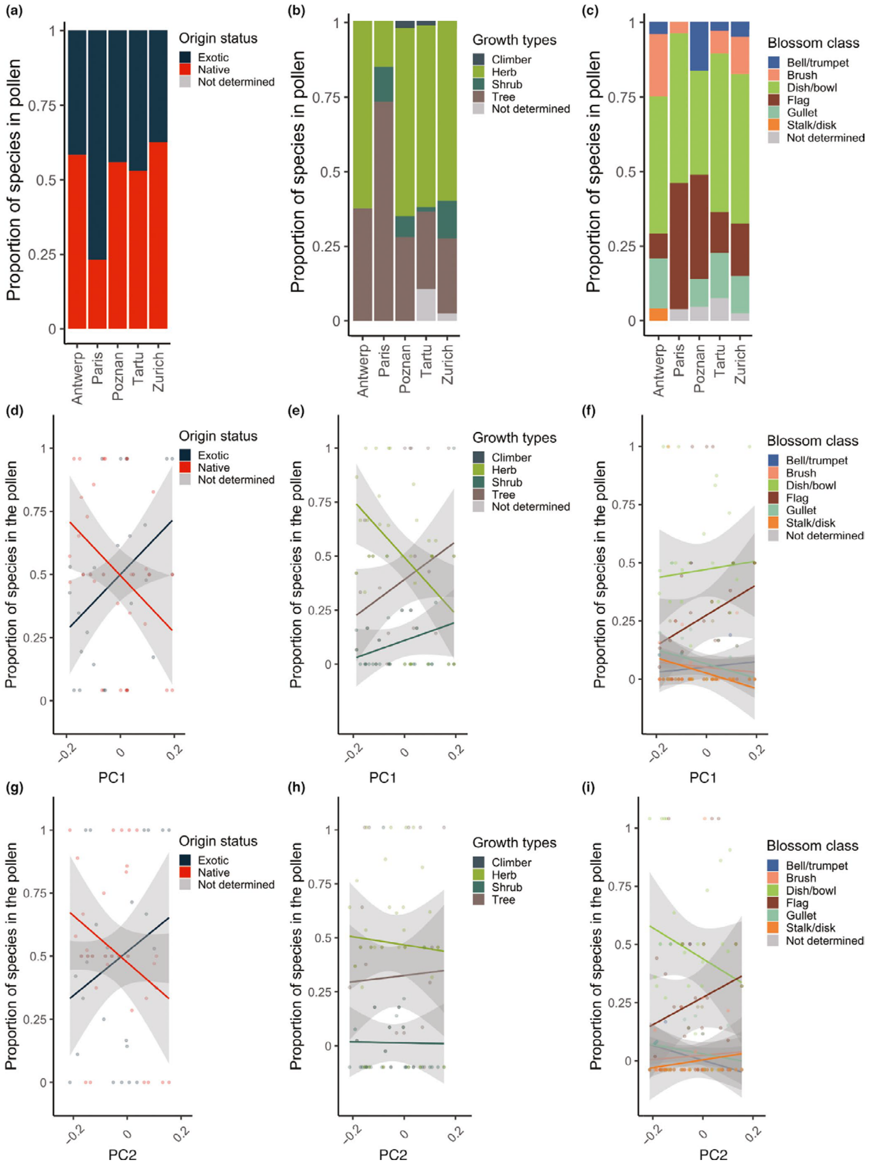
(a)
Proportion of species in pollen
0
0.25
0.5
0.75
1
Antwerp
Paris
Poznan
Tartu
Zurich
Origin status
Exotic
Native
Not determined
(b)
Proportion of species in pollen
Growth types
Climber
Herb
Shrub
Tree
Not determined
(c)
Proportion of species in pollen
Blossom class
Bell/trumpet
Brush
Dish/bowl
Flag
Gullet
Stalk/disk
Not determined
(d)
Proportion of species in the pollen
-0.2
0
0.2
PC1
Origin status
Exotic
Native
Not determined
(e)
Proportion of species in the pollen
PC1
Growth types
Climber
Herb
Shrub
Tree
Not determined
(f)
Proportion of species in the pollen
PC1
Blossom class
Bell/trumpet
Brush
Dish/bowl
Flag
Gullet
Stalk/disk
Not determined
(g)
Proportion of species in the pollen
PC2
Origin status
Exotic
Native
Not determined
(h)
Proportion of species in the pollen
PC2
Growth types
Climber
Herb
Shrub
Tree
(i)
Proportion of species in the pollen
PC2
Blossom class
Bell/trumpet
Brush
Dish/bowl
Flag
Gullet
Stalk/disk
Not determined

FIGURE 3 Trait-based larval diet composition in *Hylaeus communis*. (a–c) Composition of the diet according to the origin status (a), growth form (b) and blossom class (c) of the plant species in the larval pollen. (d–g) first-order GLMs of the proportion of the different plant trait levels in relation to the first (d–f) and second (g–i) PC axes for the origin status (d and f), growth form (e and g), and (f and i) blossom class. Grey shaded bands indicate 95% confidence intervals. Higher PC1 values indicate less vegetation (lower normalized difference vegetation index) and more artificial surfaces (urban index, land surface temperature, colour index). Higher PC2 values indicate a larger proportion of grasslands and lower proportion of deciduous trees at local scales. PC1 explained 38% of the variation and PC2 explained 12% of the variation. See Figures S7–S9 for the trait-based composition and change along urban gradients of the other three bee species

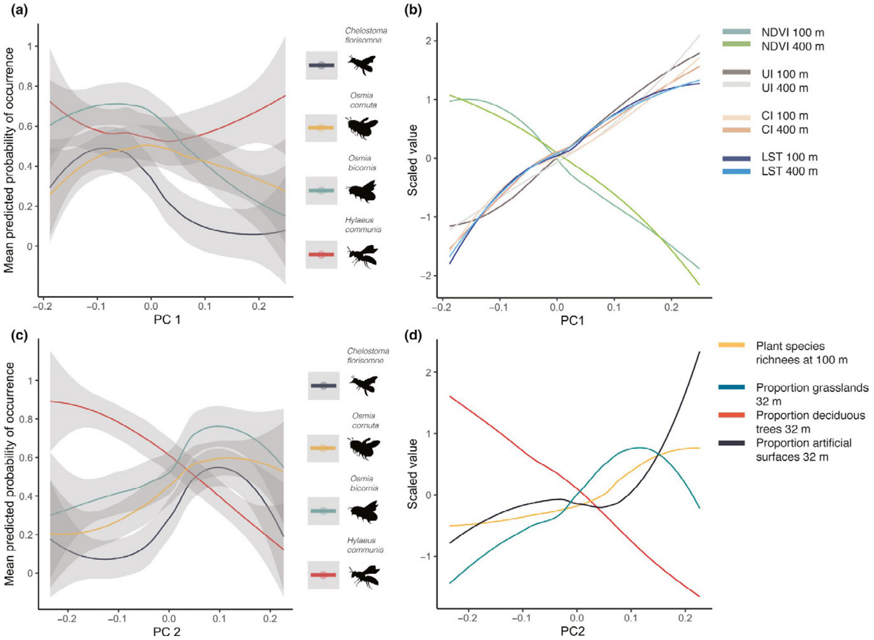

FIGURE 4 Bee distribution along urban gradients. (a and c) Loess smoothing of the mean predicted probability of occurrence of the four bee species in relation to the (a) first PCA axis (PC1) and (c) second PCA axis, performed on the explanatory variables, representing 38% and 12% of the variation, respectively. The mean predicted probability of occurrence results from the predicted probabilities of occurrence of the models with TSS > 0.4. Bands represent 95% confidence intervals. (b and d) Variation in the explanatory variables contributing the most to PC1 (b) and PC2 (d). (b) Larger values of PC1 correspond to higher values of impervious surfaces (urban index, UI), bare land (colour index, CI) and land surface temperature (LST) and lower vegetation cover (normalized difference vegetation index, NDVI) at different landscape scales (i.e. 100 and 400 m). (d) Lower values of PC2 correspond to higher proportions of deciduous trees and lower proportions of grasslands and floral resources (plant species richness) at local scales. Other scales and variables have been omitted here for simplicity (see Figure S13). See also Figure S12 for more details on the PCA

of occurrence peaked at low proportions of broad-leaved trees (Figure 4c,d; Figure S13), even though the diets of *O. cornuta* and *O. bicornis* were composed largely of tree pollen. By contrast, the probability of occurrence of *H. communis* remained constant for larger values of urban intensity (Figure 4a,b; Figure S13). Moreover, the probability of occurrence was positively affected by the amount of deciduous broad-leaved trees at local scales (Figure 4c,d; Figure S13).

4 | DISCUSSION

With biodiversity loss increasing at an unprecedented speed (Leclère et al., 2020) and urbanization expanding worldwide, there is a pressing need to better understand the niche requirements of different taxa to satisfy them in urban ecosystems through targeted planning and management (Aronson et al., 2017). Here, using trap-nests and pollen metabarcoding techniques, we studied the larval diet and distribution patterns of four wild bee species in five European cities.

The larval diet of the studied oligolectic and intermediate polylectic bees was conserved in terms of plant family composition, representing successful strategies in urban ecosystems as an alternative to generalism. As hypothesized, diet consistency decreased with decreasing wild bee degree of specialization and was relatively high at the plant family level and to lower extend at the plant genus level. Moreover, for *C. florisomne*, *O. cornuta* and *O. bicornis*, bee diet at the plant family level in the studied cities was consistent with prior studies in non-urban ecosystems (e.g. Haider et al., 2014). Diet conservatism regarding plant family composition has also been observed in other polylectic bee species such as *Bombus* spp. (Wood et al., 2021) and *Osmia* spp. (Haider et al., 2014; Vaudo et al., 2020), indicating that diet conservatism might be widespread despite a lack of data. Finally, diet consistency at the plant species level, with the exception of highly specialized *C. florisomne*, was very low, possibly because the specific trait values (e.g. pollen properties imposing cognitive or physiological restrictions; Vaudo et al., 2020) driving plant–pollinator interactions in less specialized wild bees might be relatively consistent within plant families or genera.

Across different animal taxa, broad feeding niches (i.e. low diet conservatism) have been identified as a key characteristics to pass the urban ecological filtering, and hence to thrive in cities (Fournier et al., 2020), with some species even undergoing rapid phenotypic changes to broaden their diet (e.g. Eggenberger et al., 2019). While widely distributed species inside cities are typically generalists, especially when highly mobile and with specific nesting and sociality modes (i.e. cavity nesting or social), intermediate specialization might be an alternative advantageous strategy in urban ecosystems. Focusing on wild bees, species whose preferred plant families are selected and facilitated by stakeholders (in Central European cities, e.g. Rosaceae, Fagaceae, Salicaceae; Ossola et al., 2020) could have very diversified resources, due to the co-occurrence of spontaneous and cultivated native and exotic plant species. Here, we show that this is the case for *O. cornuta* and *O. bicornis*. Consequently, wild bees could still switch pollen hosts at the species level and better exploit existing resources while avoiding the costs associated with broad niches, as some pollen types are indigestible or toxic (Eckhardt et al., 2014; Praz et al., 2008). On the other hand, strict specialization, as in *C. florisomne*, can still be a successful strategy in urban ecosystems when pollen hosts are highly facilitated and widespread in urban ecosystems. Nonetheless, strict specialists are vulnerable to the partial or total loss of pollen hosts, due to, for example, urban sprawl across the habitat of the bee or pollen host species, changes in social investment when gardening or managing greenspaces, or the arrival of pests.

The degree of specialization in bees is associated with distribution patterns along urban gradients. Our results suggest that increasing specialization leads to a higher sensitivity towards increased urban intensity. Diet specialization determines the possibility of occupying new patches, and greater specialization represents a strong limitation when the nutritional requirements are not met (e.g. with agricultural intensification; Peters et al., 2021). Rarity in bumblebees has been associated with narrower feeding niches (Goulson, 1999), and this is also the case for other wild bees (e.g. Deguines et al., 2016). Some types of urban greenspaces consistently contain high bee diversity, including several specialists (Baldock, 2020; Salisbury et al., 2015). Still, only a handful of usually broad generalists can colonize various types of urban greenspaces. Hence, these species are widespread within urban ecosystems (Casanelles-Abella, Chauvier, et al., 2021; Fournier et al., 2020), even though not only the degree of specialization but also other correlated functional traits are involved in the response to urbanization (e.g. stress tolerance, dispersal; Harrison & Winfree, 2015). To promote a larger number of bees in previously unoccupied areas of the city, wild bee habitat must be strategically increased, including enhancing the availability of high floral resource diversity. A first step to achieve this is to map the existing floral resources within the different urban land covers, making use of ongoing inventories (Ossola et al., 2020) or sampling schemes from research projects (Baldock et al., 2019; Casanelles-Abella, Frey, et al., 2021). These products could be combined and compared with wild bee diet preferences to detect where and what kind of planning actions can be taken. For instance, strategically increasing plant diversity rather than overall quantity with targeted taxonomic and trait groups is a measure that has been successful in other ecosystem types (e.g. agroecosystems; Sutter et al., 2017), although other wild bee requirements (e.g. nesting mode) must also be satisfied to successfully promote them (Requier & Leonhardt, 2020).

4.1 | Limitations and prospects

Pollen metabarcoding only yields relative abundance data and can be subject to PCR or taxon-dependent biases as discussed in several studies. (e.g. Bell et al., 2016; Keller et al., 2015) The semi-quantitative abundances obtained in metabarcoding analyses are however still useful to identify the relative proportions of taxa and differentiate dominant, common and rare contributions to a mixed pollen sample by showing correlations (even though not perfect) between read and grain numbers (Keller et al., 2015). It is further agreed that pollen metabarcoding can identify to deep taxonomic levels, is able to detect rare taxa and is well comparable between studies (Bell et al., 2016). In addition, the prevalence of certain plant families and species across cities (Figure 1), and the existing information on *C. florisomne*, *O. cornuta* and *O. bicornis* (Haider et al., 2013, 2014; Sedivy et al., 2008) showing patterns similar to those observed here support our findings. Combining molecular and morphological approaches would provide more robust relative abundance estimates as suggested by Sickel et al. (2015). Furthermore, if taking dry weight of the collected pollen samples is an option (e.g. Lihoreau et al., 2012), these relative data could be converted to absolute abundances per sample. Furthermore, we could only use morphological plant traits to investigate diet composition and shifts along urban gradients. However, bee choices when selecting larval food are likely to be influenced by the nutritional properties of the pollen, such as the content of protein, sugar or other essential nutrients (Vanderplanck et al., 2014; Vaudo et al., 2020). Evidence seems to indicate important differences in the nutritional value of the available floral resources between urban land cover types (Tew et al., 2021) and possibly between ornamental plant species (Garbuzov & Ratnieks, 2014). Incorporating nutritional traits in future dietary studies will better elucidate the mechanisms behind diet composition and trophic niche shifts.

Finally, our results open future research directions. First, further studies could consider whether there are signals of feeding behavioural changes due to anthropogenic factors (e.g. plant or management preferences by stakeholders), as seen in other taxa (e.g. Cucherousset et al., 2012), and if these are reflected in the variation of other functional traits (e.g. tongue length; Eggenberger et al., 2019). To achieve this, it would be critical to study and compare bee diets in both urban and non-urban ecosystems. Second, assessing the effects of intraspecific diet variability on fitness (e.g. number and sex ratio of offspring, adult and larval survival) would provide important mechanistic insights for anticipating how plant management choices might affect urban bee communities.

4.2 | Policy implications

The uncovered taxonomic and functional diet preferences can support the planning and management of urban greenspaces to promote wild bees, particularly in wild bee species where the diet patterns are consistent across cities. Typical common urban weeds (e.g. *Taraxacum officinale*, *Bellis perennis*, *Trifolium pratensis*, *T. repens*) that are important floral resources in urban areas (Baldock et al., 2019; Kanduth et al., 2021; Larson et al., 2014) contributed little or nothing to the larval diet of the studied bees. Conversely, both native and exotic woody species proved to be a widely used floral resource. For example, *O. cornuta* and *O. bicornis* collected large amounts of tree pollen from different plant families, which might enable them to exploit secondary pollen hosts by mixing high-quality pollens with less digestible ones (e.g. *Ranunculus* spp., Asteraceae; Eckhardt et al., 2014; Praz et al., 2008). Thus, the maintenance of different vegetation and urban habitat types (e.g. meadows, street trees, shrublands) is of major importance for preserving bees. In addition, our results indicate that the occurrence of specific plant taxa (e.g. at the family or genus level) or trait values is more important than the origin of the plants (Harrison & Winfree, 2015). For example, non-native plants have been observed to retain the blooming time of their original region (Godoy et al., 2009), and thus plant species from the Northern Hemisphere (e.g. planted urban trees or shrubs such *Acer* spp., *Salix* spp., *Crataegus* spp and *Quercus* spp.) may bloom in synchrony with natives species, providing additional resources for wild bees. Furthermore, urban trees have been shown to be an important resource for several wild bee species (Somme et al., 2016). For instance, in our study, *H. communis* increasingly collected more pollen from ornamental trees (mainly *Styphnolobium japonicum*) with decreasing amounts of greenspace. Because the tree distribution in cities is mostly driven by anthropogenic factors, it represents an important point of action for greening strategies, specifically in densely urbanized city areas with limited herbaceous vegetation. Overall, floral preferences obtained from pollen metabarcoding, particularly when combined with existing information on available floral resources, could help to improve current strategies for developing bee-friendly cities (e.g. in the EU, see Wilk et al., 2020). In particular, characterizing bee diets could inform planning, management and decision-making (e.g. what species, genera or families to plant), involving stakeholders, policymakers, nurseries and plant centres, for urban greenspaces to preserve and further promote wild bees in urban ecosystems.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

J.C.-A., S.M., M.M. and L.P. conceived the ideas; M.M., F.C., L.L., R.S., P.P. and P.T. developed the site selection methodology; J.C.-A. collected the bee data; A.K. performed the bioinformatic analyses on the pollen; J.C.-A., S.M., N.D., T.H. and M.A.O. collected the plant data; M.A.O., T.H. and L.L. provided the local land cover metrics; C.A. and P.P. provided the remote sensing data; J.C.-A. and S.M.

analysed the data; J.C.-A. led the manuscript writing, with editing and supervision by M.M. and L.P. All the authors reviewed and revised the manuscript and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data on diet composition supporting this paper available via EnviDat v.0.1 repository https://doi.org/10.16904/envidat.249 (Casanelles-Abella, Moretti, et al., 2021).

ORCID

Joan Casanelles-Abella https://orcid.org/0000-0003-1924-9298
Alexander Keller https://orcid.org/0000-0001-5716-3634
Cristiana Aleixo https://orcid.org/0000-0002-3293-476X
Marta Alós Orti https://orcid.org/0000-0002-5722-6583
François Chiron https://orcid.org/0000-0003-1958-7115
Nicolas Deguines https://orcid.org/0000-0001-6930-916X
Lauri Laanisto https://orcid.org/0000-0003-2215-7298
Pedro Pinho https://orcid.org/0000-0001-5571-9619
Roeland Samson https://orcid.org/0000-0001-7582-1450
Loïc Pellissier https://orcid.org/0000-0002-2289-8259
Marco Moretti https://orcid.org/0000-0002-5845-3198

REFERENCES

Allouche, O., Tsoar, A., & Kadmon, R. (2006). Assessing the accuracy of species distribution models: Prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology*, *43*(6), 1223–1232. https://doi.org/10.1111/j.1365-2664.2006.01214.x

Ankenbrand, M. J., Keller, A., Wolf, M., Schultz, J., & Förster, F. (2015). ITS2 database V: Twice as much. *Molecular Biology and Evolution*, *32*(11), 3030–3032. https://doi.org/10.1093/molbev/msv174

Aronson, M. F. J., Lepczyk, C. A., Evans, K. L., Goddard, M. A., Lerman, S. B., MacIvor, J. S., Nilon, C. H., & Vargo, T. (2017). Biodiversity in the city: Key challenges for urban green space management. *Frontiers in Ecology and the Environment*, *15*(4), 189–196. https://doi.org/10.1002/fee.1480

Baldock, K. C. R. (2020). Opportunities and threats for pollinator conservation in global towns and cities. *Current Opinion in Insect Science*, *38*, 63–71. https://doi.org/10.1016/j.cois.2020.01.006

Baldock, K. C. R., Goddard, M. A., Hicks, D. M., Kunin, E., Mitschunas, N., Osgathorpe, L. M., Potts, S. G., Robertson, K. M., Scott, A. V., Stone, G. N., Vaughan, I. P., & Memmott, J. (2015). Where is the UK's pollinator biodiversity ? The importance of urban areas for flower-visiting insects. *Proceedings of the Royal Society: Biologcal Sciences*, *282*, 20142849.

Baldock, K. C. R., Goddard, M. A., Hicks, D. M., Kunin, W. E., Mitschunas, N., Morse, H., Osgathorpe, L. M., Potts, S. G., Robertson, K. M., Scott, A. V., Staniczenko, P. P. A., Stone, G. N., Vaughan, I. P., & Memmott, J. (2019). A systems approach reveals urban pollinator hotspots and conservation opportunities. *Nature Ecology and Evolution*, *3*(3), 363–373. https://doi.org/10.1038/s41559-018-0769-y

Bell, K. L., De Vere, N., Keller, A., Richardson, R. T., Gous, A., Burgess, K. S., & Brosi, B. J. (2016). Pollen DNA barcoding: Current applications and future prospects. *Genome*, *59*(9), 629–640. https://doi.org/10.1139/gen-2015-0200

Buisson, L., Thuiller, W., Casajus, N., Lek, S., & Grenouillet, G. (2010). Uncertainty in ensemble forecasting of species distribution. *Global Change Biology*, *16*(4), 1145–1157. https://doi.org/10.1111/j.1365-2486.2009.02000.x

Campos, M. G., Anjos, O., Chica, M., Campoy, P., Nozkova, J., Almaraz-Abarca, N., Barreto, L. M. R. C., Nordi, J. C., Estevinho, L. M., Pascoal, A., Paula, V. B., Chopina, A., Dias, L. G., Tešić, Ž. L. J., Mosić, M. D., Kostić, A. Ž., Pešić, M. B., Milojković-Opsenica, D. M., Sickel, W., … Carreck, N. L. (2021). Standard methods for pollen research. *Journal of Apicultural Research*, *60*(4), 1–109. https://doi.org/10.1080/00218839.2021.1948240

Casanelles-Abella, J., Chauvier, Y., Zellweger, F., Villiger, P., Frey, D., Ginzler, C., Moretti, M., & Pellissier, L. (2021). Applying predictive models to study the ecological properties of urban ecosystems: A case study in Zürich. *Switzerland*. *Landscape and Urban Planning*, *214*, 104137. https://doi.org/10.1016/j.landurbplan.2021.104137

Casanelles-Abella, J., Frey, D., Müller, S., Aleixo, C., Alós Ortí, M., Deguines, N., Hallikma, T., Laanisto, L., Niinemets, Ü., Pinho, P., Samson, R., Villarroya-Villalba, L., & Moretti, M. (2021). A dataset of the flowering plants (Angiospermae) in urban green areas in five European cities. *Data in Brief*, *37*, 107243. https://doi.org/10.1016/j.dib.2021.107243

Casanelles-Abella, J., Moretti, M., Pellissier, L., Keller, A., Müller, S., Samson, R., Pinho, P., Chiron, F., Laanisto, L., Tryjanowski, P., & Villarroya Villalba, L. (2021). Larval food composition of four wild bee species in five European cities. *EnviDat*, https://doi.org/10.16904/envidat.249

Cucherousset, J., Boulêtreau, S., Azémar, F., Compin, A., Guillaume, M., & Santoul, F. (2012). 'Freshwater killer whales': Beaching behavior of an alien fish to hunt land birds. *PLoS One*, *7*(12), 1–6. https://doi.org/10.1371/journal.pone.0050840

Deguines, N., Julliard, R., de Flores, M., & Fontaine, C. (2016). Functional homogenization of flower visitor communities with urbanization. *Ecology and Evolution*, *6*(7), 1967–1976. https://doi.org/10.1002/ece3.2009

Dharmarajan, G., Gupta, P., Vishnudas, C. K., & Robin, V. V. (2021). Anthropogenic disturbance favours generalist over specialist parasites in bird communities: Implications for risk of disease emergence. *Ecology Letters*, *24*(9), 1859–1868. https://doi.org/10.1111/ele.13818

Eckhardt, M., Haider, M., Dorn, S., & Müller, A. (2014). Pollen mixing in pollen generalist solitary bees: A possible strategy to complement or mitigate unfavourable pollen properties? *Journal of Animal Ecology*, *83*(3), 588–597. https://doi.org/10.1111/1365-2656.12168

Edgar, R. (2016a). SINTAX: A simple non-Bayesian taxonomy classifier for 16S and ITS sequences. *BioRxiv*, 074161. https://doi.org/10.1101/074161

Edgar, R. (2016b). UCHIME2: Improved chimera prediction for amplicon sequencing. *BioRxiv*, 074252. https://doi.org/10.1101/074252

Edgar, R. C., & Flyvbjerg, H. (2015). Error filtering, pair assembly and error correction for next-generation sequencing reads. *Bioinformatics*, *31*(21), 3476–3482. https://doi.org/10.1093/bioinformatics/btv401

EEA. (2012). *Urban Atlas*. Retrieved from http://land.copernicus.eu/local/urban-atlas/urban-atlas-2012

Eggenberger, H., Frey, D., Pellissier, L., Ghazoul, J., Fontana, S., & Moretti, M. (2019). Urban bumblebees are smaller and more phenotypically diverse than their rural counterparts. *Journal of Animal Ecology*, *88*(10), 1522–1533. https://doi.org/10.1111/1365-2656.13051

Faeth, S. H., Warren, P. S., Shochat, E., & Marussich, W. A. (2005). Trophic dynamics in urban communities. *BioScience*, *55*(5), 399–407. https://doi.org/10.1641/0006-3568(2005)055[0399:TDIUC]2.0.CO;2

Fournier, B., Frey, D., & Moretti, M. (2020). The origin of urban communities: From the regional species pool to community assemblages in city. *Journal of Biogeography*, *47*(3), 615–629. https://doi.org/10.1111/jbi.13772

Garbuzov, M., & Ratnieks, F. L. W. (2014). Quantifying variation among garden plants in attractiveness to bees and other flower-visiting insects. *Functional Ecology*, *28*(2), 364–374. https://doi.org/10.1111/1365-2435.12178

GBIF. (2021). Data from: GBIF occurrence download. Downloaded on 18 May 2021. https://doi.org/10.15468/dl.z6fg97

Godoy, O., Richardson, D. M., Valladares, F., & Castro-Díez, P. (2009). Flowering phenology of invasive alien plant species compared with native species in three Mediterranean-type ecosystems. *Annals of Botany*, *103*(3), 485–494. https://doi.org/10.1093/aob/mcn232

Goulson, D. (1999). Foraging strategies of insects for gathering nectar and pollen, and implications for plant ecology and evolution. *Perspectives in Plant Ecology, Evolution and Systematics*, *2*(2), 185–209. https://doi.org/10.1078/1433-8319-00070

Goulson, D., Nicholls, E., Botías, C., & Rotheray, E. L. (2015). Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science*, *347*(6229), 1255957. https://doi.org/10.1126/science.1255957

Haider, M., Dorn, S., & Müller, A. (2013). Intra- and interpopulational variation in the ability of a solitary bee species to develop on non-host pollen: Implications for host range expansion. *Functional Ecology*, *27*(1), 255–263. https://doi.org/10.1111/1365-2435.12021

Haider, M., Dorn, S., Sedivy, C., & Müller, A. (2014). Phylogeny and floral hosts of a predominantly pollen generalist group of mason bees (Megachilidae: Osmiini). *Biological Journal of the Linnean Society*, *111*(1), 78–91. https://doi.org/10.1111/bij.12186

Harrison, T., & Winfree, R. (2015). Urban drivers of plant-pollinator interactions. *Functional Ecology*, *29*(7), 879–888. https://doi.org/10.1111/1365-2435.12486

Kanduth, L., Chartier, M., Schönenberger, J., & Dellinger, A. S. (2021). Red and white clover provide food resources for honeybees and wild bees in urban environments. *Nordic Journal of Botany*, *39*(3), 1–11. https://doi.org/10.1111/njb.03005

Keller, A., Danner, N., Grimmer, G., Ankenbrand, M., von der Ohe, K., von der Ohe, W., Rost, S., Härtel, S., & Steffan-Dewenter, I. (2015). Evaluating multiplexed next-generation sequencing as a method in palynology for mixed pollen samples. *Plant Biology*, *17*(2), 558–566. https://doi.org/10.1111/plb.12251

Keller, A., Hohlfeld, S., Kolter, A., Schultz, J., Schultz, J., Gemeinholzer, B., & Ankenbrand, M. J. (2020). BCdatabaser: On-the-fly reference database creation for (meta-)barcoding. *Bioinformatics*, *36*(8), 2630–2631. https://doi.org/10.1093/bioinformatics/btz960

Larson, J. L., Kesheimer, A. J., & Potter, D. A. (2014). Pollinator assemblages on dandelions and white clover in urban and suburban lawns. *Journal of Insect Conservation*, *18*(5), 863–873. https://doi.org/10.1007/s10841-014-9694-9

Leclère, D., Obersteiner, M., Barrett, M., Butchart, S. H. M., Chaudhary, A., De Palma, A., DeClerck, F. A. J., Di Marco, M., Doelman, J. C., Dürauer, M., Freeman, R., Harfoot, M., Hasegawa, T., Hellweg, S., Hilbers, J. P., Hill, S. L. L., Humpenöder, F., Jennings, N., Krisztin, T., … Young, L. (2020). Bending the curve of terrestrial biodiversity needs an integrated strategy. *Nature*, *585*(7826), 551–556. https://doi.org/10.1038/s41586-020-2705-y

Lihoreau, M., Raine, N. E., Reynolds, A. M., Stelzer, R. J., Lim, K. S., Smith, A. D., Osborne, J. L., & Chittka, L. (2012). Radar tracking and motion-sensitive cameras on flowers reveal the development of pollinator multi-destination routes over large spatial scales. *PLoS Biology*, *10*(9), e1001392. https://doi.org/10.1371/journal.pbio.1001392

Marquardt, M., Kienbaum, L., Kretschmer, L. A., Penell, A., Schweikert, K., Ruttensperger, U., & Rosenkranz, P. (2021). Evaluation of the importance of ornamental plants for pollinators in urban and suburban areas in Stuttgart. *Germany. Urban Ecosystems*, *24*(4), 811–825. https://doi.org/10.1007/s11252-020-01085-0

Ossola, A., Hoeppner, M. J., Burley, H. M., Gallagher, R. V., Beaumont, L. J., & Leishman, M. R. (2020). The global urban tree inventory: A database of the diverse tree flora that inhabits the world's cities. *Global Ecology and Biogeography*, *29*(11), 1907–1914. https://doi.org/10.1111/geb.13169

Peters, B., Keller, A., & Leonhardt, S. (2021). Diets maintained in a changing world: Does land-use intensification alter wild bee communities by selecting for flexible generalists? *Ecology and Evolution*, in review.

Pitteloud, C., Walser, J. C., Descombes, P., Novaes de Santana, C., Rasmann, S., & Pellissier, L. (2021). The structure of plant–herbivore interaction networks varies along elevational gradients in the European Alps. *Journal of Biogeography*, *48*(2), 465–476. https://doi.org/10.1111/jbi.14014

Potts, S. G., Imperatriz-Fonseca, V., Ngo, H. T., Aizen, M. A., Biesmeijer, J. C., Breeze, T. D., Dicks, L. V., Garibaldi, L. A., Hill, R., Settele, J., & Vanbergen, A. J. (2016). Safeguarding pollinators and their values to human well-being. *Nature*, *540*(7632), 220–229. https://doi.org/10.1038/nature20588

Praz, C. J., Müller, A., & Dorn, S. (2008). Specialized bees fail to develop on non-host pollen: Do plants chemically protect their pollen? *Ecology*, *89*(3), 795–804. https://doi.org/10.1890/07-0751.1

R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Requier, F., & Leonhardt, S. D. (2020). Beyond flowers: Including non-floral resources in bee conservation schemes. *Journal of Insect Conservation*, *24*(1), 5–16. https://doi.org/10.1007/s10841-019-00206-1

Rognes, T., Flouri, T., Nichols, B., Quince, C., & Mahé, F. (2016). VSEARCH: A versatile open source tool for metagenomics. *PeerJ*, *24*(4), e2584. https://doi.org/10.7717/peerj.2584

Roth, M., Oke, T. R., & Emery, W. J. (1989). Satellite-derived urban heat islands from three coastal cities and the utilization of such data in urban climatology. *International Journal of Remote Sensing*, *10*(11), 1699–1720. https://doi.org/10.1080/01431168908904002

RStudio Team. (2020). *R studio: Integrated development for R*. RStudio Inc.

Salisbury, A., Armitage, J., Bostock, H., Perry, J., Tatchell, M., & Thompson, K. (2015). Enhancing gardens as habitats for flower-visiting aerial insects (pollinators): Should we plant native or exotic species? *Journal of Applied Ecology*, *52*(5), 1156–1164. https://doi.org/10.1111/1365-2664.12499

Scheyer, A., Morville, S., Mirabel, P., & Millet, M. (2007). Pesticides analysed in rainwater in Alsace region (Eastern France): Comparison between urban and rural sites. *Atmospheric Environment*, *41*(34), 7241–7252. https://doi.org/10.1016/j.atmosenv.2007.05.025

Sedivy, C., Müller, A., & Dorn, S. (2011). Closely related pollen generalist bees differ in their ability to develop on the same pollen diet: Evidence for physiological adaptations to digest pollen. *Functional Ecology*, *25*(3), 718–725. https://doi.org/10.1111/j.1365-2435.2010.01828.x

Sedivy, C., Praz, C. J., Müller, A., Widmer, A., & Dorn, S. (2008). Patterns of host-plant choice in bees of the genus Chelostoma: The constraint hypothesis of host-range evolution in bees. *Evolution*, *62*(10), 2487–2507. https://doi.org/10.1111/j.1558-5646.2008.00465.x

Sickel, W., Ankenbrand, M. J., Grimmer, G., Holzschuh, A., Härtel, S., Lanzen, J., Steffan-Dewenter, I., & Keller, A. (2015). Increased efficiency in identifying mixed pollen samples by meta-barcoding with a dual-indexing approach. *BMC Ecology*, *15*(1), 1–9. https://doi.org/10.1186/s12898-015-0051-y

Somme, L., Moquet, L., Quinet, M., Vanderplanck, M., Michez, D., Lognay, G., & Jacquemart, A. L. (2016). Food in a row: Urban trees offer valuable floral resources to pollinating insects. *Urban Ecosystems*, *19*(3), 1149–1161. https://doi.org/10.1007/s11252-016-0555-z

Staab, M., Pufal, G., Tscharntke, T., & Klein, A.-M.-M. (2018). Trap nests for bees and wasps to analyse trophic interactions in changing environments—A systematic overview and user guide. *Methods in Ecology and Evolution*, *9*(11), 2226–2239. https://doi.org/10.1111/2041-210X.13070

Sutter, L., Jeanneret, P., Bartual, A. M., Bocci, G., & Albrecht, M. (2017). Enhancing plant diversity in agricultural landscapes promotes both rare bees and dominant crop-pollinating bees through complementary increase in key floral resources. *Journal of Applied Ecology*, *54*(6), 1856–1864. https://doi.org/10.1111/1365-2664.12907

Tew, N. E., Memmott, J., Vaughan, I. P., Bird, S., Stone, G. N., Potts, S. G., & Baldock, K. C. R. (2021). Quantifying nectar production by flowering plants in urban and rural landscapes. *Journal of Ecology*, *109*(4), 1747–1757. https://doi.org/10.1111/1365-2745.13598

Theodorou, P., Radzevičiūtė, R., Lentendu, G., Kahnt, B., Husemann, M., Bleidorn, C., Settele, J., Schweiger, O., Grosse, I., Wubet, T., Murray, T. E., & Paxton, R. J. (2020). Urban areas as hotspots for bees and pollination but not a panacea for all insects. *Nature Communications*, *11*(1), 1–13. https://doi.org/10.1038/s41467-020-14496-6

Thuiller, W., Guéguen, M., Renaud, J., Karger, D. N., & Zimmermann, N. E. (2019). Uncertainty in ensembles of global biodiversity scenarios. *Nature Communications*, *10*(1), 1446. https://doi.org/10.1038/s41467-019-09519-w

Turrini, T., & Knop, E. (2015). A landscape ecology approach identifies important drivers of urban biodiversity. *Global Change Biology*, *21*(4), 1652–1667. https://doi.org/10.1111/gcb.12825

Vanderplanck, M., Moerman, R., Rasmont, P., Lognay, G., Wathelet, B., Wattiez, R., & Michez, D. (2014). How does pollen chemistry impact development and feeding behaviour of polylectic bees? *PLoS One*, *9*(1), 1–9. https://doi.org/10.1371/journal.pone.0086209

Vaudo, A. D., Tooker, J. F., Patch, H. M., Biddinger, D. J., Coccia, M., Crone, M. K., Fiely, M., Francis, J. S., Hines, H. M., Hodges, M., Jackson, S. W., Michez, D., Mu, J., Russo, L., Safari, M., Treanore, E. D., Vanderplanck, M., Yip, E., Leonard, A. S., & Grozinger, C. M. (2020). Pollen protein: Lipid macronutrient ratios may guide broad patterns of bee species floral preferences. *Insects*, *11*(2), 132. https://doi.org/10.3390/insects11020132

Vierna, J., Doña, J., Vizcaíno, A., Serrano, D., Jovani, R., & Chain, F. (2017). PCR cycles above routine numbers do not compromise high-throughput DNA barcoding results. *Genome*, *60*(10), 868–873. https://doi.org/10.1139/gen-2017-0081

Wilk, B., Rebollo, V., & Hanania, S. (2020). *A guide for pollinator-friendly cities: Environment a guide for pollinator-friendly cities: How can spatial planners and land-use managers create favourable urban environments for pollinators?* Guidance prepared by ICLEI Europe for the European Commission.

Wilson, R. S., Keller, A., Shapcott, A., Leonhardt, S. D., Sickel, W., Hardwick, J. L., Heard, T. A., Kaluza, B. F., & Wallace, H. M. (2021). Many small rather than few large sources identified in long-term bee pollen diets in agroecosystems. *Agriculture, Ecosystems & Environment*, *310*, 107296. https://doi.org/10.1016/j.agee.2020.107296

Wood, T. J., Ghisbain, G., Rasmont, P., Kleijn, D., Raemakers, I., Praz, C., Killewald, M., Gibbs, J., Bobiwash, K., Boustani, M., Martinet, B., & Michez, D. (2021). Global patterns in bumble bee pollen collection show phylogenetic conservation of diet. *Journal of Animal Ecology*, *310*(1365–2656), 13553. https://doi.org/10.1111/1365-2656.13553

Zattara, E. E., & Aizen, M. A. (2021). Worldwide occurrence records suggest a global decline in bee species richness. *One Earth*, *4*(1), 114–123. https://doi.org/10.1016/j.oneear.2020.12.005

SUPPORTING INFORMATION

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Supporting Information for the paper "How bees find a way in European cities: pollen metabarcoding unravels multiple feeding strategies and their effects on distribution patterns in four wild bee species"

Joan Casanelles-Abella, Stefanie Müller , Alexander Keller , Cristiana Aleixo , Marta Alós Orti, François Chiron, Nicolas Deguines Tiit Hallikma, Lauri Laanisto, Pedro Pinho, Roeland Samson, Piotr Tryjanowski ,Anskje Van Mensel, Loïc Pellissier, Marco Moretti

Supplementary texts

- **Text S1.** Study organisms.
- **Text S2**. Plant phylogenetic tree.
- **Text S3.** Pollen metabarcoding laboratory workflow.
- **Text S4.** Plant sampling.
- **Text S5.** Local land cover metrics.
- **Text S6.** Remote sensing indices.
- **Text S7.** χ^2 tests.

Supplementary tables

- **Table S1.** Information on the sites and number of samples.
- **Table S2.** Plant traits.
- **Table S3.** Information on the plant traits.
- **Table S4.** Plant taxonomic metrics.
- **Table S5.** Plant trait-based metrics.
- **Table S6.** Aggregation Chi-squared.
- **Table S7.** Predictive power of the SDM variables.
- **Table S8.** Plant species composition in larval pollen.
- **Table S9.** Overview of the larval diet in the studied cities.
- **Table S10.** Pairwise Pearson correlations on bee diets.
- **Table S11.** Chi-squared results.
- **Table S12.** Pairwise Pearson correlations urban gradient.

Supplementary figures

- **Figure S1.** Study sites, trap-nests and bee nests.
- **Figure S2.** Range of values for explanatory proxies in the five cities.
- **Figure S3.** Plant list.
- **Figure S4.** Correlations between environmental predictors.
- **Figure S5.** Full phylogenetic tree.
- **Figure S6.** Histogram pollen abundance per nest

- **Figure S7.** Origin status.
- **Figure S8.** Growth form.
- **Figure S9.** Blossom class.
- **Figure S10.** Chi-squared correlations.
- **Figure S11.** Taxonomic responses along the urbanization gradient.
  Figure S12. PCA
- **Figure S13.** Probability of occurrence extended.

Supplementary data

- **Data S1.** Performance SDMs

Supplementary text

TEXT S1. ***Study organisms.*** *Osmia bicornis*, *Osmia cornuta* and *Hylaeus communis* are polylectic bees, but display differences in terms of the total number of plant families visited and the preferences for specific plant families (Haider et al., 2014). *Hylaeus communis* is the most polylectic bee species of the three, visiting a wide array of plant families (Martins et al., 2017). Both *O. bicornis* and *O. cornuta* are closely related species but display distinct preferences for pollen hosts and plant families (Haider et al., 2014; Sedivy et al., 2011). In contrast, *C. florisomne* is a strict oligolectic bee, foraging on species within the genus *Ranunculus* (Sedivy et al., 2008). *Chelostoma florisomne, O. cornuta* and *O. bicornis* fly from late winter to mid spring, whereas *H. communis* flies during late spring and summer.

TEXT S2. ***Phylogenetic tree of the plant species collected in the pollen***. The phylogenetic tree of the plant species present in the pollen of the studied bees (Fig. S5) was computed with the R package *V.phylomaker* (Jin & Qian, 2019) version 0.1.0. This package contains a mega-tree assembled from the published plant phylogeny from Smith and Brown (2018) known as the GBOTB, and contains 74 533 species and all families of extant vascular plants (Jin & Qian, 2019). The phylogenetic tree was assembled using the function ‘phylo.maker’ using all the tips in the largest cluster of the genus to define the most common recent ancestor (nodes = nodes.info.1), based on Qian and Jin (2016), using their third approach for adding genera and species to the phylogeny (scenario=”S3”).

TEXT S3. ***Pollen metabarcoding laboratory workflow.*** The total genomic DNA was isolated from all samples using either the EZNA Tissue Isolation Kit (Omega Biotek; Norcross, USA) or the Quick-DNA MicroPrep Kit (Zymo; Tustin, USA), which is specifically designed for DNA isolation from small samples. Both kits were used strictly according to the manufacturer’s instructions. For the Omega kit, DNA was eluted in a final volume of 1000 µL, whereas in the case of the Zymo kit, the final elution volume was 20 µL. A sample that contained no pollen was included in every DNA isolation round and treated as if it was a regular sample to check for cross-contamination during the experiments. DNA was quantified using the Qubit High Sensitivity dsDNA Assay (Thermo Fisher Scientific; Walthan, USA). For library preparation, a fragment of the ITS2 genomic region (of around 300 bp) was amplified using the primers ITS_S2F (5’ ATG CGA TAC TTG GTG TGA AT 3’) (Yao et al., 2010) and ITS4R (5’ TCC TCC GCT TAT TGA TAT GC 3’) (White, Bruns, Lee, & Taylor, 1990). These primers included the Illumina sequencing primer sequences attached to their 5’ ends. PCRs were carried out in a final volume of 25 µL, containing 2.5 µL of template DNA, 0.5 µM of the primers, 12.5 µL of Supreme NZYTaq 2x Green Master Mix (NZYTech; Lisboa, Portugal), and ultrapure water to reach the full 25 µL. The reaction mixture was incubated as follows: an initial denaturation step at 95°C for 5 min, followed by 35 cycles of 95°C for 30 s, 51°C for 45 s and 72°C for 30 s, and a final extension step at 72°C for 10 min. The oligonucleotide indices which are required for multiplexing different libraries in the same sequencing pool were attached in a second PCR round with identical conditions but for only 5 cycles and with 60°C as the annealing temperature. For a schematic overview of the library preparation process, see Fig. 1 in Vierna et al. (2017) and Sickel et al (2015). A negative control that contained no DNA (BPCR) was included in every PCR round to check for contamination during library preparation. The libraries were run on 2% agarose gels stained with GreenSafe (NZYTech) and imaged under UV light to verify the library size. Libraries were purified using the Mag-Bind RXNPure Plus magnetic beads (Omega Biotek), following the instructions provided by the manufacturer. Then, 338 of the total 675 libraries were pooled in equimolar amounts according to the quantification data provided by the Qubit dsDNA HS Assay (Thermo Fisher Scientific). This pool also contained a very small amount of approximately half of the extraction blanks and the PCR blanks (BPCR). The pool was sequenced in a MiSeq PE300 run (Illumina; San Diego, USA). Illumina paired-end raw files consisted of forward (R1) and reverse (R2) reads sorted by the library and their quality scores. The indices and sequencing primers were trimmed during the demultiplexing step. Moreover, we used the q2-cutadapt plugin, as implemented in QIIME2 (release 2019.10; Bolyen et al., 2018), to eliminate the part of the sequences that contained the Illumina sequencing adaptors.

TEXT S4. ***Plant sampling and traits***. We sampled all plants in a buffer of 100 m radius around each trap-nest. Sites were visited in April, May, June and July 2018. Sampling time was limited to a maximum of 2.5 hours. Each buffer was divided into 16 cells. In each cell, we documented all the plant species found, in order to obtain an estimate of both plant richness and frequency. Taxonomy assignment largely followed the criteria of the Checklist of the National Data and Information Centre of Swiss Flora (Juillerat et al., 2017) and the World Flora Online database (WFO, 2021).

We collected two plant functional traits: growth form (considering trees, shrubs, herbs and climbers; Table S2) and blossom type (following Faeregi & Pijl, (1979), classifying blossoms according to the diffusion mode and accessibility into bell-trumpet, brush, dish-bowl, flag, gullet and stalk-disk; Table S2). These two functional traits are related to the accessibility of floral resources and thus are potentially important drivers of plant–bee interactions, based on the information available in Casanelles-Abella, Frey et al. (2021). Moreover, we collected information on the origin status, which is not a functional trait itself but a main feature for assessing the importance of different social aspects (e.g. gardening preferences) in bee diet, as well as a measure of the length of shared evolutionary history where the bee and plant species are co-occurring. Plant species found in the pollen samples were classified accordingly (Table S2).

TEXT S5. ***Local land cover metrics.*** Local land cover metrics followed Alós Orti et al. (2021). We made a land cover map of each study site by photo-interpretating high-resolution (i.e. 0.5 m) aerial images from 2015 using ESRI ArcMap 10.4. Photo-interpretation was done at a scale of 1:600, which made it possible to distinguish between the different land cover types within the study sites, specifically, artificial surfaces, bare land, grasslands, shrublands, and deciduous and coniferous trees. Satellite imagery does not allow the precise classification of the extent of all land cover types, due to overlapping vertical layers. Hence, our land cover maps provided accurate information about the upper layer only (i.e. tree canopy cover and canopy percentage). After the land cover maps were complete, the proportion of each class was calculated from the focal point where the trap-nests were installed within buffers of 8, 16 and 32 m radii.

TEXT S6. *Remote-sensed indices.* Land surface temperature (LST) is an extremely relevant index for understanding several environmental phenomena, such as thermal stress, and at various spatial and temporal scales. The LST reflects the thermal response of the different Earth's surfaces and materials and is therefore often referred to as the radiative skin temperature over the Earth's surface (Weng et al., 2014). We emphasize that the LST is a surface phenomenon, whose magnitude is higher during the day and lower at night, the inverse of the atmospheric counterpart (Zhou et al., 2014). The LST can be extracted using remotely sensed thermal infrared data and depends on the albedo, vegetation cover and soil moisture.

Several Landsat-8 OLI satellite images were acquired during the most extreme seasons of the year (Table SA) to ensure that the LST is not representative of a single day only. These images were obtained from the USGS/Earth Explorer website (https://earthexplorer.usgs.gov/) with 30 m spatial resolution and whenever possible with less than 10% cloud cover.

Text S6 - Table SA. Remotely sensed thermal infrared data used to determine the land surface temperature (LST) in each of the five cities (Antwerp, Paris, Poznan, Tartu and Zurich).

City	Sensor	Tile Number	Date	Cloud Coverage
Antwerp	Landsat8 - OLI	Path: 198/ Row:24	31/07/2014	4.93%
Antwerp	Landsat8 - OLI	Path: 198/ Row:24	17/09/2014	0.30%
Antwerp	Landsat8 - OLI	Path: 198/ Row:24	12/03/2015	0.37%
Antwerp	Landsat8 - OLI	Path: 198/ Row:24	03/08/2015	2.74%
Antwerp	Landsat8 - OLI	Path: 198/ Row:24	14/04/2016	7.98%
Antwerp	Landsat8 - OLI	Path: 198/ Row:24	20/07/2016	1.77%
Antwerp	Landsat8 - OLI	Path: 198/ Row:24	26/07/2018	2.17%
Antwerp	Landsat8 - OLI	Path: 198/ Row:24	27/06/2019	7.22%
Paris	Landsat8 - OLI	Path: 199/ Row:29	16/03/2014	8.18%
Paris	Landsat8 - OLI	Path: 199/ Row:26	08/09/2014	2.36%
Paris	Landsat8 - OLI	Path: 199/ Row:28	19/01/2017	3.42%
Paris	Landsat8 - OLI	Path: 199/ Row:27	23/02/2018	0.15%
Paris	Landsat8 - OLI	Path: 199/ Row:26	02/08/2018	2.82%
Paris	Landsat8 - OLI	Path: 199/ Row:26	26/02/2019	0.04%
Paris	Landsat8 - OLI	Path: 199/ Row:26	04/07/2019	0.00%
Paris	Landsat8 - OLI	Path: 199/ Row:26	06/09/2019	7.73%
Poznan	Landsat8 - OLI	Path: 190/ Row:24	11/08/2015	0.03%
Poznan	Landsat8 - OLI	Path: 190/ Row:24	14/09/2016	0.51%

Poznan	Landsat8 - OLI	Path: 190/ Row:24	08/02/2018	30.99%
Poznan	Landsat8 - OLI	Path: 190/ Row:24	20/09/2018	2.30%
Poznan	Landsat8 - OLI	Path: 190/ Row:24	27/02/2019	8.93%
Tartu	Landsat8 - OLI	Path: 187/ Row:22	15/03/2015	0.07%
Tartu	Landsat8 - OLI	Path: 187/ Row:19	28/12/2015	2.35%
Tartu	Landsat8 - OLI	Path: 187/ Row:20	26/07/2017	11.79%
Tartu	Landsat8 - OLI	Path: 186/ Row:19	22/07/2018	18.65%
Tartu	Landsat8 - OLI	Path: 186/ Row:19	23/08/2018	6.05%
Tartu	Landsat8 - OLI	Path: 187/ Row:21	17/08/2019	29.48%
Tartu	Landsat8 - OLI	Path: 187/ Row:19	02/09/2019	1.08%
Zurich	Landsat8 - OLI	Path: 194/ Row:24	30/08/2015	1.29%
Zurich	Landsat8 - OLI	Path: 194/ Row:27	18/03/2016	1.04%
Zurich	Landsat8 - OLI	Path: 194/ Row:25	16/08/2016	9.46%
Zurich	Landsat8 - OLI	Path: 194/ Row:26	25/08/2016	0.51%
Zurich	Landsat8 - OLI	Path: 194/ Row:27	08/03/2018	8.59%
Zurich	Landsat8 - OLI	Path: 195/ Row:27	14/02/2019	0.49%
Zurich	Landsat8 - OLI	Path: 195/ Row:27	24/07/2019	2.13%
Zurich	Landsat8 - OLI	Path: 194/ Row:27	09/08/2019	9.42%
Zurich	Landsat8 - OLI	Path: 194/ Row:27	18/08/2019	0.89%
Zurich	Landsat8 - OLI	Path: 195/ Row:27	25/08/2019	1.80%
Zurich	Landsat8 - OLI	Path: 194/ Row:27	03/09/2019	2.95%

In this work, we adopted the Radiative Transfer Equation model to estimate the LST, since it can reach an accuracy of 0.6°C (Sobrino et al., 2004; Yu et al., 2014), which is given by:

$$\mathrm{LST} = \frac{c_2}{\lambda \ln \left\{ \dfrac{c_1}{\lambda^5 \left[\dfrac{L_{TIR} - Lu - \tau\,(1-\varepsilon)\,Ld}{\tau\,\varepsilon} \right]} + 1 \right\}}$$

where LST is the land surface temperature; c_1 and c_2 are constants; λ is the thermal infrared (TIR) band wavelength; L_{TIR} corresponds to the spectral radiance value at the top-of-atmosphere; Lu and Ld are the upwelling and the downwelling atmospheric radiance, respectively; τ is the atmospheric transmittance; and ε is the land surface emissivity. To simulate atmospheric transmittance and upwelling and downwelling radiances, we used the spatial and temporal closest atmospheric profile from the MODTRAN model. The land surface emissivity was derived from a normalized difference vegetation index (NDVI) threshold method, using the following equation:

$$\varepsilon = \begin{cases} \varepsilon_w, & \text{NDVI} < 0.0 \\ a + \mathrm{b} \cdot \rho_{red}, & 0.0 \geq \text{NDVI} < 0.2 \\ \varepsilon_v \cdot \mathrm{P}_v + \varepsilon_s (1 - \mathrm{P}_v) + \mathrm{C}, & 0.2 \geq \text{NDVI} \leq 0.5 \\ \varepsilon_v + \mathrm{C}, & \text{NDVI} > 0.5 \end{cases}$$

where a and b are constants (0.979 and 0.046 respectively); ρ_{red} is the land surface reflectance in the red band; and ε_w, ε_v and ε_s are the emissivity of water, vegetation and soil, respectively. P_v refers to the proportion of vegetation and can be calculated using the following equation:

$$\mathrm{P}_v = \left[\frac{\mathrm{NDVI} - \mathrm{NDVI}_{min}}{\mathrm{NDVI}_{max} - \mathrm{NDVI}_{min}}\right]^2$$

where NDVI_{min} and NDVI_{max} represent minimum and maximum NDVI, respectively, and can be obtained from the histogram of NDVI image. C is a term which takes the cavity effect into account, due to the surface roughness, and can be estimated using the following equation:

$$\mathrm{C} = (1 - \varepsilon_s) \cdot \varepsilon_v \cdot F \cdot (1 - \mathrm{Pv})$$

where F is the geometrical factor between 0 and 1 (Yu et al., 2014). After processing all indices, we calculated the average of each index for summer and for winter.

ArcMap (v.10.5.1) was used to process Landsat-8 OLI images, including radiometric calibration and atmospheric correction, but also the entire process through the final LST calculation.

In addition to LST, other remote sensing indices were calculated based on Sentinel-2 images. This satellite has a high spatial resolution (10 m) and a 5-day revisit time, therefore offering enormous potential for the analysis of vegetation in urban landscapes (Kopecká et al., 2017). Thus, remote sensing indices derived from Sentinel-2 images can be used as a surrogate for the amount of habitat available to urban wild bees. Sentinel-2 images are obtained from the USGS/Earth Explorer website (https://earthexplorer.usgs.gov/), whenever possible with less than 10% cloud cover and no clouds under greenspaces. For more information about the Sentinel-2 images see Table SB.

Text S6 - Table SB. Sentinel-2 data used to determine several remote sensing indices in each of the five cities (Antwerp, Greater Paris, Poznan, Tartu and Zurich).

City	Sensor	Tile Number	Date	Cloud Coverage
Antwerp	Sentinel-2A	T31UES	12/03/2016	3.22%
Antwerp	Sentinel-2A	T31UES	20/07/2016	0.00%
Antwerp	Sentinel-2A	T31UES	27/12/2016	0.01%
Antwerp	Sentinel-2B	T31UES	25/02/2018	0.00%

Antwerp	Sentinel-2A	T31UES	30/06/2018	0.00%
Antwerp	Sentinel-2B	T31UES	15/07/2018	0.68%
Antwerp	Sentinel-2A	T31UES	18/09/2018	6.56%
Antwerp	Sentinel-2B	T31UES	21/01/2019	6.34%
Antwerp	Sentinel-2A	T31UES	15/02/2019	0.00%
Antwerp	Sentinel-2A	T31UES	25/02/2019	0.00%
Antwerp	Sentinel-2A	T31UES	25/07/2019	3.50%
Antwerp	Sentinel-2A	T31UES	24/08/2019	2.44%
Paris	Sentinel-2A	T31UDQ	16/07/2015	0.00%
Paris	Sentinel-2A	T31UDQ	27/12/2016	0.00%
Paris	Sentinel-2A	T31UDQ	26/01/2017	0.00%
Paris	Sentinel-2A	T31UDQ	15/02/2017	0.01%
Paris	Sentinel-2B	T31UDQ	25/02/2018	0.10%
Paris	Sentinel-2B	T31UDQ	25/07/2018	0.00%
Paris	Sentinel-2A	T31UDQ	19/08/2018	5.57%
Paris	Sentinel-2B	T31UDQ	21/01/2019	0.00%
Paris	Sentinel-2A	T31UDQ	15/02/2019	0.00%
Paris	Sentinel-2A	T31UDQ	25/02/2019	0.00%
Poznan	Sentinel-2A	T33UXU	10/08/2015	0.01%
Poznan	Sentinel-2A	T33UXU	20/08/2015	0.02%
Poznan	Sentinel-2A	T33UXU	30/07/2017	0.00%
Poznan	Sentinel-2A	T33UXU	27/12/2017	96.11%
Poznan	Sentinel-2A	T33UXU	25/02/2018	4.45%
Poznan	Sentinel-2B	T33UXU	02/03/2018	6.95%
Poznan	Sentinel-2A	T33UXU	15/07/2018	3.41%
Poznan	Sentinel-2B	T33UXU	29/08/2018	7.50%
Poznan	Sentinel-2B	T33UXU	25/02/2019	88.55%
Poznan	Sentinel-2A	T33UXU	30/06/2019	0.00%
Poznan	Sentinel-2B	T33UXU	24/08/2019	0.00%
Poznan	Sentinel-2A	T33UXU	16/01/2020	0.00%
Tartu	Sentinel-2A	T35VME	04/08/2015	0.01%
Tartu	Sentinel-2A	T35VME	24/08/2015	3.55%
Tartu	Sentinel-2A	T35VME	14/02/2017	0.06%
Tartu	Sentinel-2A	T35VME	06/03/2017	0.85%
Tartu	Sentinel-2A	T35VME	16/03/2017	0.07%
Tartu	Sentinel-2A	T35VME	31/07/2017	49.73%
Tartu	Sentinel-2A	T35VME	30/08/2017	0.15%
Tartu	Sentinel-2A	T35VME	07/01/2018	1.97%
Tartu	Sentinel-2B	T35VME	23/08/2018	1.52%
Tartu	Sentinel-2B	T35VME	19/09/2018	0.00%

Tartu	Sentinel-2B	T35VME	18/08/2019	10.15%
Tartu	Sentinel-2B	T35VME	28/08/2019	18.82%
Zurich	Sentinel-2A	T32TMT	29/08/2015	1.52%
Zurich	Sentinel-2A	T32TMT	13/08/2016	0.00%
Zurich	Sentinel-2A	T32TMT	16/02/2017	2.36%
Zurich	Sentinel-2A	T32TMT	06/07/2017	6.54%
Zurich	Sentinel-2A	T32TMT	18/08/2017	0.44%
Zurich	Sentinel-2A	T32TMT	24/07/2018	3.75%
Zurich	Sentinel-2A	T32TMT	12/09/2018	0.05%
Zurich	Sentinel-2B	T32TMT	14/02/2019	0.07%
Zurich	Sentinel-2A	T32TMT	16/02/2019	2.79%
Zurich	Sentinel-2B	T32TMT	24/02/2019	0.78%
Zurich	Sentinel-2A	T32TMT	26/02/2019	2.44%
Zurich	Sentinel-2A	T32TMT	28/08/2019	2.07%

We performed an atmospheric correction using the Sen2Cor plugin (Sen2Cor, v2.1.2.) from the Sentinel-2 toolbox (SNAP, 7.0.4). This type of correction is essential because the atmosphere between the satellite and the Earth's surface reduces the range of possible digital numbers recorded by the sensor. In addition, it decreases the contrast between adjacent surfaces and changes the brightness of each image pixel. Consequently, spectral indices are, on average, underestimated. This can lead to a weak differentiation of various urban surfaces, becoming a problem in extremely heterogeneous environments.

After completing the atmospheric correction, we estimated four spectral indices with the same software (SNAP, 7.0.4): the urban index (UI), the colour index (CI), the normalized difference water index (NDWI) and the normalized difference vegetation index (NDVI). These indices can be used to characterize existing vegetation and urban infrastructure.

The UI was developed by Kawamura et al. (1996) to effectively detect the structural details of urban cores and is calculated using the following equation:

$$\mathrm{UI} = \frac{\rho_{SWIR2} - \rho_{NIR}}{\rho_{SWIR2} + \rho_{NIR}}$$

where ρ_{SWIR2} and ρ_{NIR} are the responses in the second short wave and near-infrared bands, respectively. Thus, it is a good index for detecting built and non-built areas and can also be used to identify building densities. The built-up area tends to have UI values greater than 0, while negative values close to -1 tend to be green areas.

The CI was introduced by Pouget et al. (1991) and results from the following equation:

$$\mathrm{CI} = \frac{\rho_{Red} - \rho_{Green}}{\rho_{Red} + \rho_{Green}}$$

where ρ_{Red} and ρ_{Green} are the responses in the red and green bands, respectively. Although this index was developed to differentiate various types of soils in arid environments, it can help to compute better vegetation indices for incomplete canopies. In most cases, the CI provides complementary information to the NDVI, making it possible to differentiate plants and soil more effectively, especially in study areas with less than 10% vegetation (Pouget et al., 1991). Typically, low CI values have been shown to be correlated with the presence of a high concentration of carbonates or sulfates, nutrients that can serve as fertilizers for plant growth. Meanwhile, higher values have been correlated with crusty and sandy soils and with a low content of organic matter (Escadafal, 1989). Thus, this index seems to be a good indicator of soil degradation.

The NDWI was developed by Gao (1996) and is useful to monitor drought stress. It is computed from the near-infrared (ρ_{NIR}) and the short-wave infrared (ρ_{SWIR}) reflectance, and results from the following equation:

$$\text{NDWI} = \frac{\rho_{NIR} - \rho_{SWIR}}{\rho_{NIR} + \rho_{SWIR}}$$

The NDWI is a measure of liquid water molecules in vegetation canopies that interact with the incoming solar radiation content. It represents an adequate indicator for vegetation liquid water content and is less sensitive to atmospheric scattering effects than NDVI (Gao, 1996). Negative values correspond to water bodies. Low positive values correspond to vegetation canopies with a comparatively small number of water molecules and high positive values to canopies containing more water molecules.

Finally, the NDVI was developed by Tucker (1979) and is one of the most common indices widely applied for monitoring vegetation dynamics. This index results from the following equation:

$$\text{NDWI} = \frac{\rho_{NIR} - \rho_{Red}}{\rho_{NIR} + \rho_{Red}}$$

where ρ_{NIR} and ρ_{Red} are the responses in near-infrared and red bands, respectively. This index represents the photosynthetic capacity, or the energy absorbed by plant canopies, and hence the amount of healthy vegetation. Thus, higher NDVI values indicate a higher density of green vegetation. Specifically, in urban environments, NDVI values greater than 0.5 correspond to vigorous green areas, while NDVI values between 0.2 and 0.5 indicate moisture stressed vegetation, such as natural meadows (Ha and Weng, 2018). NDVI values near zero and negative values indicate non-vegetated features, such as artificial and barren surfaces, water bodies, snow and clouds.

After processing all indices, we calculated the average of each index for summer and for winter for each city under study. All indices were computed at different spatial scales (50, 100, 200, 400, 800, 1600 m). ArcMap (v.10.5.1) was used for these processes.

TEXT S7. χ^2 tests. For the χ^2 tests, to guarantee a sufficient number of observations (> 4) per class, we aggregated: (1) certain families with low proportions in the pollen (based on occurrence at the city site), keeping apart the most frequent ones; (2) growth into herbaceous and non-herbaceous species; and (3) blossom class into dish-bowl and non-dish-bowl (see Table S6 for details on the aggregation). Due to the strict specialization of *Chelostoma florisomne* on *Ranunculus* spp., we did not include this species in the χ^2 tests.

Supplementary Tables

TABLE S1. Information on the study sites and the samples used. For every site the area, proximity index and coordinates of the trap-nest position (latitude and longitude) are given. For every bee, the number of pollen samples analysed at a site is given (1), as well as the occurrence of the bee species at the given site (2).

						Chelostoma florisomne		***Osmia cornuta***		***Osmia bicornis***		***Hylaeus communis***	
City	**Site**	**Area (m^2)**	**Proximity index**	**Latitude**	**Longitude**	**(1)**	**(2)**	**1**	**2**	**1**	**2**	**1**	**2**
Antwerp	An011	1085854	23.57	51.16	4.36	0	0	10	1	0	1	5	1
Antwerp	An016	12426	931.47	51.18	4.42	21	1	0	0	1	1	0	0
Antwerp	An020	20169	6.82	51.18	4.37	0	0	14	1	0	0	1	1
Antwerp	An056	1054885	247.14	51.21	4.48	5	1	0	0	0	0	1	1
Antwerp	An057	6704	1.52	51.21	4.39	0	0	0	0	0	0	0	0
Antwerp	An062	11116	3.31	51.22	4.44	0	0	0	0	0	0	0	1
Antwerp	An068	93542	2.31	51.22	4.42	0	0	0	0	0	0	0	0
Antwerp	An073	56928	6.78	51.22	4.39	0	0	0	0	0	1	2	1
Antwerp	An082	60943	4.48	51.24	4.47	0	0	2	1	2	1	0	0
Antwerp	An088	14401	7.69	51.25	4.46	0	0	0	1	0	0	0	0
Antwerp	An092	56167	91.92	51.26	4.45	0	0	5	1	4	1	0	0
Antwerp	An102	52059	3995.62	51.29	4.43	0	0	3	1	0	0	0	0
Paris	Pa282	9890	3.80	48.83	2.38	0	0	7	1	5	1	0	0
Paris	Pa013	126628	24.13	48.70	2.17	0	0	0	0	25	1	5	1
Paris	Pa191	24993	29.42	48.80	2.30	0	0	0	1	7	1	0	0
Paris	Pa245	5933064	2792.45	48.84	2.42	0	0	1	1	17	1	1	1
Paris	Pa265	3553	2.00	48.83	2.37	0	0	1	1	2	1	4	1

Paris	Pa269	159611	5.39	48.82	2.34	0	0	0	0	1	1	0	0
Paris	Pa295	8339	5.55	48.83	2.37	0	0	5	1	3	1	1	1
Paris	Pa398	169327	2.98	48.84	2.36	0	1	2	1	1	1	1	1
Paris	Pa418	4630	9.83	48.84	2.29	0	0	0	0	0	0	0	1
Paris	Pa492	9148	45794.28	48.85	2.26	0	0	2	1	6	1	0	0
Paris	Pa535	164101	49.76	48.87	2.32	0	0	0	0	0	0	4	1
Paris	Pa573	4607	1.79	48.88	2.32	0	0	0	0	0	0	0	0
Poznan	Po001	30443	862.43	52.31	16.98			0	0	1	1	5	1
Poznan	Po037	48772	11.66	52.36	16.90			0	1	4	1	5	1
Poznan	Po059	8200	5.96	52.37	16.88			0	0	1	1	5	1
Poznan	Po137	187103	31.09	52.39	16.93			0	0	0	0	0	0
Poznan	Po179	56886	3.46	52.40	16.90			0	0	0	0	1	1
Poznan	Po183	10423	2136.45	52.40	16.95			0	0	8	1	0	0
Poznan	Po210	13222	7.95	52.41	16.93			0	0	0	0	11	1
Poznan	Po227	8406	10.50	52.41	16.87			0	0	10	1	0	1
Poznan	Po267	1059825	325.97	52.43	16.95			0	0	10	1	0	1
Poznan	Po348	18721	18.63	52.44	16.93			0	0	5	1	0	0
Poznan	Po406	5624	468.47	52.46	16.92			0	0	0	0	0	1
Poznan	Po423	27974	12829.47	52.47	16.93			0	0	9	1	0	0
Tartu	Ta008	6338	14.27	58.35	26.77	0	0			0	1	7	1
Tartu	Ta013	2776	2.74	58.35	26.74	0	0			0	0	2	1
Tartu	Ta025	6225	2.87	58.37	26.70	0	0			0	0	1	1
Tartu	Ta033	33237	5.78	58.38	26.68	0	0			0	0	0	1
Tartu	Ta040	36590	314.56	58.37	26.73	0	0			0	1	0	1
Tartu	Ta047	131100	57.84	58.38	26.72	0	0			0	1	2	1
Tartu	Ta057	5066	5.36	58.38	26.69	0	0			0	0	7	1

Tartu	Ta064	183227	14.97	58.37	26.74	1	1			0	0	2	1
Tartu	Ta102	13236	22.54	58.39	26.70	0	0			0	0	1	1
Tartu	Ta104	37412	5.32	58.38	26.76	0	0			0	1	1	1
Tartu	Ta110	8623	7.02	58.39	26.73	0	0			1	1	0	1
Tartu	Ta125	245706	26.38	58.39	26.73	0	0			0	0	10	1
Zurich	Zu006	104871	104.93	47.35	8.52	1	1	1	1	3	1	0	1
Zurich	Zu007	3717	7.01	47.35	8.56	0	0	0	0	0	0	0	0
Zurich	Zu015	39215	167.23	47.36	8.56	23	1	0	1	3	1	0	1
Zurich	Zu018	57666	56.97	47.36	8.53	1	1	1	1	0	1	0	1
Zurich	Zu033	10400	28.24	47.36	8.56	10	1	0	0	0	1	3	1
Zurich	Zu039	36842	10.96	47.36	8.54	0	0	0	0	0	0	3	1
Zurich	Zu057	13040	6.74	47.37	8.53	0	0	0	0	6	1	1	1
Zurich	Zu062	18017	6.16	47.37	8.54	0	0	0	0	0	1	0	0
Zurich	Zu067	275320	14.78	47.37	8.51	6	1	0	0	1	1	1	1
Zurich	Zu080	26855	8.75	47.38	8.54	0	0	0	1	0	0	0	0
Zurich	Zu082	13854	17.51	47.38	8.49	4	1	0	0	2	1	0	1
Zurich	Zu087	22711	4.87	47.39	8.52	0	0	0	0	0	0	1	1
Zurich	Zu094	96182	974.64	47.39	8.47	1	1	0	0	0	1	5	1
Zurich	Zu105	9576	67.97	47.40	8.50	0	1	1	1	1	1	0	1
Zurich	Zu113	46486	34334.06	47.40	8.52	12	1	2	1	0	0	0	0
Zurich	Zu119	107938	108059.38	47.40	8.54	6	1	0	0	0	0	1	1
Zurich	Zu126	11737	15.67	47.40	8.50	0	0	1	1	7	1	0	0
Zurich	Zu133	3511	13.91	47.41	8.54	4	1	0	0	3	1	0	0
Zurich	Zu155	4346	6.51	47.41	8.55	0	0	0	0	0	0	3	1
Zurich	Zu158	5929	7.75	47.41	8.53	1	1	2	1	0	0	0	0
Zurich	Zu173	5600	25.03	47.42	8.51	0	0	0	0	10	1	0	0

Zurich	Zu179	103083	2778.23	47.42	8.53	9	1	0	0	0	1	0	0
Zurich	Zu901	15459	32.08	47.41	8.48	0	0	0	0	1	1	0	0
Zurich	Zu903	58342	332.17	47.41	8.51	4	1	3	1	0	1	0	1
Zurich	Zu904	8253	5.04	47.39	8.52	0	0	0	0	0	0	0	0
Zurich	Zu905	10987	7.02	47.41	8.56	0	0	0	0	0	0	0	0
Zurich	Zu906	10629	9.10	47.40	8.59	0	0	1	1	3	1	0	0
Zurich	Zu907	22894	25.21	47.40	8.49	0	0	0	0	0	1	0	1
Zurich	Zu908	102401	262.43	47.35	8.58	3	1	0	0	6	0	0	0
Zurich	Zu910	53898	14.50	47.34	8.53	10	1	1	1	6	1	0	0
Zurich	Zu911	3219	18.09	47.43	8.50	0	0	0	0	1	1	0	0
Zurich	Zu912	26567	8.86	47.35	8.55	0	0	0	0	2	1	0	0

TABLE S2. Trait values of the plant species in pollen. Plant species are sorted according to family. See Fig. 4 and Figs S6–S8 for the composition. For definitions of the traits, see Table S3.

Plant family	**Plant species**	**Origin status**	**Growth form**	**Blossom class**
Adoxaceae	*Viburnum lantana*	N	shrub	dish_bowl
	Viburnum tinus	N	shrub	dish_bowl
Alismataceae	*Alisma plantago-aquatica*	N	herb	dish_bowl
Altingiaceae	*Liquidambar styraciflua*	E	tree	not determined
Amaryllidaceae	*Allium cepa*	E	herb	dish_bowl
Apiaceae	*Ammi visnaga*	E	herb	dish_bowl
	Bupleurum fruticosum	E	herb	dish_bowl
	Daucus carota	E	shrub	dish_bowl
	Foeniculum vulgare	N	herb	dish_bowl
	Heracleum sphondylium	N	herb	dish_bowl
	Levisticum officinale	N	herb	dish_bowl
	Pastinaca sativa	N	herb	dish_bowl
Asteraceae	*Achillea millefolium*	E	herb	dish_bowl
	Bellis perennis	E	herb	dish_bowl
	Cichorium intybus	E	herb	dish_bowl
	Crepis biennis	N	herb	dish_bowl
	Helianthus pauciflorus	N	herb	dish_bowl
	Hypochaeris radicata	N	herb	dish_bowl
	Jacobaea vulgaris	N	herb	dish_bowl
	Picris hieracioides	N	herb	dish_bowl
	Pilosella officinarum	N	herb	dish_bowl

	Solidago canadensis	N	herb	dish_bowl
	Solidago gigantea	N	herb	dish_bowl
	Taraxacum officinale	N	herb	dish_bowl
Balsaminaceae	*Impatiens acuminata*	E	herb	gullet
Berberidaceae	*Berberis aquifolium*	E	herb	dish_bowl
	Berberis julianae	E	shrub	dish_bowl
	Epimedium pinnatum	E	shrub	dish_bowl
Betulaceae	*Betula pendula*	E	tree	brush
	Carpinus betulus	N	tree	brush
	Carpinus laxiflora	N	tree	brush
Boraginaceae	*Borago officinalis*	N	herb	bell_trumpet
	Echium vulgare	N	herb	stalk_disk
	Myosotis arvensis	N	herb	dish_bowl
	Raphanus raphanistrum	N	herb	bell_trumpet
	Raphanus sativus	N	herb	dish_bowl
	Sinapis alba	N	herb	dish_bowl
	Sisymbrium loeselii	N	herb	dish_bowl
Cactaceae	*Opuntia sp.*	E	shrub	not determined
Cornaceae	*Cornus sericea*	N	shrub	dish_bowl
Cucurbitaceae	*Bryonia cretica*	E	herb	bell_trumpet
	Cucurbita pepo	N	herb	dish_bowl
Cupressaceae	*Cupressus sempervirens*	N	tree	not determined
Elaeagnaceae	*Elaeagnus angustifolia*	N	shrub	dish_bowl
Fabaceae	*Indigofera heterantha*	E	climber	flag
	Medicago sativa	E	shrub	flag
	Melilotus albus	E	tree	flag

	Robinia pseudoacacia	E	tree	flag
	Styphnolobium japonicum	N	herb	flag
	Trifolium repens	N	herb	flag
	Vigna unguiculata	N	herb	flag
Fagaceae	*Castanea dentata*	E	tree	brush
	Castanea sativa	E	tree	brush
	Fagus sylvatica	E	tree	brush
	Quercus ilex	N	tree	brush
	Quercus robur	N	tree	brush
	Quercus rubra	N	tree	brush
Hydrangeaceae	*Deutzia scabra*	E	shrub	dish_bowl
Iridaceae	*Iris dichotoma*	E	herb	gullet
	Iris hookeri	E	herb	gullet
Juglandaceae	*Carya glabra*	E	tree	brush
	Juglans regia	E	tree	brush
Lamiaceae	*Glechoma hederacea*	E	shrub	gullet
	Lamium purpureum	N	herb	gullet
	Satureja montana	N	herb	gullet
Lythraceae	*Lythrum salicaria*	N	herb	stalk_disk
Malvaceae	*Firmiana simplex*	E	tree	dish_bowl
	Theobroma speciosum	E	tree	dish_bowl
	Tilia dasystyla	E	tree	dish_bowl
	Tilia hyrcana	E	tree	dish_bowl
	Tilia oliveri	E	tree	dish_bowl
	Tilia platyphyllos	N	tree	dish_bowl
	Tilia tomentosa	N	tree	dish_bowl

Oleaceae	*Fraxinus americana*	E	tree	brush
	Fraxinus excelsior	N	tree	brush
	Fraxinus ornus	N	tree	brush
Paeoniaceae	*Paeonia suffruticosa*	E	shrub	dish_bowl
Papaveraceae	*Chelidonium majus*	E	herb	dish_bowl
	Papaver dubium	N	herb	dish_bowl
	Papaver nudicaule	N	herb	dish_bowl
	Papaver rhoeas	N	herb	dish_bowl
Phyllanthaceae	*Flueggea sp.*	E	tree	not determined
Pinaceae	*Abies lasiocarpa*	E	tree	not determined
Plantaginaceae	*Linaria vulgaris*	N	herb	gullet
	Plantago media	N	herb	brush
Platanaceae	*Platanus orientalis*	E	tree	dish_bowl
	Platanus occidentalis	N	tree	dish_bowl
	Platanus x hispanica	N	herb	dish_bowl
Poaceae	*Phragmites australis*	E	herb	brush
	Triticum turgidum	N	herb	brush
Polygonaceae	*Rumex stenophyllus*	N	herb	dish_bowl
Ranunculaceae	*Ficaria verna*	N	herb	dish_bowl
	Ranunculus acris	N	herb	dish_bowl
	Ranunculus bulbosus	N	herb	dish_bowl
	Ranunculus repens	N	herb	dish_bowl
	Ranunculus sardous	N	herb	dish_bowl
	Ranunculus sp.	N	herb	dish_bowl
Rosaceae	*Chaenomeles japonica*	E	shrub	dish_bowl
	Chaenomeles speciosa	E	shrub	dish_bowl

	Crataegus monogyna	E	shrub	dish_bowl
	Dasiphora fruticosa	E	shrub	dish_bowl
	Exochorda racemosa	E	shrub	dish_bowl
	Malus domestica	E	shrub	dish_bowl
	Physocarpus opulifolius	E	shrub	dish_bowl
	Potentilla anserina	E	tree	dish_bowl
	Prunus avium	E	tree	dish_bowl
	Prunus laurocerasus	N	herb	dish_bowl
	Prunus lusitanica	N	shrub	dish_bowl
	Prunus padus	N	shrub	brush
	Prunus pseudocerasus	N	shrub	dish_bowl
	Prunus serotina	N	shrub	dish_bowl
	Prunus serrulata	N	tree	dish_bowl
	Prunus sogdiana	N	tree	dish_bowl
	Prunus x dasycarpa	N	tree	dish_bowl
	Rosa xanthina	N	tree	dish_bowl
	Rubus caesius	N	tree	dish_bowl
	Rubus idaeus	N	tree	dish_bowl
	Rubus plicatus	N	tree	dish_bowl
Rutaceae	*Citrus limon*	E	tree	dish_bowl
Salicaceae	*Salix alba*	E	shrub	brush
	Salix caprea	N	shrub	brush
	Salix fragilis	N	shrub	brush
	Salix helvetica	N	tree	brush
	Salix rehderiana	N	tree	brush
Sapindaceae	*Acer campestre*	E	tree	dish_bowl

	Acer macrophyllum	E	tree	flag
	Acer pseudoplatanus	E	tree	flag
	Acer velutinum	E	tree	dish_bowl
	Aesculus glabra	E	tree	dish_bowl
	Aesculus hippocastanum	N	tree	dish_bowl
	Aesculus x carnea	N	tree	dish_bowl
	Koelreuteria paniculata	N	tree	flag
Solanaceae	*Solanum lycopersicum*	E	climber	bell_trumpet
Violaceae	*Viola tianschanica*	E	herb	gullet
Vitaceae	*Vitis riparia*	E	climber	brush

TABLE S3. Description of the three plant traits used. For each trait, we provide a description of the trait regarding plant–bee interactions, a description of the levels considered and the references used.

Trait	Description	Level	References
Growth form	A trait related to the accessibility of the flowers considering the height where flowers occur	Four broad categories were defined: tree, shrub, herb and climber. - Trees included woody species typically classified as phanerophytes, including species described as small trees or tall shrubs. - Shrubs included mostly chamerophytes. - Herbs included all herbaceous plants regardless of their height or growth form. - Climbers included woody and non-woody epiphytes such as lianas and vines.	
Blossom class	A trait related to accessibility of the flowers considering their morphology	Six general blossom classes were defined according to the accessibility of the floral rewards: - Dish-bowl: - Stalk-dish: - Bell-trumpet: for blossoms with deep corollas - Brush: for blossom classes where the pollen exchange is generally external, such as catkins. - Gullet: - Flag: For Papilionaceae species	Faegri & van der Pijl (1979)

Origin status	Not a functional trait itself but a key feature to assess the importance of the social investment (e.g. gardening and other horticultural activities) in wild bee diet.	A species was considered native if its origin was Europe and exotic if it originated elsewhere.	To document the origin status of each plant species, we used the Global Biodiversity Information System (GBIF: The Global Biodiversity Information Facility, 2019).

TABLE S4. Plant taxonomic-based metrics. For each site and bee, the number of collected plant families, genera and species, and the Shannon's pollen diversity are provided.

Bee species	**City**	**Site**	**Number of families**	**Number of genera**	**Number of species**	**Pollen diversity**
Chelostoma florisomne	Antwerp	An016	1	1	2	0.690
	Antwerp	An056	1	1	2	0.683
	Tartu	Ta064	1	1	2	0.693
	Zurich	Zu006	1	1	2	0.693
	Zurich	Zu015	1	1	2	0.693
	Zurich	Zu018	1	1	1	0.000
	Zurich	Zu033	1	1	1	0.000
	Zurich	Zu067	1	1	2	0.637
	Zurich	Zu082	1	1	2	0.500
	Zurich	Zu094	1	1	1	0.000
	Zurich	Zu113	1	1	2	0.658
	Zurich	Zu119	1	1	2	0.693
	Zurich	Zu133	1	1	2	0.500
	Zurich	Zu158	1	1	2	0.693
	Zurich	Zu179	1	1	2	0.673
	Zurich	Zu903	1	1	2	0.562
	Zurich	Zu908	1	1	2	0.562
	Zurich	Zu910	1	1	2	0.691
Osmia cornuta	Antwerp	An011	8	9	13	2.344
	Antwerp	An020	4	4	7	1.811
	Antwerp	An082	2	2	2	0.637

	Antwerp	An092	1	2	2	0.410
	Antwerp	An102	4	4	6	1.748
	Paris	Pa013	4	4	5	1.505
	Paris	Pa265	3	3	4	1.386
	Paris	Pa269	3	3	3	1.099
	Paris	Pa295	3	3	4	1.168
	Paris	Pa398	3	3	3	1.099
	Paris	Pa492	2	2	2	0.637
	Zurich	Zu006	1	1	1	0.000
	Zurich	Zu018	2	2	2	0.693
	Zurich	Zu105	2	2	3	1.099
	Zurich	Zu113	2	2	4	1.332
	Zurich	Zu126	2	2	2	0.693
	Zurich	Zu158	2	2	2	0.637
	Zurich	Zu903	3	3	4	1.332
	Zurich	Zu906	2	2	2	0.693
	Zurich	Zu910	1	1	1	0.000
Osmia bicornis	Antwerp	An016	1	1	1	0.000
	Antwerp	An082	2	2	2	0.693
	Antwerp	An092	2	2	2	0.693
	Paris	Pa013	8	8	8	1.569
	Paris	Pa191	5	6	8	1.928
	Paris	Pa192	3	3	3	1.099
	Paris	Pa245	8	10	10	1.978
	Paris	Pa265	2	2	2	0.637
	Paris	Pa269	2	2	2	0.693

Paris	Pa282	4	4	7	1.831
Paris	Pa295	8	8	8	2.079
Paris	Pa398	1	1	1	0.000
Paris	Pa492	6	6	7	1.845
Poznan	Po001	1	1	1	0.000
Poznan	Po037	3	4	4	1.277
Poznan	Po059	3	3	3	1.099
Poznan	Po183	4	5	5	1.292
Poznan	Po227	9	12	13	2.441
Poznan	Po267	8	9	9	2.035
Poznan	Po348	4	4	5	1.523
Poznan	Po423	5	6	8	1.859
Tartu	Ta110	2	2	2	0.693
Zurich	Zu006	3	3	3	0.950
Zurich	Zu015	4	4	5	1.550
Zurich	Zu057	4	6	10	2.096
Zurich	Zu067	1	1	1	0.000
Zurich	Zu082	2	2	3	1.040
Zurich	Zu105	1	1	1	0.000
Zurich	Zu126	3	3	3	0.937
Zurich	Zu133	2	2	2	0.637
Zurich	Zu173	6	6	7	1.675
Zurich	Zu901	2	2	2	0.693
Zurich	Zu906	2	2	2	0.562
Zurich	Zu908	5	5	5	1.367
Zurich	Zu910	4	5	6	1.609

	Zurich	Zu911	2	2	3	1.099
	Zurich	Zu912	3	3	3	1.099
Hylaeus communis	Antwerp	An011	10	12	14	2.558
	Antwerp	An020	2	2	2	0.693
	Antwerp	An056	1	1	1	0.000
	Antwerp	An073	4	4	4	1.386
	Paris	Pa191	1	1	1	0.000
	Paris	Pa265	2	2	2	0.693
	Paris	Pa269	4	6	6	1.733
	Paris	Pa295	1	1	1	0.000
	Paris	Pa398	3	3	3	1.099
	Paris	Pa535	3	3	4	1.352
	Poznan	Po001	2	2	2	0.693
	Poznan	Po037	6	6	6	1.581
	Poznan	Po054	3	3	3	1.099
	Poznan	Po059	3	3	3	1.011
	Poznan	Po179	1	1	1	0.000
	Poznan	Po210	6	7	7	1.699
	Tartu	Ta008	10	10	10	2.246
	Tartu	Ta013	4	4	4	1.386
	Tartu	Ta025	1	2	2	0.693
	Tartu	Ta047	4	4	4	1.386
	Tartu	Ta057	8	8	9	2.008
	Tartu	Ta064	3	3	3	1.099
	Tartu	Ta102	3	3	3	1.099
	Tartu	Ta104	2	2	2	0.693

Tartu	Ta125	12	13	13	2.424
Zurich	Zu033	4	5	7	1.906
Zurich	Zu039	5	5	5	1.561
Zurich	Zu057	2	2	2	0.693
Zurich	Zu067	2	2	2	0.693
Zurich	Zu087	2	2	2	0.693
Zurich	Zu094	8	8	8	1.979
Zurich	Zu119	1	1	1	0.000
Zurich	Zu155	7	7	7	1.946

TABLE S5. Plant-trait-based metrics: the proportion of the different trait classes in the four bee species in the studied cities. For each trait level, the proportion in a given city for each bee species is provided. 1 = Antwerp; 2 = Paris; 3 = Poznan; 4 = Tartu; 5 = Zurich.

		Chelostoma florisomne			***Osmia cornuta***			***Osmia bicornis***					***Hylaeus communis***				
Trait	**Level**	**1**	**4**	**5**	**1**	**2**	**5**	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**
Origin status	Native	0	0	0	0.64	0.91	0.92	0.86	0.72	0.59	1.00	0.86	0.58	0.23	0.57	0.53	0.63
	Exotic	1	1	1	0.36	0.09	0.08	0.14	0.28	0.41	0.00	0.14	0.42	0.77	0.43	0.47	0.35
	Not determined	0	0	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03
Growth form	Trees	0	0	0	0.70	0.79	0.58	1.00	0.79	0.81	0.50	0.72	0.33	0.69	0.29	0.26	0.25
	Shrubs	0	0	0	0.25	0.06	0.13	0.00	0.01	0.04	0.00	0.03	0.04	0.15	0.05	0.12	0.15
	Climbers	0	0	0	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.02	0.02	0.00
	Herbs	1	1	1	0.05	0.15	0.29	0.00	0.21	0.14	0.50	0.25	0.63	0.15	0.64	0.61	0.58
	Not determined	0	0	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03
Blossom class	Bell-trumpet	0	0	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.17	0.03	0.03
	Brush	0	0	0	0.48	0.24	0.17	0.29	0.32	0.31	0.50	0.31	0.21	0.00	0.00	0.08	0.15
	Dish-bowl	1	1	1	0.47	0.76	0.83	0.71	0.49	0.46	0.50	0.67	0.46	0.50	0.36	0.42	0.48
	Flag	0	0	0	0.03	0.00	0.00	0.00	0.18	0.19	0.00	0.01	0.08	0.42	0.36	0.14	0.18
	Gullet	0	0	0	0.03	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.17	0.00	0.10	0.15	0.13
	Stalk-disk	0	0	0	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.04	0.00	0.00	0.00	0.00
	Not determined	0	0	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.08	0.02	0.18	0.05

TABLE S6. Aggregation criteria for the χ^2 test.

	Levels
Taxonomic	
Osmia cornuta	Rosaceae
	Salicaceae
	Sapindaceae
	Other families
Osmia bicornis	Fagaceae
	Juglandaceae & Betulaceae
	Ranunculaceae
	Sapindaceae
	Other families
Hylaeus communis	Apiaceae
	Other families
Trait-based	
Origin status	Native
	Exotic
Growth form	Herb
	Other growth forms
Blossom class	Dish-bowl
	Other blossoms

TABLE S7. Results from the χ^2 test.

Bee species	**Comparison**	***P*-value**	**Degrees of freedom**	χ^2
Hylaeus communis	Family	0.0065	4	14.26
Osmia bicornis	Family	0.0000	8	38.61
Osmia cornuta	Family	0.0097	6	16.89
Hylaeus communis	Origin status	0.0201	4	11.66
Hylaeus communis	Growth form	0.0002	4	22.29
Hylaeus communis	Blossom class	0.4419	4	3.74
Osmia bicornis	Origin status	0.0001	2	18.37
Osmia bicornis	Growth form	0.1026	3	6.19
Osmia bicornis	Blossom class	0.0054	3	12.69
Osmia cornuta	Origin status	0.0017	2	12.71
Osmia cornuta	Growth form	0.0069	2	9.94
Osmia cornuta	Blossom class	0.0007	2	14.40

TABLE S8. Proportion of plant species in the pollen of the four bee species for each city based on the relative abundance. Plant species are sorted according to family. 1 = Antwerp; 2 = Paris; 3 = Poznan; 4 = Tartu; 5 = Zurich.

			Cf			Oc			Ob					Hc				
Plant family	**Plant genus**	**Plant species**	**1**	**4**	**5**	**1**	**2**	**5**	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**
Adoxaceae	*Viburnum*	*Viburnum lantana*														0.01		
	Viburnum	*Viburnum tinus*																0.06
Alismataceae	*Alisma*	*Alisma plantago-aquatica*							0.01									
Altingiaceae	*Liquidambar*	*Liquidambar styraciflua*													0			
Amaryllidaceae	*Allium*	*Allium cepa*							0.01									
Apiaceae	*Ammi*	*Ammi visnaga*								0.01								
	Bupleurum	*Bupleurum fruticosum*					0.07											
	Daucus	*Daucus carota*				0.04	0.01			0.05								
	Foeniculum	*Foeniculum vulgare*							0.09	0.05								
	Heracleum	*Heracleum sphondylium*				0.13												
	Levisticum	*Levisticum officinale*								0.11								
	Pastinaca	*Pastinaca sativa*							0.01									
Asteraceae	*Achillea*	*Achillea millefolium*						0.01	0.03									
	Bellis	*Bellis perennis*						0.04										

	Cichorium	*Cichorium intybus*					0.02						
	Crepis	*Crepis biennis*						0					
	Helianthus	*Helianthus pauciflorus*					0.01						
	Hypochaeris	*Hypochaeris radicata*											0.01
	Jacobaea	*Jacobaea vulgaris*	0.01	0.03									
	Picris	*Picris hieracioides*		0.04									
	Pilosella	*Pilosella officinarum*									0		
	Solidago	*Solidago canadensis*			0.1	0.02	0.02						
	Solidago	*Solidago gigantea*	0.02										
	Taraxacum	*Taraxacum officinale*						0.01					0.05
Balsaminaceae	*Impatiens*	*Impatiens acuminata*				0.07					0.02		
Berberidaceae	*Berberis*	*Berberis aquifolium*									0		
	Berberis	*Berberis julianae*										0.01	
	Epimedium	*Epimedium pinnatum*											0.02
Betulaceae	*Betula*	*Betula pendula*								0.01			
	Carpinus	*Carpinus betulus*						0		0.01			
	Carpinus	*Carpinus laxiflora*								0.02			
Boraginaceae	*Borago*	*Borago officinalis*					0.01						
	Echium	*Echium vulgare*			0.08	0.01	0.02						
	Myosotis	*Myosotis arvensis*							0.03				

Brassicaceae	*Raphanus*	*Raphanus raphanistrum*	0.1									
	Raphanus	*Raphanus sativus*				0.03						
	Sinapis	*Sinapis alba*	0.02				0.02					
	Sisymbrium	*Sisymbrium loeselii*			0.09							
Cactaceae	*Opuntia*	*Opuntia sp.*				0.05	0.01					
Cornaceae	*Cornus*	*Cornus sericea*				0.03						
Cucurbitaceae	*Bryonia*	*Bryonia cretica*			0.04							
	Cucurbita	*Cucurbita pepo*	0.02			0						
Cupressaceae	*Cupressus*	*Cupressus sempervirens*				0.03						
Elaeagnaceae	*Elaeagnus*	*Elaeagnus angustifolia*		0.01								
Fabaceae	*Indigofera*	*Indigofera heterantha*		0.05								
	Medicago	*Medicago sativa*					0.06					
	Melilotus	*Melilotus albus*	0.05		0.09	0.14	0.12					
	Robinia	*Robinia pseudoacacia*					0.01		0.06	0.05		
	Styphnolobium	*Styphnolobium japonicum*		0.52	0.37		0.06					
	Trifolium	*Trifolium repens*				0.03						
	Vigna	*Vigna unguiculata*				0						
Fagaceae	*Castanea*	*Castanea dentata*										0
	Castanea	*Castanea sativa*	0.13									
	Fagus	*Fagus sylvatica*										0.02

	Quercus	*Quercus ilex*							0.11				
	Quercus	*Quercus robur*					0.01	0.26	0.07	0.19	0.7	0.21	0
	Quercus	*Quercus rubra*							0.01			0	
Hydrangeaceae	*Deutzia*	*Deutzia scabra*							0				
Iridaceae	*Iris*	*Iris dichotoma*				0.04			0.02				
	Iris	*Iris hookeri*	0.02		0.04	0.01							
Juglandaceae	*Carya*	*Carya glabra*							0				
	Juglans	*Juglans regia*				0.01			0.09	0.08		0.01	0
Lamiaceae	*Glechoma*	*Glechoma hederacea*	0.04										
	Lamium	*Lamium purpureum*	0.01										
	Satureja	*Satureja montana*					0.01						
Lythraceae	*Lythrum*	*Lythrum salicaria*	0.09										
Malvaceae	*Firmiana*	*Firmiana simplex*		0.03									
	Theobroma	*Theobroma speciosum*				0							
	Tilia	*Tilia dasystyla*	0.03				0.08						
	Tilia	*Tilia hyrcana*	0.05				0.02						
	Tilia	*Tilia oliveri*		0.05									
	Tilia	*Tilia platyphyllos*			0.01	0.13							
	Tilia	*Tilia tomentosa*	0.03	0.05			0.01						

Oleaceae	*Fraxinus*	*Fraxinus americana*											0.01					
	Fraxinus	*Fraxinus excelsior*								0.01								0.02
	Fraxinus	*Fraxinus ornus*				0.01						0						
Paeoniaceae	*Paeonia*	*Paeonia suffruticosa*											0.01					
Papaveraceae	*Chelidonium*	*Chelidonium majus*											0.03					
	Papaver	*Papaver dubium*											0.02					
	Papaver	*Papaver nudicaule*										0						
	Papaver	*Papaver rhoeas*										0						
Phyllanthaceae	*Flueggea*	*Flueggea sp.*					0.01											
Pinaceae	*Abies*	*Abies lasiocarpa*							0.03									
Plantaginaceae	*Linaria*	*Linaria vulgaris*								0.12								
	Plantago	*Plantago media*				0.03												
Platanaceae	*Platanus*	*Platanus cf. Orientalis*										0						
	Platanus	*Platanus occidentalis*										0						
	Platanus	*Platanus x hispanica*										0						
Poaceae	*Phragmites*	*Phragmites australis*															0.01	
Poaceae	*Triticum*	*Triticum turgidum*								0.03								
Polygonaceae	*Rumex*	*Rumex stenophyllus*					0.06	0.01	0.03									
Ranunculaceae	*Ficaria*	*Ficaria verna*											0.01					
	Ranunculus	*Ranunculus acris*	0.68	0.25					0.01									
	Ranunculus	*Ranunculus bulbosus*			0.61			0.03		0.02			0.03		0.17			0.09

	Ranunculus	*Ranunculus repens*	0.32	0.75				0.03					0.3		0		
	Ranunculus	*Ranunculus sardous*									0.16					0.13	
	Ranunculus	*Ranunculus sp.*			0.39				0.01					0.06			0.1
Rosaceae	*Chaenomeles*	*Chaenomeles japonica*										0.01					
	Chaenomeles	*Chaenomeles speciosa*										0.01					
	Crataegus	*Crataegus monogyna*				0.05											
	Dasiphora	*Dasiphora fruticosa*					0.01										
	Exochorda	*Exochorda racemosa*												0.02			0.01
	Malus	*Malus domestica*										0.03					
	Physocarpus	*Physocarpus opulifolius*												0			
	Potentilla	*Potentilla anserina*						0.01									
	Prunus	*Prunus avium*						0.01			0.01				0	0.03	0.07
	Prunus	*Prunus laurocerasus*								0.09					0.18		
	Prunus	*Prunus lusitanica*									0.04			0		0.33	
	Prunus	*Prunus padus*										0.03					0.06
	Prunus	*Prunus pseudocerasus*														0.01	0.01
	Prunus	*Prunus serotina*										0.03					
	Prunus	*Prunus serrulata*										0.02					
	Prunus	*Prunus sogdiana*													0.01		

	Prunus	*Prunus x dasycarpa*								0					
	Rosa	*Rosa xanthina*				0.01						0			
	Rubus	*Rubus caesius*			0.05										
	Rubus	*Rubus idaeus*					0.05								
	Rubus	*Rubus plicatus*					0.02								
Rutaceae	*Citrus*	*Citrus limon*				0.02									
Salicaceae	*Salix*	*Salix alba*				0.08			0.02	0.04		0.01	0.09	0.17	0.12
	Salix	*Salix caprea*					0.04						0.04		0.09
	Salix	*Salix fragilis*											0.07		
	Salix	*Salix helvetica*											0.06	0.01	
	Salix	*Salix rehderiana*											0.09		
Sapindaceae	*Acer*	*Acer campestre*													0.04
	Acer	*Acer macrophyllum*												0.09	
	Acer	*Acer pseudoplatanus*	0.09		0.01	0.01		0.65	0.33	0.22		0.44	0.37	0.21	0.24
	Acer	*Acer velutinum*										0.01			
	Aesculus	*Aesculus glabra*											0.04		
	Aesculus	*Aesculus hippocastanum*							0.02						
	Aesculus	*Aesculus x carnea*							0.01	0.15		0			
	Koelreuteria	*Koelreuteria paniculata*		0.07											

Solanaceae	*Solanum*	*Solanum lycopersicum*		0.02	
Violaceae	*Viola*	*Viola tianschanica*	0.01		
Vitaceae	*Vitis*	*Vitis riparia*			0.01

TABLE S9. Overview of the larval diet in the studied cities. For each bee species and each city where the larval pollen was sampled, we provide summary statistics on the larval diet concerning the study design (number of sites and samples), the taxonomic features (number of plant families, genera and species; most common species and family) and trait-based features (most common origin status, growth form and blossom class).

		Bee species			
		Chelostoma florisomne	*Osmia cornuta*	*Osmia bicornis*	*Hylaeus communis*
Antwerp	Number of sites with sample	2	5	3	4
	Total number of samples	46	73	7	24
	N. families (mean; min – max)	1; 1 – 1	4; 1 – 8	2; 1 – 2	4; 1 – 10
	N. genera (mean; min – max)	1; 1 – 1	4; 2 – 9	2; 1 – 2	5; 1 – 12
	N. species (mean; min – max)	2; 2 – 2	6; 2 – 13	2; 1 – 2	5; 1 – 14
	Most common species	*Ranunculus acris*	*Acer pseudoplatanus*	*Acer pseudoplatanus*	*Castanea sativa*
	Most common family	Ranunculaceae	Salicaceae	Sapindaceae	Fagaceae
	Most common origin status	Native	Native	Native	Native
	Most common growth form	Herb	Tree	Tree	Herb
	Most common blossom class	Dish-bowl	Dish-bowl	Dish-bowl	Dish-bowl
Paris	Number of sites with sample		6	10	6
	Total number of samples		33	141	26
	N. families		3; 2 – 4	5; 1 – 8	2; 1 – 4
	N. genera		3; 2 – 4	5; 1 – 10	3; 1 – 6

	N. species		4; 2 – 5	6; 1 – 10	3; 1 – 6
	Most common species		*Prunus lusitanica*	*Acer pseudoplatanus*	*Styphnolobium japonicum*
	Most common family		Rosaceae	Sapindaceae	Fabaceae
	Most common origin status		Native	Native	Exotic
	Most common growth form		Tree	Tree	Tree
	Most common blossom class		Dish-bowl	Dish-bowl	Dish-bowl
Poznan	Number of sites with sample			8	6
	Total number of samples			101	42
	N. families			5; 1 – 9	4; 1 – 6
	N. genera			6; 1 – 12	4; 2 – 7
	N. species			6; 1 – 13	4; 2 – 7
	Most common species			*Acer pseudoplatanus*	*Styphnolobium japonicum*
	Most common family			Sapindaceae	Asteraceae
	Most common origin status			Native	Native
	Most common growth form			Tree	Herb
	Most common blossom class			Dish-bowl	Dish-bowl
Tartu	Number of sites with sample	1		1	9
	Total number of samples	2		2	66
	N. families	1; 1 – 1		2; 2 – 2	5; 1 – 12
	N. genera	1; 1 – 1		2; 2 – 2	5; 2 – 12
	N. species	2; 2 – 2		2; 2 – 2	6; 2 – 13

	Most common species	*Ranunculus acris / repens*		*Quercus robur / Ranunculus repens*	*Opuntia sp.*
	Most common family	Ranunculaceae		Fagaceae/Ranunculaceae	Fabaceae
	Most common origin status	Native		Native	Native
	Most common growth form	Herb		Tree / Herb	Herb
	Most common blossom class	Dish-bowl		Dish-bowl	Dish-bowl
Zurich	Number of sites with sample	15	9	15	8
	Total number of samples	127	24	96	40
	N. families	1; 1 – 1	2; 1 – 3	3; 1 – 5	4; 1 – 8
	N. genera	1; 1 – 1	2; 1 – 3	3; 1 – 6	4; 1 – 8
	N. species	2; 2 – 2	3; 1 – 4	4; 1 – 10	4; 1 – 8
	Most common species	*Ranunculus bulbosus*	*Acer pseudoplatanus*	*Acer pseudoplatanus*	*Linaria vulgaris*
	Most common family	Ranunculaceae	Rosaceae	Sapindaceae	Fabaceae
	Most common origin status	Native	Native	Native	Native
	Most common growth form	Herb	Tree	Tree	Herb
	Most common blossom class	Dish-bowl	Dish-bowl	Dish-bowl	Dish-bowl
Total	N. families	1	12	18	32
	N. genus	1	17	31	67
	N. species	4*	33	51	81

* three species and one species aggregate

TABLE S10. Results of the pairwise Pearson correlations between pairs of cities regarding the composition of the bee larval diet.

Plant taxonomic level	**Bee species**	**Pairwise comparison**		**Pearson correlation**
Family level	*Chelostoma florisomne*	Antwerp	Tartu	1
	Chelostoma florisomne	Antwerp	Zurich	1
	Chelostoma florisomne	Tartu	Zurich	1
	Hylaeus communis	Antwerp	Paris	0.26
	Hylaeus communis	Antwerp	Poznan	0.40
	Hylaeus communis	Antwerp	Tartu	0.10
	Hylaeus communis	Antwerp	Zurich	0.47
	Hylaeus communis	Paris	Poznan	0.36
	Hylaeus communis	Paris	Tartu	0.21
	Hylaeus communis	Paris	Zurich	0.14
	Hylaeus communis	Poznan	Tartu	0.49
	Hylaeus communis	Poznan	Zurich	0.29
	Hylaeus communis	Tartu	Zurich	0.20
	Osmia bicornis	Antwerp	Paris	0.39
	Osmia bicornis	Antwerp	Poznan	0.44
	Osmia bicornis	Antwerp	Tartu	0.37
	Osmia bicornis	Antwerp	Zurich	0.57
	Osmia bicornis	Paris	Poznan	0.55
	Osmia bicornis	Paris	Tartu	0.31
	Osmia bicornis	Paris	Zurich	0.55
	Osmia bicornis	Poznan	Tartu	0.35
	Osmia bicornis	Poznan	Zurich	0.49
	Osmia bicornis	Tartu	Zurich	0.46
	Osmia cornuta	Antwerp	Paris	0.57
	Osmia cornuta	Antwerp	Zurich	0.72
	Osmia cornuta	Paris	Zurich	0.67
Genus level	*Chelostoma florisomne*	Antwerp	Tartu	1
	Chelostoma florisomne	Antwerp	Zurich	1
	Chelostoma florisomne	Tartu	Zurich	1
	Hylaeus communis	Antwerp	Paris	0.04
	Hylaeus communis	Antwerp	Poznan	0.12
	Hylaeus communis	Antwerp	Tartu	0.06
	Hylaeus communis	Antwerp	Zurich	0.05

	Hylaeus communis	Paris	Poznan	0.08
	Hylaeus communis	Paris	Tartu	0.12
	Hylaeus communis	Paris	Zurich	0.02
	Hylaeus communis	Poznan	Tartu	0.25
	Hylaeus communis	Poznan	Zurich	0.17
	Hylaeus communis	Tartu	Zurich	0.01
	Osmia bicornis	Antwerp	Paris	0.39
	Osmia bicornis	Antwerp	Poznan	0.39
	Osmia bicornis	Antwerp	Tartu	0.39
	Osmia bicornis	Antwerp	Zurich	0.42
	Osmia bicornis	Paris	Poznan	0.50
	Osmia bicornis	Paris	Tartu	0.31
	Osmia bicornis	Paris	Zurich	0.40
	Osmia bicornis	Poznan	Tartu	0.31
	Osmia bicornis	Poznan	Zurich	0.32
	Osmia bicornis	Tartu	Zurich	0.34
	Osmia cornuta	Antwerp	Paris	0.58
	Osmia cornuta	Antwerp	Zurich	0.41
	Osmia cornuta	Paris	Zurich	0.47
Species level	*Chelostoma florisomne*	Antwerp	Tartu	1
	Chelostoma florisomne	Antwerp	Zurich	0.01
	Chelostoma florisomne	Tartu	Zurich	0.01
	Hylaeus communis	Antwerp	Paris	0.07
	Hylaeus communis	Antwerp	Poznan	0.03
	Hylaeus communis	Antwerp	Tartu	0.04
	Hylaeus communis	Antwerp	Zurich	0.08
	Hylaeus communis	Paris	Poznan	0.04
	Hylaeus communis	Paris	Tartu	0.12
	Hylaeus communis	Paris	Zurich	0.01
	Hylaeus communis	Poznan	Tartu	0.24
	Hylaeus communis	Poznan	Zurich	0.09
	Hylaeus communis	Tartu	Zurich	0.07
	Osmia bicornis	Antwerp	Paris	0.19
	Osmia bicornis	Antwerp	Poznan	0.21
	Osmia bicornis	Antwerp	Tartu	0.40
	Osmia bicornis	Antwerp	Zurich	0.23
	Osmia bicornis	Paris	Poznan	0.12
	Osmia bicornis	Paris	Tartu	0.10
	Osmia bicornis	Paris	Zurich	0.26
	Osmia bicornis	Poznan	Tartu	0.12

Osmia bicornis	Poznan	Zurich	0.18
Osmia bicornis	Tartu	Zurich	0.13
Osmia cornuta	Antwerp	Paris	0.23
Osmia cornuta	Antwerp	Zurich	0.15
Osmia cornuta	Paris	Zurich	0.26

TABLE S11. Predictive power of the predictors used in the SDMs for each bee species.

	Predictor	**D^2**
Chelostoma florisomne	NDVI at 200 m	0.44
	Plant frequency	0.36
	LST at 200 m	0.33
Osmia cornuta	NDVI at 200 m	0.22
	Plant richness	0.18
	LST at 1600 m	0.16
Osmia bicornis	NDVI at 200 m	0.18
	Plant richness	0.16
	LST at 400 m	0.09
Hylaeus communis	Proximity index	0.17
	Grasslands at 8 m	0.15
	NDVI at 1600 m	0.12

TABLE S12. Pairwise Pearson correlations between taxonomic and trait-based metrics and proxies of urban gradients. For *Osmia cornuta*, *Osmia bicornis* and *Hylaeus communis*, we provide the Pearson correlations between the number of plant families (N. families) and plant species (N. species), the Shannon diversity of the pollen (Pollen diversity), and the proportion of the different levels of origin status (P. exotic), growth form (P. trees, P. herbs, P. shrub and P. climbers) and blossom class (P. bell-trumpet, P. brush, P. dish-bowl, P. flag, P. gullet, P. stalk-dish), and six proxies of urban intensity. The six proxies are related to stress (land surface temperature, LST), amount of available habitat (normalized difference vegetation index, NDVI) and resource availability (plant species richness and Shannon diversity). LST and NDVI are measured at 400 and 1600 m from the focal sites. The plant species richness and Shannon diversity are measured within 100 m radius. Note that *C. florisomne* has not been included in the calculations due to its strict specialization on *Ranunculus* spp.

Bee species	**Explanatory variable**	**City**	**N. families**	**N. species**	**Pollen diversity**	**P. exotic**	**P. trees**	**P. herbs**	**P. shrubs**	**P climbers**	**P. bell-trumpet**	**P. brush**	**P. dish-bowl**	**P. flag**	**P. gullet**	**P. stalk-disk**
Osmia cornuta	LST 400 m	Antwerp	-0.11	-0.12	0.13	0.28	-0.70	-0.29	0.85			0.80	-0.72	-0.74	0.08	
		Paris	-0.23	0.15	0.09	-0.49	0.35	-0.33	0.15			0.07	-0.07			
		Zurich	0.64	0.29	0.41	-0.14	0.62	-0.07	-0.58			-0.23	0.23			
		All	0.04	0.11	0.20	0.20	0.14	-0.20	0.08			0.25	-0.23	-0.29	0.25	
	LST 1600 m	Antwerp	-0.18	-0.19	-0.09	-0.18	-0.58	-0.17	0.66			0.57	-0.53	-0.52	0.16	
		Paris	-0.13	-0.06	0.12	-0.72	-0.26	0.28	-0.28			0.03	-0.03			
		Zurich	0.85	0.74	0.85	0.19	0.56	-0.34	-0.19			-0.39	0.39			
		All	0.33	0.38	0.51	0.19	0.38	-0.36	-0.01			0.01	-0.04	0.13	0.39	
	NDVI 400 m	Antwerp	0.12	0.13	-0.13	-0.29	0.71	0.31	-0.86			-0.80	0.71	0.76	-0.05	
		Paris	0.49	0.23	0.21	0.79	-0.14	0.08	0.19			0.23	-0.23			
		Zurich	-0.28	0.14	0.01	-0.01	-0.46	0.14	0.32			0.00	0.00			
		All	0.04	0.11	-0.08	0.20	-0.18	0.04	0.16			-0.02	-0.03	0.46	0.08	
	NDVI 1600 m	Antwerp	0.11	0.15	0.04	0.21	0.67	0.12	-0.74			-0.60	0.54	0.61	-0.16	
		Paris	0.40	0.35	0.20	0.85	0.21	-0.26	0.40			0.24	-0.24			

		Zurich	0.15	0.14	0.12	-0.71	0.17	-0.45	0.36		0.21	-0.21			
		All	0.01	0.11	-0.03	0.17	0.02	-0.28	0.34		0.19	-0.23	0.28	0.11	
	Species richness	Antwerp	0.77	0.73	0.85	0.71	-0.51	0.46	0.34		0.51	-0.48	-0.52	0.38	
		Paris	0.08	-0.18	-0.03	-0.14	-0.10	0.14	-0.27		-0.38	0.38			
		Zurich	-0.24	-0.78	-0.67	-0.27	-0.44	0.30	0.11		0.34	-0.34			
		All	0.00	-0.12	-0.03	-0.20	-0.05	0.16	-0.14		-0.18	0.20	-0.16	-0.15	
	Shannon diversity	Antwerp	0.69	0.65	0.85	0.72	-0.82	0.36	0.71		0.84	-0.79	-0.83	0.44	
		Paris	0.18	-0.09	0.04	-0.03	-0.05	0.08	-0.17		-0.28	0.28			
		Zurich	-0.22	-0.75	-0.66	-0.24	-0.31	0.22	0.07		0.42	-0.42			
		All	-0.07	-0.24	-0.13	-0.27	-0.19	0.27	-0.11		-0.08	0.13	-0.42	-0.27	
Osmia bicornis	LST 400 m	Antwerp	-0.03	-0.03	-0.03	0.85					-0.88	0.88			
		Paris	-0.19	-0.13	0.11	0.13	-0.37	0.39	-0.31		0.21	-0.25	0.20	-0.08	
		Poznan	-0.20	-0.21	-0.04	-0.08	-0.49	0.69	-0.74	0.11	-0.36	-0.06	0.27		0.36
		Zurich	-0.11	0.34	0.18	0.33	-0.02	-0.06	0.08		-0.12	0.07	0.64		
		All	-0.20	-0.06	0.00	0.22	-0.04	0.01	0.05	0.02	-0.24	0.18	0.02	-0.09	0.07
	LST 1600 m	Antwerp	0.41	0.41	0.41	0.99					-0.58	0.58			
		Paris	-0.58	-0.41	-0.23	-0.43	0.15	-0.12	-0.61		0.24	-0.05	-0.10	-0.46	
		Poznan	0.28	0.21	0.43	0.42	-0.44	0.49	-0.25	-0.01	-0.22	-0.35	0.56		0.28
		Zurich	-0.58	-0.24	-0.50	0.46	0.05	-0.41	0.32		0.20	-0.21	0.40		
		All	-0.25	-0.15	-0.21	0.30	0.26	-0.43	0.14	-0.03	-0.02	-0.01	0.10	-0.12	-0.01
	NDVI 400 m	Antwerp	0.06	0.06	0.06	-0.83					0.90	-0.90			
		Paris	0.37	0.25	0.03	0.10	0.08	-0.11	0.55		-0.31	0.18	0.10	0.03	
		Poznan	0.01	0.03	-0.12	-0.17	0.42	-0.60	0.66	-0.18	0.30	0.21	-0.52		-0.21

		Zurich	-0.08	-0.55	-0.44	-0.37	0.11	-0.01	-0.13			0.26	-0.21	-0.73		
		All	-0.03	-0.16	-0.22	-0.21	0.05	-0.09	0.04	-0.01		0.01	0.13	-0.28	-0.12	0.01
	NDVI 1600 m	Antwerp	-0.48	-0.48	-0.48	-1.00						0.52	-0.52			
		Paris	0.62	0.56	0.42	0.38	-0.32	0.29	0.69			-0.17	-0.03	0.25	0.17	
		Poznan	-0.18	-0.10	-0.27	-0.53	0.40	-0.49	0.35	-0.02		0.29	0.37	-0.64		-0.35
		Zurich	0.13	-0.31	-0.13	-0.22	-0.17	0.36	-0.14			-0.50	0.51	-0.57		
		All	-0.01	-0.10	-0.10	-0.16	-0.19	0.20	0.04	0.05		-0.25	0.33	-0.28	-0.09	0.02
	Species richness	Antwerp	0.79	0.79	0.79	0.93						-0.14	0.14			
		Paris	-0.51	-0.57	-0.71	-0.58	0.40	-0.40	-0.06			-0.65	0.75	-0.42	-0.17	
		Poznan	0.18	0.25	0.22	0.56	-0.41	0.27	0.21	0.24		-0.27	0.00	0.12		0.30
		Zurich	0.29	0.23	0.37	-0.27	0.14	0.09	-0.25			0.13	-0.12	-0.02		
		All	-0.17	-0.16	-0.19	-0.28	0.08	-0.03	-0.07	-0.08		-0.14	0.25	-0.20	-0.06	-0.14
	Shannon diversity	Antwerp	-0.13	-0.13	-0.13	0.79						-0.92	0.92			
		Paris	-0.45	-0.58	-0.72	-0.53	0.33	-0.34	0.09			-0.66	0.77	-0.47	-0.16	
		Poznan	0.20	0.26	0.20	0.52	-0.42	0.28	0.20	0.30		-0.24	0.02	0.02		0.33
		Zurich	0.36	0.38	0.53	-0.37	0.27	0.12	-0.43			0.10	-0.11	0.11		
		All	-0.07	-0.05	-0.06	-0.22	-0.07	0.13	-0.05	-0.07		-0.06	0.20	-0.24	0.00	-0.19
Hylaeus communis	LST 400 m	Antwerp	-0.34	-0.33	-0.26	0.58	0.73	-0.45	-0.36		1.00	-0.57	0.37	-0.29	-0.56	-0.34
		Paris	-0.90	-0.81	-0.84	0.08	0.03	-0.54	0.24				0.12	0.21		
		Poznan	0.30	0.37	0.11	0.66	0.75	-0.77	-0.04		-0.64		-0.01	0.33	0.41	
		Tartu	-0.14	-0.10	-0.20	0.65	-0.43	0.36	0.24		-0.30	-0.35	-0.40	0.12	0.78	
		Zurich	-0.27	-0.21	-0.14	0.18	0.65	-0.38	-0.41		-0.38	-0.23	0.33	0.23	-0.48	
		All	-0.32	-0.28	-0.31	0.28	0.17	-0.22	0.05		0.28	-0.17	-0.21	0.35	-0.23	-0.04

LST 1600 m	Antwerp	-0.45	-0.39	-0.49	0.49	0.37	0.05	-0.72	0.86	-0.86	-0.11	-0.26	-0.89	0.12
	Paris	-0.79	-0.73	-0.80	0.06	-0.27	-0.25	0.44			-0.20	0.40		
	Poznan	-0.09	-0.01	-0.28	0.83	0.95	-0.94	-0.26	-0.62		-0.20	0.60	0.06	
	Tartu	-0.59	-0.56	-0.59	-0.10	0.59	-0.50	-0.31	-0.06	0.17	0.33	-0.19	-0.20	
	Zurich	-0.48	-0.61	-0.47	0.72	0.19	-0.32	0.22	-0.16	-0.32	0.08	0.10	-0.47	
	All	-0.40	-0.35	-0.39	0.34	0.21	-0.31	0.14	0.17	-0.10	-0.24	0.28	-0.36	0.19
NDVI 400 m	Antwerp	0.31	0.39	0.07	0.05	-0.53	0.81	-0.63	-0.52	-0.11	-0.65	0.55	-0.24	0.60
	Paris	0.48	0.53	0.41	-0.03	-0.21	0.74	-0.13			-0.54	0.39		
	Poznan	-0.30	-0.38	-0.12	-0.61	-0.74	0.75	0.13	0.51		0.10	-0.33	-0.40	
	Tartu	0.45	0.42	0.38	-0.13	-0.32	0.32	0.02	0.37	-0.22	0.05	-0.34	0.04	
	Zurich	0.10	0.12	-0.02	-0.16	-0.47	0.14	0.41	-0.61	0.00	-0.08	-0.13	0.05	
	All	0.29	0.31	0.21	-0.36	-0.47	0.56	-0.09	-0.09	0.08	-0.08	-0.24	0.13	0.30
NDVI 1600 m	Antwerp	0.25	0.35	0.03	0.43	-0.17	0.64	-0.92	-0.06	-0.37	-0.48	0.54	-0.53	0.44
	Paris	-0.30	-0.16	-0.34	0.06	-0.24	0.34	0.10			-0.57	0.67		
	Poznan	0.05	-0.04	0.18	-0.87	-0.85	0.83	0.41	0.65		-0.02	-0.37	-0.01	
	Tartu	0.46	0.43	0.39	0.34	-0.47	0.43	0.18	0.06	-0.35	-0.34	-0.05	0.56	
	Zurich	0.35	0.44	0.25	-0.56	-0.31	0.27	0.01	-0.52	0.22	-0.09	-0.01	0.24	
	All	0.38	0.36	0.26	-0.49	-0.52	0.68	-0.20	0.09	0.12	-0.14	-0.12	0.31	0.10
Species richness	Antwerp	0.89	0.90	0.88	0.86	0.67	-0.44	-0.29	0.09	0.48	0.64	0.88	0.32	-0.68
	Paris	0.29	0.07	0.22	0.43	0.31	-0.16	-0.28			-0.29	-0.09		
	Poznan	-0.50	-0.46	-0.30	0.33	-0.10	0.20	-0.75	-0.06		0.51	-0.38	-0.74	
	Tartu	0.80	0.80	0.84	0.47	-0.51	0.27	0.70	0.21	0.34	-0.81	0.73	0.21	
	Zurich	0.20	0.40	0.37	-0.16	0.41	-0.38	-0.25	-0.17	-0.11	0.50	-0.34	0.08	
	All	-0.06	-0.05	0.02	0.34	0.36	-0.36	-0.05	-0.14	-0.07	-0.05	0.05	-0.14	-0.07

Shannon diversity	Antwerp	0.58	0.58	0.65	0.94	0.94	-0.71	-0.25	0.53	0.23	0.81	0.55	0.13	-0.83
	Paris	0.34	0.12	0.26	0.42	0.32	-0.12	-0.31			-0.19	-0.19		
	Poznan	-0.57	-0.53	-0.39	0.39	-0.01	0.11	-0.81	-0.05		0.42	-0.27	-0.79	
	Tartu	0.76	0.75	0.80	0.44	-0.55	0.32	0.67	0.15	0.34	-0.79	0.76	0.19	
	Zurich	0.10	0.33	0.32	-0.13	0.54	-0.40	-0.38	-0.04	-0.20	0.54	-0.28	-0.01	
	All	-0.04	0.00	0.05	0.40	0.28	-0.37	0.09	-0.25	0.04	0.09	-0.02	-0.15	-0.12

Supplementary Figures

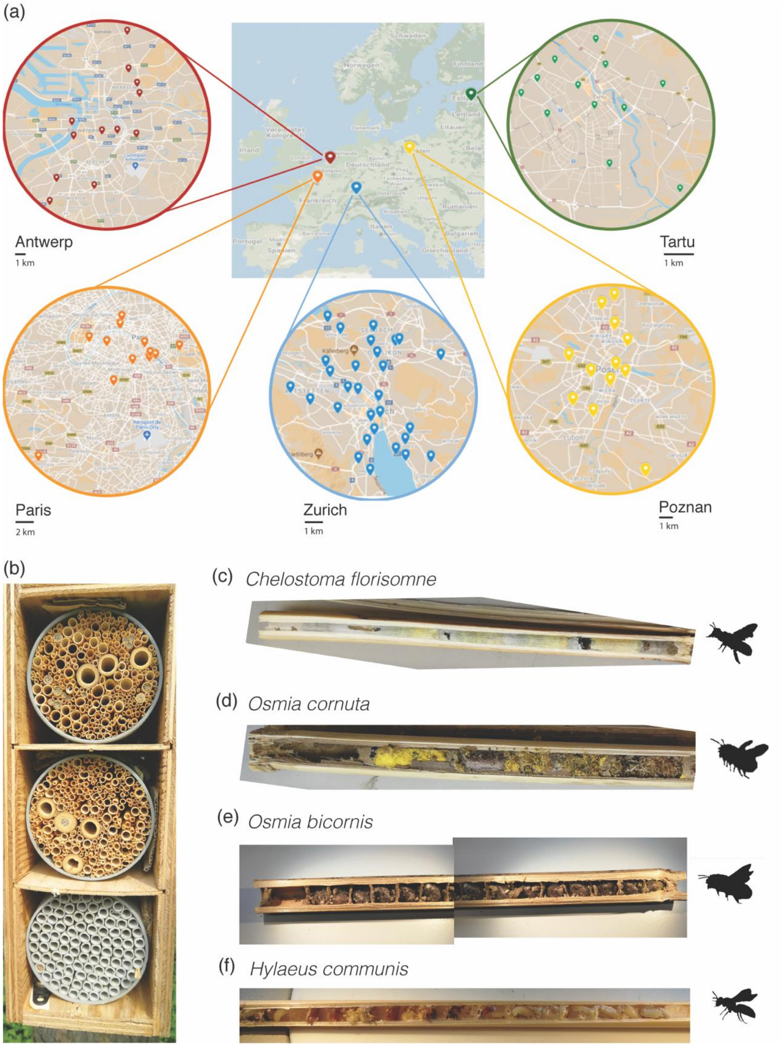
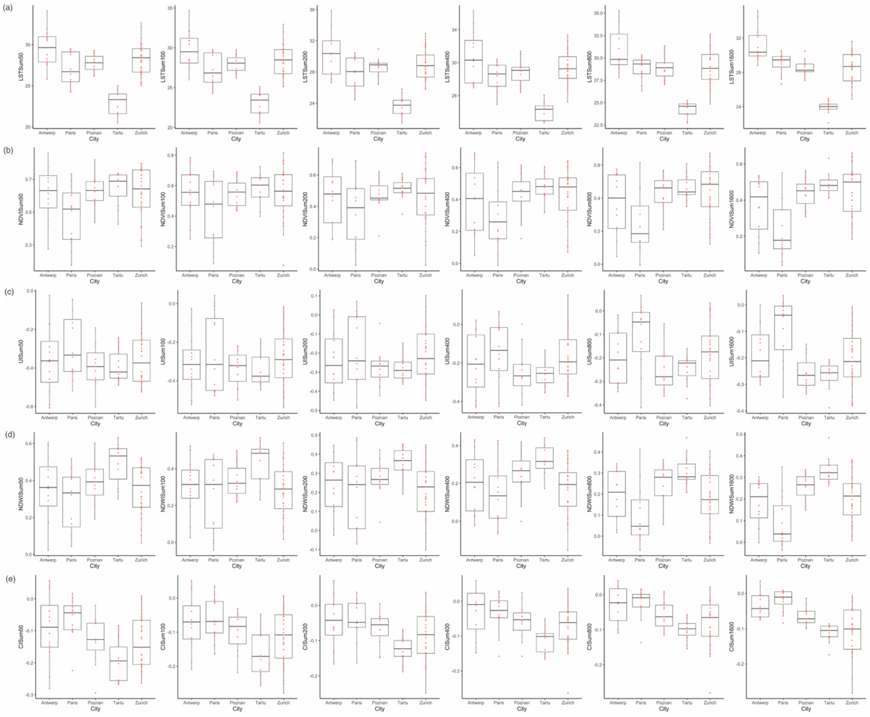


FIGURE S1. Study sites, trap-nests and bee nests. (a) Distribution of the study sites in the five studied cities, i.e. Antwerp (Belgium), Paris (France), Poznan (Poland), Tartu (Estonia) and Zurich (Switzerland). (b) Photograph of one of the installed trap-nests where bee data was collected. (c–f) Photograph of a nest of *Chelostoma florisomne* (c), *Osmia cornuta* (d), *Osmia bicornis* (e) and *Hylaeus communis* (f).


(a)
LSTSum50
LSTSum100
LSTSum200
LSTSum400
LSTSum800
LSTSum1600
(b)
NDVISum50
NDVISum100
NDVISum200
NDVISum400
NDVISum800
NDVISum1600
(c)
UISum50
UISum100
UISum200
UISum400
UISum800
UISum1600
(d)
NDWISum50
NDWISum100
NDWISum200
NDWISum400
NDWISum800
NDWISum1600
(e)
CISum50
CISum100
CISum200
CISum400
CISum800
CISum1600
Antwerp
Paris
Poznan
Tartu
Zurich
City

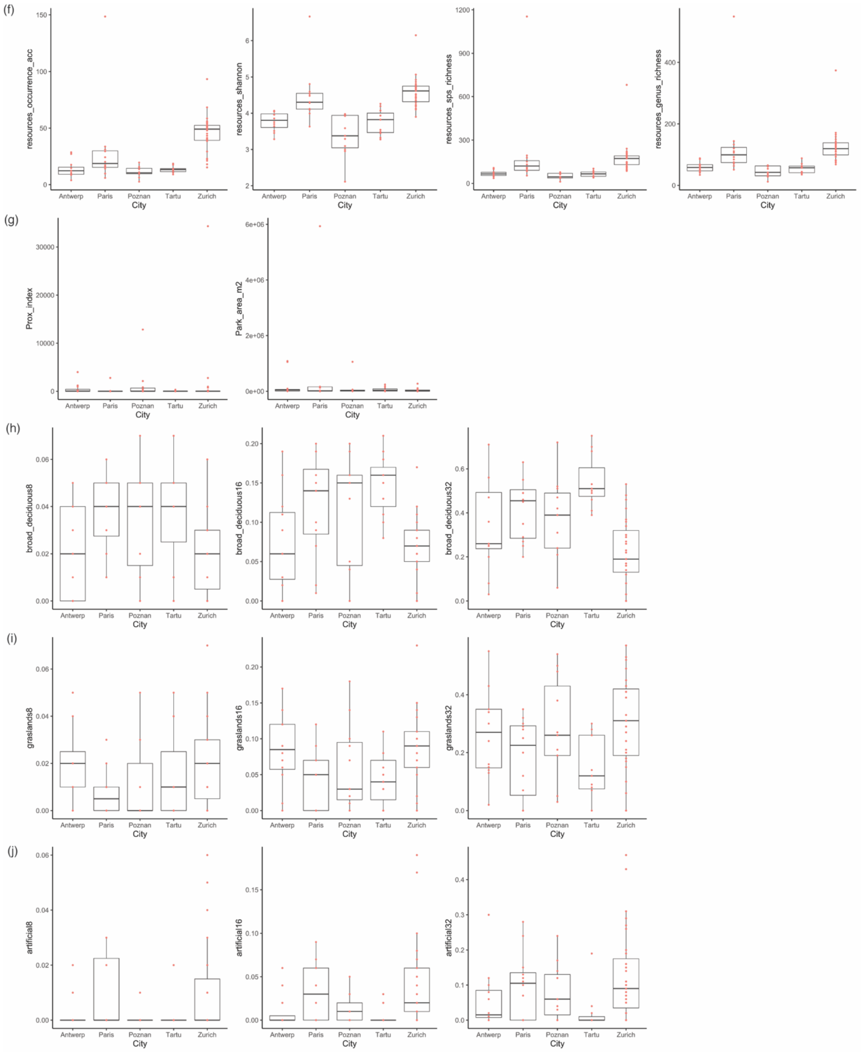


FIGURE S2. Boxplots and points depicting the distribution of the values of the environmental predictors in each city. For each city, we provide the distribution of the values of each predictor at all the spatial scales considered. (a–e) remote sensing variables at 50, 100, 200, 400, 800 and 1600 m from the focal sites, specifically (a) LST, (b) NDVI, (c) UI, (d) NDWI and (e) CI. (f) floral resources, (g) connectivity metrics and (h–j) local land cover at 8, 16 and 32 m, specifically, (h) the proportion of deciduous trees, (i) the proportion of grasslands, and (j) the proportion of artificial surfaces. NDVI =

normalized difference vegetation index; UI = urban intensity; LST = land surface temperature; CI = colour index; NDWI = normalized difference water index.

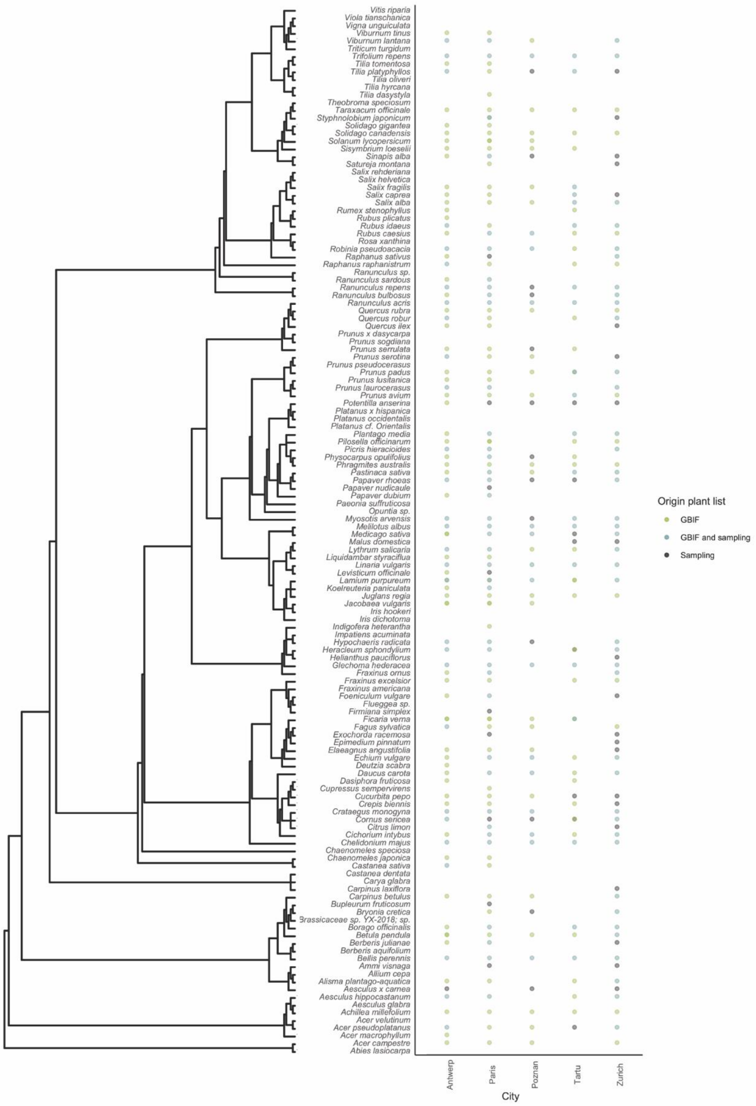


FIGURE S3. Origin of the plant list used for the study of the trophic matrix. For each plant species in the pollen in each of the five studied cities we indicate whether the species was obtained from the floral resource sampling within a 100-m radius at each site, from the species records extracted from GBIF (GBIF, 2021) or from both sources. Data from: GBIF Occurrence Download. Downloaded on 18 May 2021 doi: https://doi.org/10.15468/dl.z6fg97.

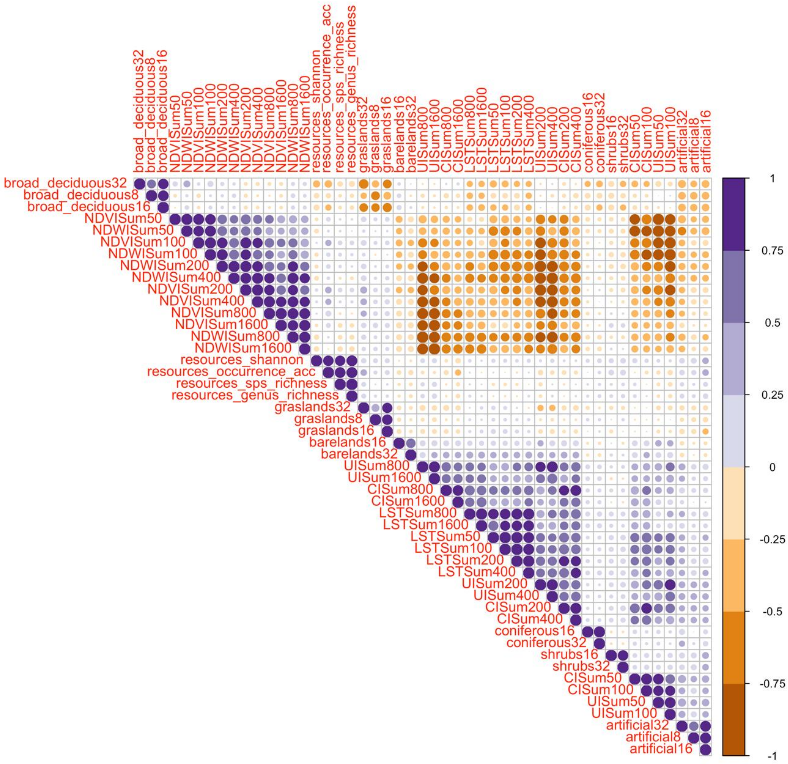


FIGURE S4. Pearson correlations between the environmental predictors (see Methods and Supplementary Text S3-S5 for a description on the predictors). LSTSum = Land Surface Temperature; NDVISum = Normalised Difference Vegetation Index; NDWISum = Normalised Difference Water Index; CISum = Color Index; UISum = Urban Index; artificial = artificial surfaces; coniferous = coniferous trees; shrubs = shrub vegetation; broad_deciduous = broad deciduous trees; grasslands = grassland vegetation; resources_shannon = Shannon diversity of the floral resources; resources_occurrence_acc = Sum frequency of all flowering plant species; resources_sps_richness = species richness flowering plants; resources_genus_richness = genus richness flowering plants. Numbers indicate the radius of the measuring buffer in meters.

FIGURE S5. Phylogenetic tree of all the plant species found in the pollen of the four bee species (*Chelostoma florisomne*, *Osmia cornuta*, *Osmia bicornis*, *Hylaeus communis*). The tree was assembled using the R package *V.phylomaker* (Jin & Qian, 2019). The interaction with bee species identity is depicted in Fig. 1. See also Text S1.

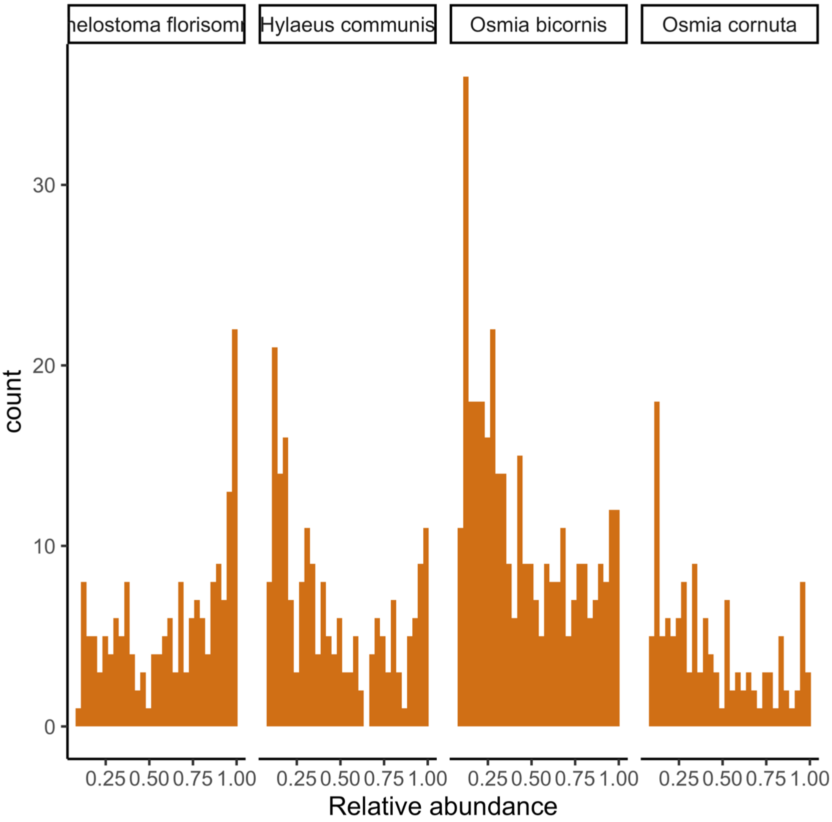


FIGURE S6. Histograms of the relative pollen abundances of each taken plant species per nest for each of the four studied bees.

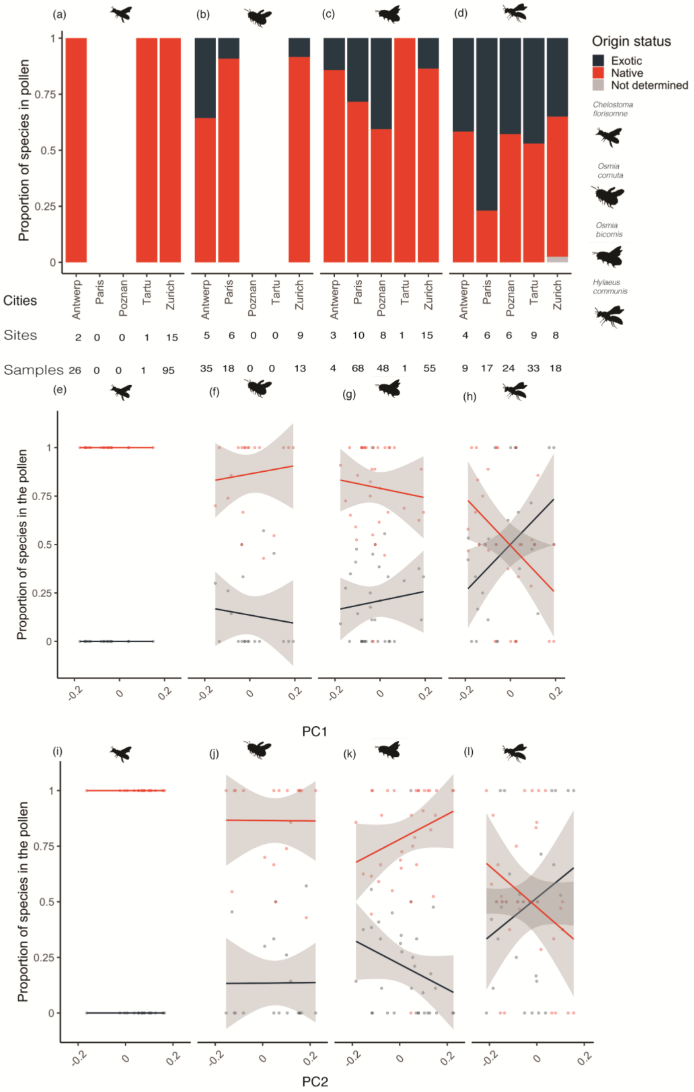


FIGURE S7. Diet composition and variability based on the origin status of the plant species. (a–d) The proportion of exotic and native plant species for each bee species in each city. The category "Not determined" refers to plant taxa at the genus or family level that could not unequivocally be classified. (e–l) Change in the proportion of exotic and native species along the urban intensity gradient, based on the first (PC1, e-h) and second (PC2, i-l) principal component analysis axes. See Methods and Figure S11 for more details.

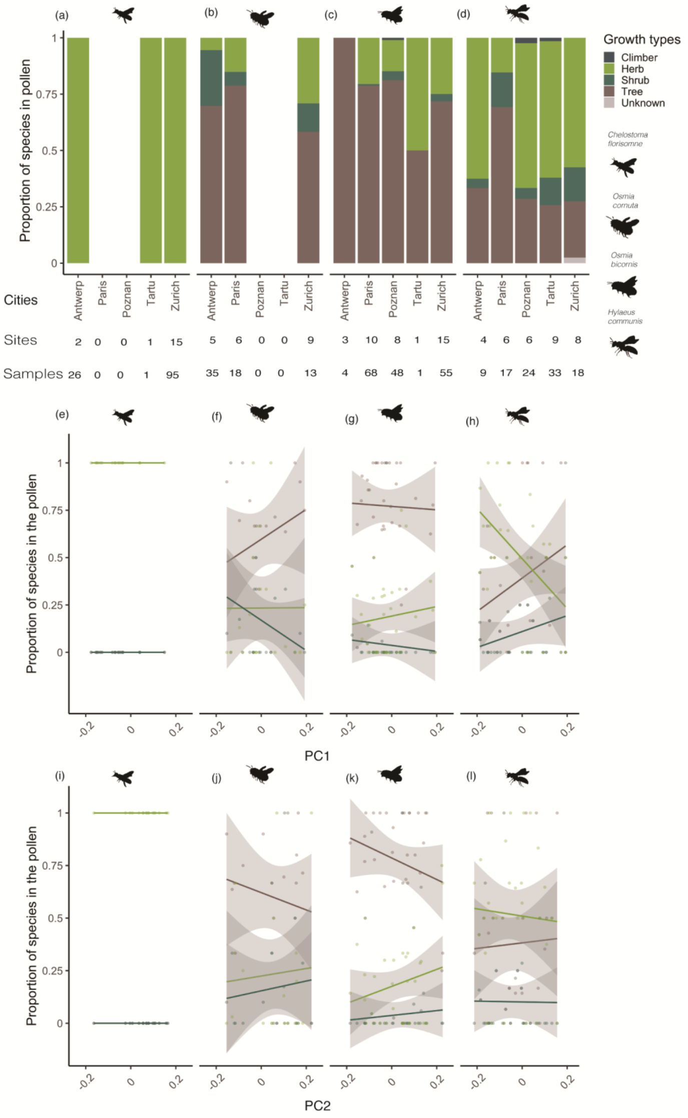


FIGURE S8. Diet composition and variability based on the growth form of the plant species. (a–d) Proportion of tree, shrub, herb and climber plant species in each city for each bee species. The category “Unknown” refers to plant taxa at the genus or family level that could not be classified unequivocally. (e–l) Change in the proportion of growth form categories along the urban intensity gradient based on the first (PC1, e-h) and second (PC2, i-l) principal component analysis axes. See Methods and Figure S11 for more details.

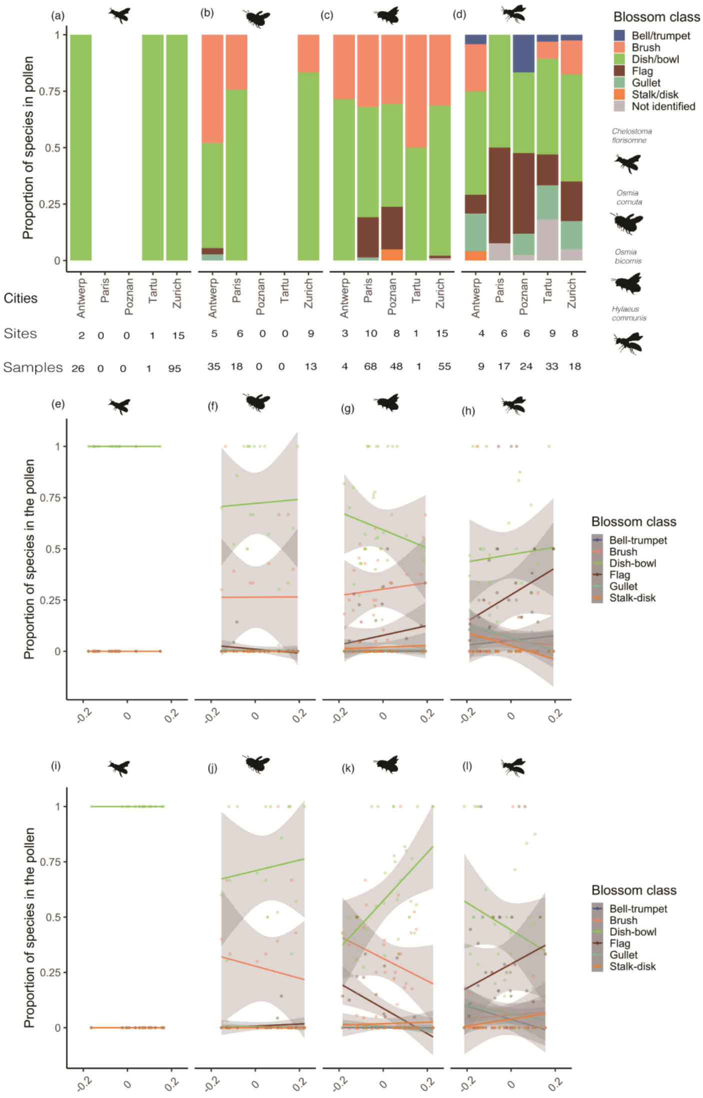


FIGURE S9. Diet composition and variability based on the blossom class of the plant species. (a–d) Proportion species with bell-trumpet, brush, dish-bowl, flag, gullet and stalk-disk blossom classes in each city for each bee species. The category “Not determined” refers to plant taxa at the genus or family level that could not be classified unequivocally. (e–l) Change in the proportion of blossom classes along the urban intensity gradient based on the first (PC1, e-h) and second (PC2, i-l) principal component analysis axes. See Methods and Figure S11 for more details.

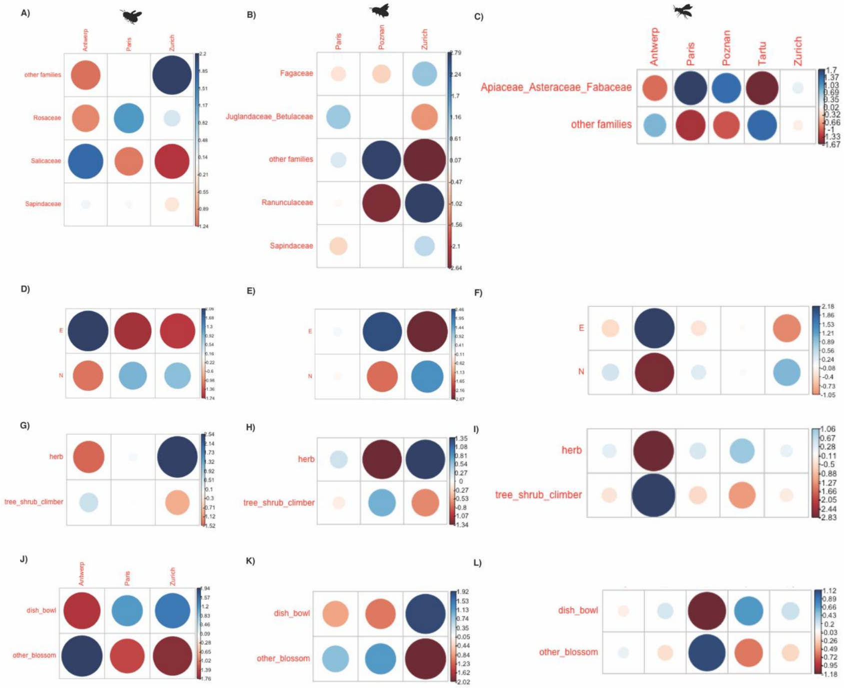


FIGURE S10. Contribution of the different plant taxonomic and trait classes on χ^2 tests for *Osmia cornuta*, *Osmia bicornis* and *Hylaeus communis*. Each plot depicts the Pearson residuals from the χ^2 tests on plant family (A–C) and trait (origin status, D–F; growth form, G–I; blossom class, J–L) composition for *Osmia cornuta* (A, D, G, J), *Osmia bicornis* (B, E, H, K) and *Hylaeus communis* (C, F, I, L). Blue colours (positive residuals) indicate a positive association between the taxonomic or trait class and a city, whereas red colours (negative residuals) indicate a negative association. E = exotic; N = native.

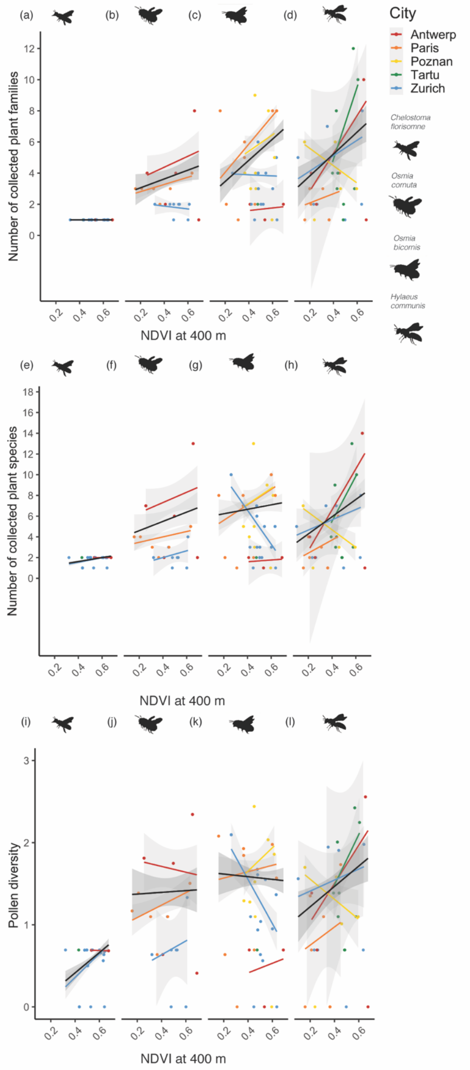


FIGURE S11. Taxonomic metrics along urban gradients. For each bee species and each city, lines represent the linear models depicting the relationship between the number of collected plant families (a–d), number of collected plant species (e–h) and pollen diversity (i–l with NDVI measured at 400 m from the focal sites is plotted. Dark lines correspond to the estimated response pooling all cities together. Shaded gray bands represent 95% confidence interval.

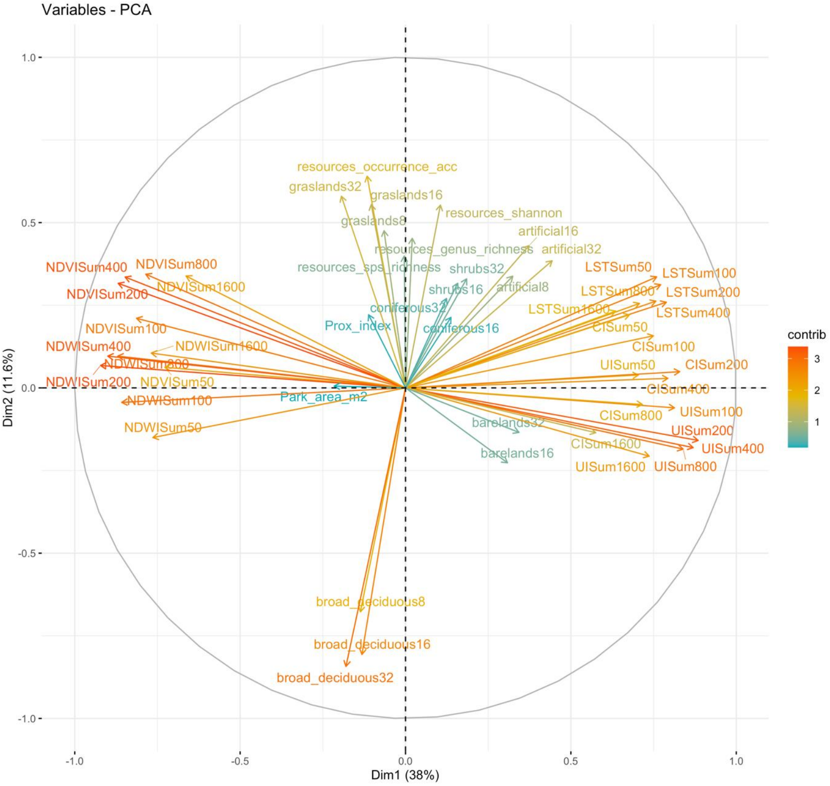
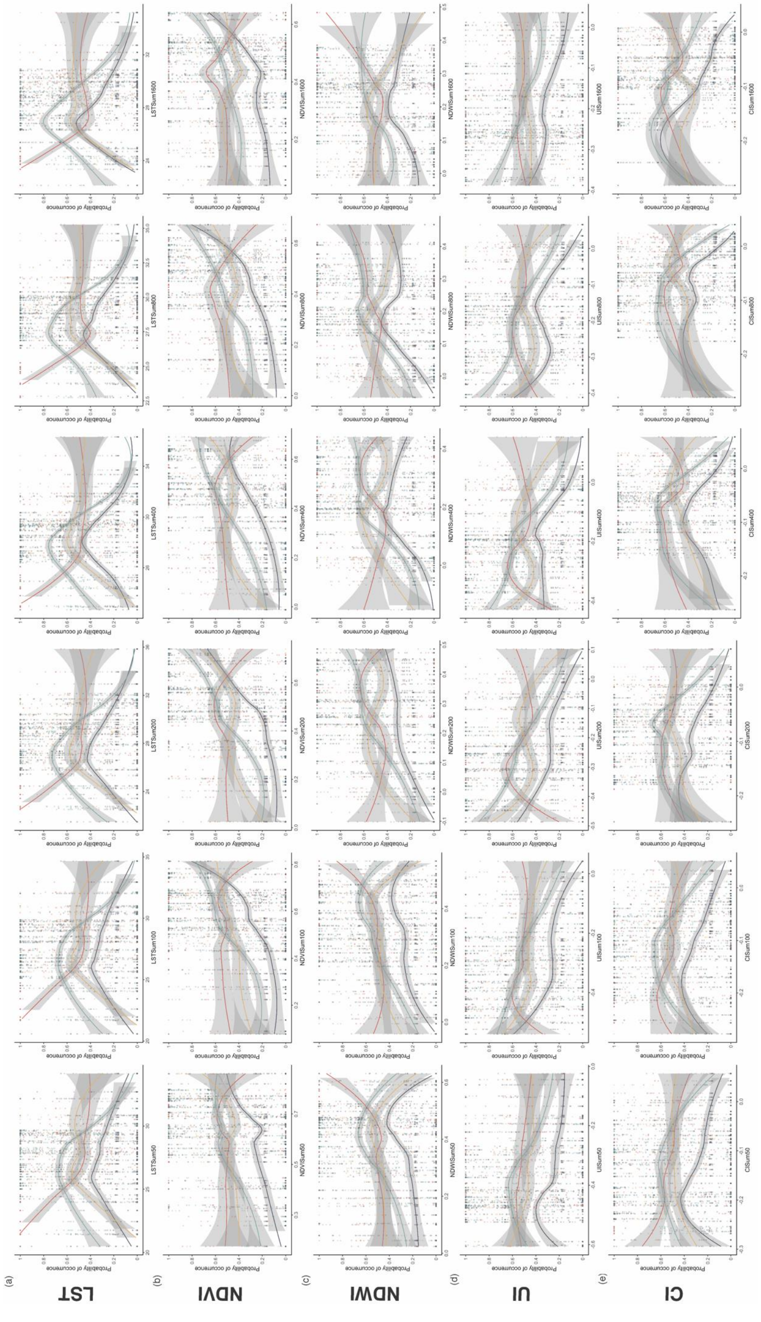


FIGURE S12. Results from the principal component analyses on the 53 explanatory variables. PC1 accounts for 38% of the variation, whereas PC2 accounts for 11.6%. The colour of each arrow indicates the contribution to the axis, with warm colours (red) indicating the highest contribution and cold colours (blue) indicating the lowest. LSTSum = Land Surface Temperature; NDVISum = Normalised Difference Vegetation Index; NDWISum = Normalised Difference Water Index; CISum = Color Index; UISum = Urban Index; artificial = artificial surfaces; coniferous = coniferous trees; shrubs = shrub vegetation; broad_deciduous = broad deciduous trees; grasslands = grassland vegetation; resources_shannon = Shannon diversity of the floral resources; resources_occurrence_acc = Sum frequency of all flowering plant species; resources_sps_richness = species richness flowering plants; resources_genus_richness = genus richness flowering plants. Numbers indicate the radius of the measuring buffer in meters.


(a)
LST
(b)
NDVI
(c)
NDWI
(d)
UI
(e)
CI
Probability of occurrence
LSTSum50
LSTSum100
LSTSum200
LSTSum400
LSTSum800
LSTSum1600
NDVISum50
NDVISum100
NDVISum200
NDVISum400
NDVISum800
NDVISum1600
NDWISum50
NDWISum100
NDWISum200
NDWISum400
NDWISum800
NDWISum1600
UISum50
UISum100
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CISum400
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CISum1600

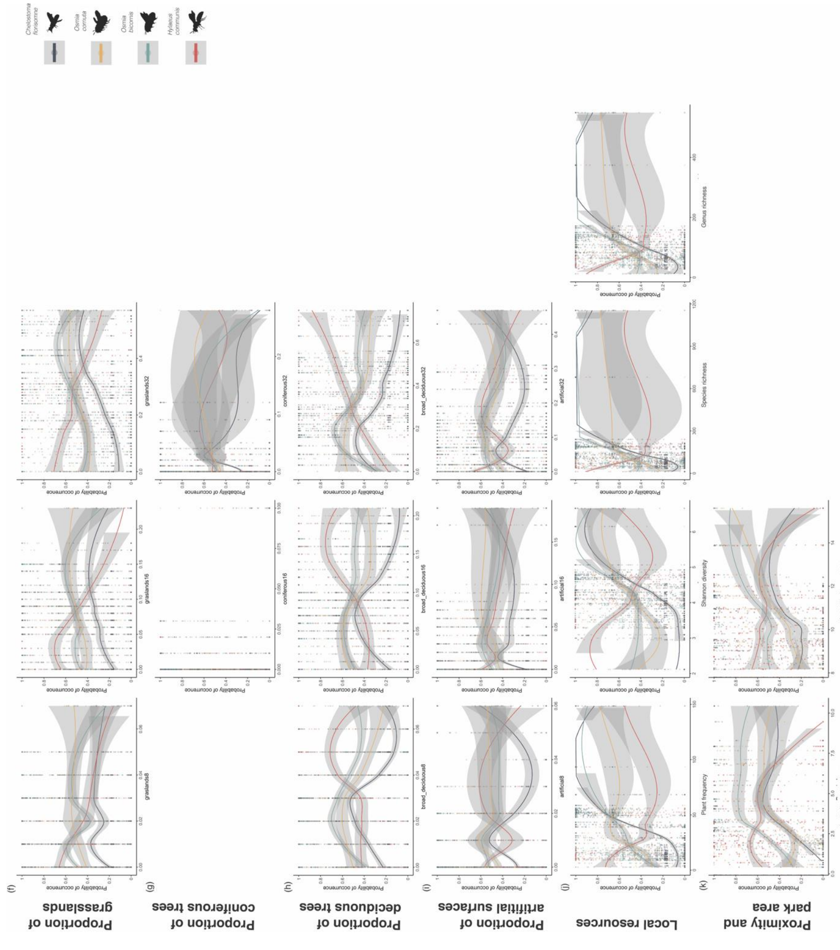(f)
Proportion of grasslands
(g)
Proportion of coniferous trees
(h)
Proportion of deciduous trees
(i)
Proportion of artifitial surfaces
(j)
Local resources
(k)
Proximity and park area
Probability of occurrence
grasslands8
grasslands16
grasslands32
coniferous16
coniferous32
broad_deciduous8
broad_deciduous16
broad_deciduous32
artificial8
artificial16
artificial32
Plant frequency
Shannon diversity
Species richness
Genus richness
log10(Proximity index)
log10(Park area (m2))
Chelostoma florisomne
Osmia cornuta
Osmia bicornis
Hylaeus communis

FIGURE S13. Predicted probability of occurrence of *C. florisomne*, *O. cornuta*, *O. bicornis* and *H. communis* along urban intensity, habitat amount and local resource proxies. (a–e) Probability of occurrence in relation to the LST, NDVI, NDWI, UI and CI measured at 50, 100, 200, 400, 800 and 1600 m from the focal sites. (g–i) Probability of occurrence in relation to the local land cover variables (i.e. the proportion of grasslands, artificial surfaces, bare land, and coniferous and deciduous trees). (j) Probability of occurrence in relation to local resource availability (i.e. plant frequency, plant Shannon diversity, plant species and genus richness). (k) Probability of occurrence in relation to the proximity index and the park area. NDVI = normalized difference vegetation index; UI = urban intensity; LST = land surface temperature; CI = colour index; NDWI = normalized difference water index. Numbers in the x-axis label indicate the radius of the measuring buffer in meters.

SUPPLEMENTARY REFERENCES

Alós Ortí, M., Casanelles-Abella, J., Chiron, F., Deguines, N., Hallikma, T., Jaksi, P., … Laanisto, L. (2021). Negative relationship between woody species density and urban green areas in seven European cities. *Urban Forestry and Urban Greening*, *in review*.

Casanelles-Abella, J., Frey, D., Müller, S., Aleixo, C., Alós Ortí, M., Deguines, N., … Moretti, M. (2021). A dataset of the flowering plants (Angiospermae) in urban green areas in five European cities. Data in Brief, 37, 107243. doi: 10.1016/j.dib.2021.107243

Escadafal, R., Girard, M-C., Courault, D. (1989). Munsell soil color and soil reflectance in the visible spectral bands of landsat MSS and TM data. Remote Sensing of Environment, 27(1): 37-46. https://doi.org/10.1016/0034-4257(89)90035-7

Faegri, K & van der Pijl, L. (1979). Structural Blossom Classes, Princ. Pollinat. Ecol. 88–95 .

Gao, B. (1996) - NDWI—A normalized difference water index for remote sensing of vegetation liquid water from space. Remote Sensing of Environment, 58(3): 257-266. https://doi.org/10.1016/S0034-4257(96)00067-3

GBIF. (2021). Data from: GBIF Occurrence Download. Downloaded on 18 May 2021 doi: https://doi.org/10.15468/dl.z6fg97.

Ha H.Q.; Weng, Q. (2018) - Mapping impervious surfaces in the Greather Hanoi Area, Vietnam, from time series Landsat images 1988-2015. In: Weng, W., Quattrochi, D., Gamba, P.E. (Eds.), Urban Remote Sensing, Second Edition. CRC Press, Boca Raton, 22pp. https://doi.org/10.1201/9781138586642

Haider, M., Dorn, S., & Müller, A. (2014). Better safe than sorry? A Fabaceae species exhibits unfavourable pollen properties for developing bee larvae despite its hidden anthers. Arthropod-Plant Interactions, 8(3), 221–231. doi: 10.1007/s11829-014-9299-y

Jin, Y., & Qian, H. (2019). V.PhyloMaker: an R package that can generate very large phylogenies for vascular plants. *Ecography*, *42*(8), 1353–1359. doi: 10.1111/ecog.04434

Juillerat, P., Bäumler, B., Bornand, C., Gygax, A., Jutzi, M., Möhl, A., … Eggenberg, S. (2017). *Flora Helvetica Checklist 2017 der Gefässpflanzenflora der Schweiz*.

Kawamura, M., Jayamana, S., Tsujiko, Y. (1996). Relation between social and environmental conditions in Colombo Sri Lanka and the Urban Index estimated by satellite remote sensing data. The International Archives of Photogrammetry and Remote Sensing, 31(PART B7), 321–326.

Kopecká, M., Szatmári, D., Rosina, K. (2017). Analysis of Urban Green Spaces based on Sentinel-2A: Case studies from Slovakia. Land, 6(25):1-17. https://doi.org/10.3390/land6020025

Martins, K. T., Normandin, É., & Ascher, J. S. (2017). Hylaeus communis (Hymenoptera: Colletidae), a new exotic bee for North America with generalist foraging and habitat preferences. Canadian Entomologist, 149(3), 377–390. doi: 10.4039/tce.2016.62

Pouget, M., Madeira, J., Le Floc'H, E., Kamal, S. (1991). Caractéristiques spectrales des surfaces sableuses de la région côtière Nord-Ouest de l'Egypte: Application aux données satellitaires SPOT. In : Caractérisation et suivi des milieux terrestres en régions arides et tropicales. Paris: ORSTOM, p. 27-38. (Colloques et Séminaires). Journées de Télédétection, 2., Bondy (FRA), 1990/12/04-06. ISBN 2-7099-1051-9.

Qian, H., & Jin, Y. (2016). An updated megaphylogeny of plants, a tool for generating plant phylogenies and an analysis of phylogenetic community structure. *Journal of Plant Ecology*, *9*(2), 233–239. doi: 10.1093/jpe/rtv047

Sedivy, C., Müller, A., & Dorn, S. (2011). Closely related pollen generalist bees differ in their ability to develop on the same pollen diet: Evidence for physiological adaptations to digest pollen. Functional Ecology, 25(3), 718–725. doi: 10.1111/j.1365-2435.2010.01828.x

Sedivy, C., Praz, C. J., Müller, A., Widmer, A., & Dorn, S. (2008). Patterns of host-plant choice in bees of the genus Chelostoma: The constraint hypothesis of host-range evolution in bees. Evolution, 62(10), 2487–2507. doi: 10.1111/j.1558-5646.2008.00465.x

Sickel, W., Ankenbrand, M. J., Grimmer, G., Holzschuh, A., Härtel, S., Lanzen, J., … Keller, A. (2015). Increased efficiency in identifying mixed pollen samples by meta-barcoding with a dual-indexing approach. *BMC Ecology*, *15*(1), 1–9. doi: 10.1186/s12898-015-0051-y

Sobrino, J.A., Jiménez-Munoz, J.C., Paolini, L. (2004). Land surface temperature retrieval from LANDSAT TM-5. Remote Sensing of Environment, 90: 434–440. https://doi.org/10.1016/j.rse.2004.02.003

Smith, S. A., & Brown, J. W. (2018). Constructing a broadly inclusive seed plant phylogeny. *American Journal of Botany*. doi: 10.1002/ajb2.1019

Tucker, C.J. (1979). Red and Photographic Infrared Linear Combinations for Monitoring Vegetation. Remote Sensing of Environment, 8:127:150. https://doi.org/10.1016/0034-4257(79)90013-0

Vierna, J., Doña, J., Vizcaíno, A., Serrano, D., Jovani, R., & Chain, F. (2017). PCR cycles above routine numbers do not compromise high-throughput DNA barcoding results. *Genome*, *60*(10), 868–873. doi: 10.1139/gen-2017-0081

WFO. (2021). World Flora Online.

Weng, Q., Fu, P., Gao, F. (2014). Generating daily land surface temperature at Landsat resolution by fusing Landsat and MODIS data. Remote Sensing of Environment, 145: 55-67. https://doi.org/10.1016/j.rse.2014.02.003

White, T. J., Bruns, T., Lee, S., & Taylor, J. (1990). Amplification and Direct Sequencing of Fungal Ribosomal Rna Genes for Phylogenetics. *PCR Protocols*, (January), 315–322. doi: 10.1016/b978-0-12-372180-8.50042-1

Yao, H., Song, J., Liu, C., Luo, K., Han, J., Li, Y., … Chen, S. (2010). Use of ITS2 region as the universal DNA barcode for plants and animals. *PLoS ONE*, *5*(10). doi: 10.1371/journal.pone.0013102

Yu, X., Guo, X., Wu, Z. (2014). Land Surface Temperature retrieval from Landsat 8 TIRS – Comparison between Radiative Transfer Equation-Based Method, Split Window Algorithm and Single Channel Method. Remote Sensing, 6: 9829-9852. https://doi.org/10.3390/rs6109829

Zhou, D., Zhao, S., Liu, S., Zhang, L., Zhu, C. (2014). Surface urban heat island in China's 32 major cities: Spatial patterns and drivers. Remote Sensing of Environment, 152: 51-61. https://doi.org/10.1016/j.rse.2014.05.017

CURRICULUM VITAE

Name	Marta M.
Surnames	Alós Ortí
Date of Birth	19.01.1989
Email	martaalosorti@gmail.com

Academic degrees

2018-2022	PhD studies in Environmental Sciences and Applied Biology. Institute of Agricultural and Environmental Sciences. Estonian University of Life Sciences (EMÜ)
2014	MSc in Biodiversity: Conservation and Evolution. University of Valencia (UV)
2013	B.S. in Environmental Sciences. University of Valencia (UV)

Additional training

2018	Urban Ecology: the green within the city. Lisbon, Portugal
2018	Forest disturbances and ecosystem services: data and modeling. Tartu, Estonia
2018	Multivariate Data Analysis Using PC-ORD. Tartu, Estonia
2017	Environmental legislation: Waste, Soil and Atmosphere. Online, Spain
2016	Introduction to Climate Change. Online, United Nations Climate Change (UNCC) Learning
2016	Forest Management and Policy in the General State Administration. Online, Spanish Ministry of Agriculture, Food and Environment.

Languages

Spanish (Mother tongue)
English (Advanced)
Italian (Advanced)

Professional employment

2014-2018	Sapienza University of Rome. Department of Environmental Biology. Rome, Italy
2014	Traineeship. Desertification Research Center (CIDE). Moncada, Spain.

Projects

2017-2020	BioVeins: Living veins for biodiverse cities. H2020 BiodivERsA32015104
2014-2018	Mapping and Assessment of Ecosystems and their Services (MAES). Italy

Scientific publications

2022	**Alós Ortí, M.**, Casanelles J, Chiron F, Deguines N, Hallikma T, Jaksi P, Kwiatkowska P, Moretti M, Muyshdont B, Niinemets Ü, Pinho P, Pinto MM, Saar P, Samson R, Tryjanowski P, Van Mensel A, Laanisto L. (2022). Negative relationship between woody species density and urban green spaces in seven European cities. Urban Forestry & Urban Greening. https://doi.org/10.1016/j.ufug.2022.127650
2022	Casanelles-Abella, J; Keller, A; Müller, S; Aleixo, C; **Alós Ortí, M**; Chiron, F; Laanisto, L; Myczko, Ł; Pinho, P; Samson, R; Tryjanowski, P; Van Mensel, A; Villarroya-Villalba, L; Pellissier, L; Moretti, M. Wild bee larval food composition in five European cities. Ecology, e3740. DOI: 10.1002/ecy.3740

2021	Pinho, P; Casanelles-Abella, J; Luz, A; Kubicka, AM; Branquinho, C; Laanisto, L; Neuenkamp, L; **Alós Ortí, M**; Obrist, M; Deguines, N; Tryjanowski, P; Samson, R; Niinemets, Ü; Moretti, M. Research agenda on biodiversity and ecosystem functions and services in European cities. Basic and Applied Ecology, 53, 124–133. DOI: 10.1016/j.baae.2021.02.014.
2021	Casanelles-Abella, J; Frey, D; Mueller, S; Aleixo, C; **Alós Ortí, M**; Deguines, N; Hallikma, T; Laanisto, L; Niinemets, U; Pinho, Pedro; Samson, R; Villarroya-Villalba, L; Moretti, M. A dataset of the flowering plants (Angiospermae) in urban green areas in five European cities. Data in Brief, 37, 107243. DOI: 10.1016/j.dib.2021.107243.
2021	Casanelles-Abella, J; Müller, S; Keller, A; Aleixo, C; **Alós Ortí, M**; Chiron, F; Deguines, N; Hallikma, T; Laanisto, L; Pinho, P; Samson, R; Tryjanowski, P; Van Mensel, A; Pellissier, L; Moretti, M. How wild bees find a way in European cities: Pollen metabarcoding unravels multiple feeding strategies and their effects on distribution patterns in four wild bee species. Journal of Applied Ecology. DOI: 10.1111/1365-2664.14063.
2019	Capotorti, G; Copiz, R; Fusaro, L; Mollo, B; **Alós Ortí, MM**; Salvatori, E; Zavattero, L. Biodiversity and ecosystem services in urban green infrastructure planning: A case study from the metropolitan area of Rome (Italy). Urban Forestry & Urban Greening, 37, 87–96. DOI: 10.1016/j.ufug.2017.12.014.

2019	Capotorti, G; De Lazzari, V; **Alos Orti, M**. Local Scale Prioritisation of Green Infrastructure for Enhancing Biodiversity in Peri-Urban Agroecosystems: A Multi-Step Process Applied in the Metropolitan City of Rome (Italy). Sustainability, 11 (12), ARTN 3322. DOI: 10.3390/su11123322.
2017	Blasi, C; Capotorti, G; **Alós Ortí, MM**; Anzellotti, I; Attore, F; Azzella, MM; Carli, E; Copiz, R; Garfì, V; Manes, F; Marando, F; Marchetti, M; Mollo, B, Zavattero, L. Ecosystem mapping for the implementation of the European Biodiversity Strategy at the national level: The case of Italy. Environmental Science & Policy, 78, 173−184. DOI: 10.1016/j.envsci.2017.09.002.
2016	Capotori, G**; Alós Ortí, MM**; Anzellotti, I; Azzella, MM; Copiz, R; Mollo, B; Zavattero, L. The MAES process in Italy: Contribution of vegetation science to implementation of European Biodiversity Strategy to 2020. Plant Biosystems, 149(6), 949−953. DOI: 10.1080/11263504.2015.1095253.

Other publications

2018	Blasi, C; Zavattero, L; Capotorti, G; Copiz, R; Manes, F; Mollo, B; **Alós Ortí, MM**. Urban and rural green infrastructure: two projects for the metropolitan city of Rome. In: Paracchini M.L., Zingari P.C., Blasi C. (Eds.), Reconnecting Natural and Cultural Capital, Contributions from science and policy, Office of Publications of the European Union. ISBN 978-92-79-59948-4

2016	Maes, J; Zulian, G; Thijssen, M; Castell, C; Baró, F; Ferreira, AM; Melo, J; Garrett, CP; David, N; Alzetta, C; Geneletti, D; Cortinovis, C; Zwierzchowska, I; Louro Alves, F; Souto Cruz, C; Blasi, C; **Alós Ortí, MM**, Attorre, F; Azzella, MM; Capotorti, G; Copiz, R; Fusaro, L; Manes, F; Marando, F; Marchetti, M; Mollo, B; Salvatori, E; Zavattero, L; Zingari, PC; Giarratano, MC; Bianchi, E; Duprè, E; Barton, D; Stange, E; Perez-Soba, M; van Eupen, M; Verweij, P; de Vries, A; Kruse, H; Polce, C; Cugny-Seguin, M; Erhard, M; Nicolau, R; Fonseca, A; Fritz, M; Teller, A. Mapping andAssessment of Ecosystems and their Services. Urban Ecosystems. Publications Office of the European Union, Luxembourg.

CURRICULUM VITAE

Nimi	Marta M.
Perekonnanimi	Alós Ortí
Sünniaeg	19.01.1989
Email	martaalosorti@gmail.com

Haridustee

2018-2022	Doktorantuur keskkonnateaduste ja rakendusbioloogia erialal Eesti Maaülikoolis
2014	MSc Elurikkuse, looduskaitse ja evolutsiooni erialal Valencia ülikoolis
2013	B.S. Keskkonnateaduste erialal Valencia ülikoolis

Koolitused ja lisakursused

2018	Urban Ecology: the green within the city. Lissabon, Portugal
2018	Forest disturbances and ecosystem services: data and modeling. Tartu, Eesti
2018	Multivariate Data Analysis Using PC-ORD. Tartu, Eesti
2017	Environmental legislation: Waste, Soil and Atmosphere. Veebikoolitus, Hispaania
2016	Introduction to Climate Change. Veebikoolitus, United Nations Climate Change (UNCC) Learning programmi kaudu
2016	Forest Management and Policy in the General State Administration. Veebikoolitus, Hispaania

Keeleoskus	Hispaania (emakeel) Inglise (vilunud) Itaalia (vilunud)

Töökohad

2014-2018	Teadur. Sapienza ülikool Roomas. Keskkonnabioloogia osakond. Rooma, Itaalia
2014	Praktikant. Kõrbestumise uurimiskeskus (CIDE). Moncada, Hispaania.

Osalus teadusprojektides

2017-2020	BioVeins: Living veins for biodiverse cities. H2020 BiodivERsA 32015104
2014-2018	Mapping and Assessment of Ecosystems and their Services (MAES).

Publikatsioonid

2022	**Alós Ortí, M**., Casanelles J, Chiron F, Deguines N, Hallikma T, Jaksi P, Kwiatkowska P, Moretti M, Muyshdont B, Niinemets Ü, Pinho P, Pinto MM, Saar P, Samson R, Tryjanowski P, Van Mensel A, Laanisto L. (2022). Negative relationship between woody species density and urban green spaces in seven European cities. Urban Forestry & Urban Greening. https://doi.org/10.1016/j.ufug.2022.127650
2022	Casanelles-Abella, J; Keller, A; Müller, S; Aleixo, C; **Alós Ortí, M**; Chiron, F; Laanisto, L; Myczko, Ł; Pinho, P; Samson, R; Tryjanowski, P; Van Mensel, A; Villarroya-Villalba, L; Pellissier, L; Moretti, M. Wild bee larval food composition in five European cities. Ecology, e3740. DOI: 10.1002/ecy.3740
2021	Pinho, P; Casanelles-Abella, J; Luz, A; Kubicka, AM; Branquinho, C; Laanisto, L; Neuenkamp, L; **Alós Ortí, M**; Obrist, M; Deguines, N; Tryjanowski, P; Samson, R; Niinemets, Ü; Moretti, M. Research agenda on biodiversity and ecosystem functions and services in European cities. Basic and Applied Ecology, 53, 124−133. DOI: 10.1016/j.baae.2021.02.014.

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Muud publikatsioonid

2018	Blasi, C; Zavattero, L; Capotorti, G; Copiz, R; Manes, F; Mollo, B; **Alós Ortí, MM**. Urban and rural green infrastructure: two projects for the metropolitan city of Rome. In: Paracchini M.L., Zingari P.C., Blasi C. (Eds.), Reconnecting Natural and Cultural Capital, Contributions from science and policy, Office of Publications of the European Union. ISBN 978-92-79-59948-4
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VIIS VIIMAST KAITSMIST

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NISU SAAGI JA KÜPSETUSKVALITEEDI STABIILSUS BALTI REGIOONIS
Dotsent Evelin Loit, vanemteadur Mati Koppel
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PATTERN OF URBAN PARK USE,SPATIAL ACCESSIBILITY AND PREFERANCES OF URBAN PARK USERS IN TEHRAN, IRAN
LINNAPARKIDE KASUTUSMUSTRID, RUUMILINE LIGIPÄÄSETAVUS JA KASUTAJAEELISTUSED IRAANI PEALINNAS TEHERANIS
Professor Simon Bell
10. juuni 2022

ASSAR LUHA
OCCUPATIONAL NOISE EXPOSURE AND HEARING PROBLEMS AMONG ACTIVE MILITARY SERVICE PERSONNEL IN ESTONIA
MILITAARMÜRA EKSPOSITSIOON JA KUULMISPROBLEEMID EESTI TEGEVVÄELASTEL
Professor Eda Merisalu, kaasprofessor Hans Orru
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HENRI JÄRV
THE IMPACT OF PROTECTED AREAS GOVERNANCE AND MANAGEMENT PRACTICES ON HUMAN WELL-BEING AND LOCAL SOCIOECONOMIC CONDITIONS
KAITSEALADE HALDUSSÜSTEEMI JA KAITSEKORRALDUSLIKE MEETMETE MÕJU INIMESTE HEAOLULE NING KOHALIKELE SOTSIAALMAJANDUSLIKELE OLUDELE
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PÕLLUMULLAST ERALDUVA DILÄMMASTIKOKSIIDI VÄHENDAMINE
Kaasprofessor Merrit Shanskiy, kaasprofessor Kaido Soosaar, professor Alar Astover
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MARTA ALÓS ORTÍ

URBAN ECOLOGY: NOVEL ECOSYSTEMS, NOVEL CHALLENGES

Eesti Maaülikool
Estonian University of Life Sciences

URBAN ECOLOGY: NOVEL ECOSYSTEMS, NOVEL CHALLENGES

LINNAÖKOLOOGIA: UUED ÖKOSÜSTEEMID, UUED VÄLJAKUTSED

MARTA ALÓS ORTÍ

A Thesis
for applying for the degree of Doctor of Philosophy
in Applied Biology

Väitekiri
filosoofiadoktori kraadi taotlemiseks
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